

Chapter 2

Neurobiology: Language By, In, Through and Across the Brain

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Language has come to be commonly understood as something accomplished *by the brain*. Much scientific investigation has consequently focused on looking for language *in the brain*. Although it may sound intuitive, this approach suggests that language is an object located inside another object. This spatial metaphor has generated important insights into the brain sites important for language, from nineteenth century studies of brain-damaged patients to more recent and refined evidence from brain imaging. However, with this refinement has come the realization that brains are not truly maps, and that language is not simply the inhabitant of a localized part of the brain. On the time scale of lifetime development, this is supported by evidence of plasticity in the brain's organization for language, prompted by maturation, experience, or localized damage. On the smaller time scale of an individual language process *through the brain*, the participation of many brain regions can be observed. Some of these regions are known for their role in perceptual, motor, and other seemingly non-linguistic functions. It remains uncertain whether any brain regions are exclusively dedicated to language. As examples, the classical language areas of Broca and Wernicke participate in many functions, such as imitation, action understanding, perception of biological motion that are not specifically linguistic. This suggests that language acquisition is built upon and embedded in precursor and component functions that emerge during the first years of life from networks distributed *across the brain*.

2.1 By the Brain: Language as a Biological Object

In 1959, the young linguist Noam Chomsky reviewed B. F. Skinner's book *Verbal Behavior* (Skinner 1957), in which behaviorist principles of conditioning and reinforcement were applied to the question of language acquisition in children.

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Chomsky's review (1959) is remembered for debunking behaviorist linguistics in an uncompromising way. As an alternative, Chomsky put forth a 'generative grammar' in an attempt to transform linguistics into a science on a par with mathematics or physics (Chomsky 1965, 1972a). This approach proposes a set of rules and principles capable of generating an infinite number of sentences, and dramatically changed the concept of language in the second half of the twentieth century. Chomsky's views about the biological basis of these grammatical principles were equally revolutionary. In the mentioned review Chomsky accounts for children's ability to develop mental grammars through innate tendencies, which endow human beings with specific types of learning. He then tied these thoughts to the view of mind and body as separate and independent realms, as proposed earlier by Descartes (Chomsky 1966).¹ From the contemporary point of view, Cartesian innatism (the belief that the mind is born with ideas) and mind-body dualism may be considered strange bedfellows of linguistics as an exact science. This appears to be reflected in the ultimately ambivalent attitude towards a biological explanation of language that has characterized Chomsky's work and that of many fellow generative grammarians. While the presumed genetic bases of universal grammar have been a mantra for decades in generative linguistics, actual efforts to identify relevant genes remained modest for a long time (see Chap. 7 for recent advances).

Chomsky's views not only opposed behaviorist teachings, which he directly attacked, but also the tradition of Ferdinand de Saussure, which had dominated early twentieth century linguistics. While Saussure's structural linguistics foreshadowed Chomsky (Newmeyer 1986) by viewing language ("langue") as a system that could be subjected to exact scientific study ("un objet de nature concrète"), he considered this object of language as a social entity, "exterior to the individual" (Saussure 1915/1972). To Saussure, the core object of linguistics was social, whereas the study of "parole", the "grammatical system that exists in every brain", was considered secondary. Chomsky reversed these priorities, declaring the language ability (which he called "universal grammar") to be the core object of linguistics—a biological entity that matured in similar ways as other bodily organs (Chomsky 1976, 1980). Pragmatic and sociological approaches to language, such as Searle's theory of speech acts (Searle 1969), were dismissed with disdain: "You can also collect butterflies and make many observations. If you like butterflies, that's fine; but such work must not be confounded with research..." (Chomsky and Ronat 1979).

Given Chomsky's strong views on the biological and innate nature of language, generative grammarians showed surprisingly little initiative to bridge the gap between linguistic theory and neuroscience or genetics. Lenneberg's *Biological Foundations of Language* (1967) attempted to link principles of generative grammar with biological, neurological, and evolutionary evidence. However, Lenneberg's conclusion, according to which human language abilities reflected "an adaptation of a ubiquitous process (among vertebrates) of categorization and extraction of similari-

¹ Chomsky's forays into dualistic rationalism were blended with and at least partly motivated by his political views, which eclectically (and bizarrely) equated empiricism with US imperialism of the Vietnam era and rationalism with progressive enlightenment (Chomsky 1972b).

ties”, was hard to reconcile with Chomsky’s strong views of the autonomy of language with respect to nonverbal cognition (Chomsky 1957, 1976). Lenneberg furthermore dismissed the idea of “genes for language”, pointing out that species-specific changes in genes during hominid evolution may have resulted in protracted infancy, enhanced brain plasticity, and “a peculiar ontogenetic phase of an optimal confluence of various abilities... [and] thus a critical period for language acquisition” (ibid.; see also Sect. 2.2.5). As will become clear in Sect. 2.4, these ideas are surprisingly modern and still capture the gist of neurobiological evidence that has accumulated in the past four decades.

2.2 In the Brain: Language as a Spatial Location

2.2.1 History

Chomsky’s critique of Skinner came in the context of a mid-twentieth century “cognitive revolution” in linguistics, philosophy, psychology, and artificial intelligence. This revolution aimed to replace behaviorist views of the mind as a “black box” with cognitive models of the mind (Gardner 1987). Yet, the brain was surely not new territory at the time. On the contrary, neurology had an extensive track record in the study of brain-behavior relationships. Overcoming empirically dubious early attempts (such as medieval ventricular theory or phrenology in the late eighteenth century; Clarke and Dewhurst 1972), modern neurology had accumulated a large literature relating localized brain damage to specific types of cognitive-behavioral impairment. As neuroimaging techniques identifying local damage in living patients were yet unavailable, the link was usually established after death. Broca’s (1861) landmark case of Leborgne, also called “tan-tan” for his repetitive utterances, serves as a slightly ironic example. First, Leborgne conveniently died only 6 days after his case had been declared a litmus test of the theory of functional localization at the Parisian ‘Société d’Anthropologie’ in 1861 (Harrington 1987). Secondly, while results from his autopsy prompted the notion of the left inferior frontal gyrus (“Broca’s area”) as a language area critically involved in speech production, the actual damage in Leborgne’s brain was far more extensive, including underlying white matter, and parts of the frontal and parietal lobes (Dronkers et al. 2007; Signoret et al. 1984). Nonetheless, 150 years later the inferior frontal cortex is still considered a core region for language processing or simply a “language area”, for valid (though not necessarily compelling) reasons, as will become clear below (brain regions are shown in Fig. 2.1). Regardless of its empirical accuracy in the specific case of Leborgne, the basic logic of the localizationist approach is apparent: The damaged brain is equated to the healthy minus the injured part, and similarly the impaired mind of a lesion patient is equal to its healthy counterpart minus the function attributed to the site of injury. For example, if Leborgne’s loss of speech production resulted from damage to Broca’s area, the function of this region in the healthy brain was inferred to be

speech production. This “patho-normal inference” (Müller 1996) survives in modern cognitive neuropsychology (see Shallice 1988 for a thorough review).

The case of Leborgne attracted great interest in 1861 because it was considered a test case in the ongoing debate between those who believed in functional brain localization, such as Jean-Baptiste Bouillaud, and others who considered the brain a unitary organ, without distinct functional subdivisions, such as Pierre Flourens.² Critics of the localizationist program have made contributions to the debate about brain-behavior relationships that remain of interest today. The British neurologist John Hughlings-Jackson (1878) goes beyond the traditional emphasis on the lesion patient’s “negative condition” (e.g., loss of expressive speech) and highlights the importance of the “positive condition”. Jackson describes the example of a paraphasia, such as the production of the word “table” instead of “chair”. In Jackson’s view, this utterance is not “the direct result of the disease”, as typically assumed. Instead it is “the best speech under the circumstances... owing to activity of healthy... nervous elements” (ibid.: 316”).

Although Jackson’s statement may appear trivial, it reflects a crucial change in perspective that contrasts with localizationism, as described above. Rather than equating the effect of brain damage with a simple subtraction of a specific function, Jackson considered it as a regression into a more primitive and automated state that reflected an earlier stage of evolution. More generally, Jackson’s emphasis of the positive condition following brain damage underscores the importance of plasticity, which complicates any inference based on subtractions. These implications were further elaborated by Henry Head, who (1920) defined Jackson’s “positive effects” as follows: “A negative lesion produces positive effects by releasing activities, normally held under control by the functions of the affected level” (ibid.: 805”). In order to fully understand cognitive processes in a lesion patient, it is therefore necessary to accept that brain damage triggers functional *reorganization*. Head’s account of plasticity remains a crucial insight today, because it implies that lesion effects are not simply subtractive. Later, Head (1926) adopted the term *diaschisis* from Constantin von Monakow to describe alterations in the brain far away from the site of the damage. Diaschisis contradicts the idea of strictly local effects of brain damage.³

Although skepticism over subtractive arguments in the works of Jackson, Head, Marie (1906) and Goldstein (1948) raised many deep and important issues, it did not put an end to the idea of localization. One consideration in favor of localizationism has been its strength in generating clear and falsifiable hypotheses. As argued by Popper (1965), true science resembles trial and error, or “conjectures and refutations”.

² Interestingly, this scientific debate had political and ideological undertones in mid-nineteenth century France of the second empire, as holistic views were considered a conservative and theologically warranted reflection of the unity of the soul, whereas localizationism was associated with antimonarchic and anticlerical left-wing views at the time (Harrington 1987).

³ Modern neurology has provided evidence in support of diaschisis. For example, in patients with damage in cerebral cortex, reduced glucose metabolism is often seen far away from the site of damage, in the opposite hemisphere of the cerebellum. This phenomenon, called ‘crossed cerebellar diaschisis’, is attributed to contralateral (“crossed”) connections between forebrain and cerebellum (Gold and Lauritzen 2002; Pantano et al. 1986).

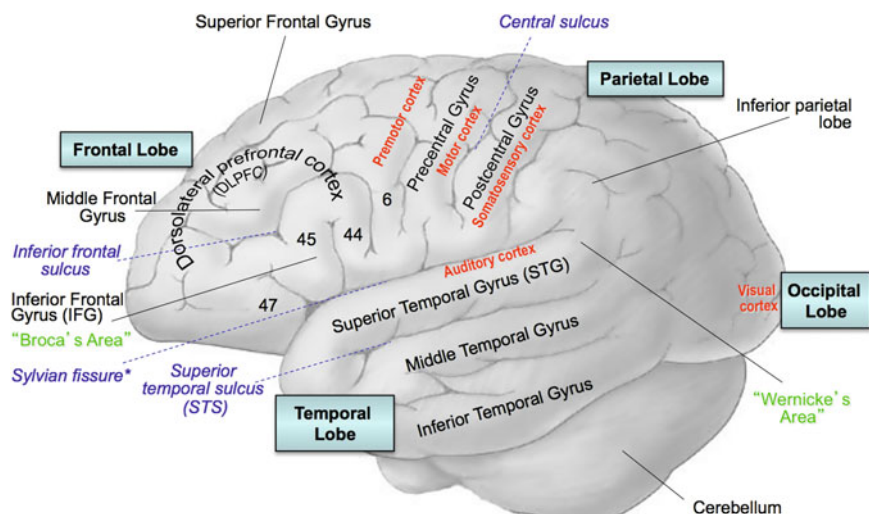


Fig. 2.1 Outline of left hemisphere with anatomical terms used in text

Conversely, any school of thinking that does not generate falsifiable hypotheses may be considered unscientific, as it is impossible to produce empirical evidence that could refute it. The latter may apply to many of the insights provided by critics of localizationism. Hughlings-Jackson (1878), for example, emphasized that conclusions on brain-behavior relationships were ultimately limited to each individual patient: “There is... no single well-defined entity—loss of speech or aphasia—and thus... such a question as, ‘Can an aphasic make a will?’ cannot be answered any more than the question, ‘Will a piece of string reach across the room?’... The question should be, ‘Can this or that aphasic person make a will?’ ” (ibid.: 314). In Goldstein’s work (1948), this focus on the individual appears to become an explicit denial of theory construction: “Experience showed that I must free myself from any definitive theory and investigate patients in a way as unbiased from any of them as possible”.

Localizationist approaches, on the other hand, provided explicit models and predictions. A prime example is Ludwig Lichtheim’s ‘house model’, which transparently predicts seven different types of language impairment (aphasia), based on lesion sites hitting either of the classical language areas (Broca’s or Wernicke’s), or connections between these and other nodes of a simple network (Fig. 2.1). Modern classifications of aphasia (e.g., Broca’s, Wernicke’s, transcortical sensory and motor, conduction, global) still resemble Lichtheim’s model (e.g., Benson and Ardila 1996). A review by Norman Geschwind in *Science* (1970) was most instrumental in reintroducing Broca’s, Wernicke’s, and Lichtheim’s localizationist approach to the general community of cognitive psychology and neuroscience; this review praised the concept of functionally specialized centers for language as “one of the greatest achievements of the last half of the nineteenth century”.

2.2.2 Localizationism Afresh: Functional Neuroimaging

While this revitalized localizationism did not share much scientific heritage with Chomsky's claim of the autonomy of syntax, there is some common ground. For an interesting example, Grodzinsky (1990) reviews Geschwind's "appealing" model, which was based on Lichtheim's house diagram (Fig. 2.1), and argues against it because it does not implement adequate theoretical concepts. The point is well-taken. How can a neurological model localize language, if the latter is not even fully understood, but construed in simplistic terms of speech comprehension, production etc.? The inverse approach, which prioritizes linguistic models and then looks for corresponding neural substrates, however, faces a similar problem.

How do we know whether a linguistic theory that adequately models empirical facts about language behavior actually relates to the way the brain is organized? In an influential article in *Behavioral and Brain Sciences*, Grodzinsky (2000) illustrates the issue. Stating that Broca's area "is more specialized than previously thought", he explains that this specialization pertains to grammatical relations within sentences⁴ and that "syntactic abilities... are represented entirely and exclusively in the left hemisphere" (ibid.: 1). An empirical evaluation of these statements will follow further below. The justified critique of Geschwind's approach encounters a complementary problem: superimposing a theoretical concept (transformation) onto brain tissue without adequate understanding of brain function. While there is no perfect resolution to the tension between linguistic theory-driven 'top-down' and neuroscience data-driven 'bottom-up' approaches, it appears that extreme positions may hamper progress and only careful consideration of both can advance cognitive neurolinguistics.⁵ Moreover, neuroscience is not a discipline of unassorted data, but is itself shaped by theoretical models, which may be usefully applied in cognitive neurolinguistics, as I will discuss later.

The views on the brain organization for syntax described above reflect a modern version of localizationism often called *modularity*. This concept was most influentially propagated by Fodor (1983), who portrayed cognitive modules as independent ("encapsulated") systems that are "innate" (genetically specified) and supported by localized brain structures. How compatible are such views with evidence from cognitive neuroscience? Functional imaging techniques, such as PET and fMRI (Box 1),

⁴ In more technical verbatim terms: Broca's area "handles only intrasentential dependency relations" (Grodzinsky 2000: 21) and "is the neural home to receptive mechanisms involved in the computation of the relation between transformationally moved phrasal constituents and their extraction sites..." (ibid.: 1).

⁵ Corresponding issues have been debated in artificial intelligence for decades. Computational models informed by cognitive theories may approximate the behavior of a human being, but their internal organization in no way resembles functional brain organization. The cognitive model-driven approach in AI (e.g., Newell and Simon 1963) was countered in the 1980s by parallel-distributed ("connectionist") models (McClelland and Rumelhart 1986). These were inspired 'bottom-up' by simplified features of neurons and their connections and aspired to demonstrate complex input-output behaviors mimicking human cognition as emergent properties of such very simple neural networks.

have greatly enhanced the investigation of brain-behavior relationships in recent decades. Note that in conventional applications these techniques have a localizationist bias, as they are typically used to generate “maps” of cognitive functions on the brain (similar in principle to phrenological maps or those of classical localizationism). Some early neuroimaging results in the study of syntax indeed appeared consistent with a modular view. Several PET studies by Caplan and colleagues (1998, 1999; Stromswold et al. 1996) implemented comparisons of sentences at different levels of complexity. Both identified activity in left inferior frontal area 44, presenting prominent illustrations with exclusive activity in this portion of Broca’s area (Fig. 2.2a). Closer inspection, however, shows that stronger activations were identified in other parts of the brain, but were deemed irrelevant because they occurred elsewhere.

Box 1. The two most important functional brain imaging techniques are positron emission tomography (PET) and functional magnetic resonance imaging (fMRI). In **PET**, a small amount of radioactive tracer is injected into the bloodstream and biological measures, such as blood flow or glucose metabolism, can be taken based on the distribution of the tracer in the brain, which is detected by the PET scanner. **fMRI** does not involve radioactivity and is therefore more broadly used (even in children). This technique takes advantage of the relative increase of oxygen in the blood during regional brain activation, which results in slight changes in magnetic resonance that can be detected with an MRI scanner. This blood oxygen level dependent (**BOLD**) effect indirectly reflects local neuronal activity. A more recent development is **event-related fMRI**, in which the BOLD effect is detected for single trials of a task (rather than long blocks of trials), resulting in improved temporal resolution (see Box 2).

In a PET study by Caplan and colleagues (1999) for example, participants made plausibility judgments for more complex cleft object sentences (“It was the juice that the child enjoyed”) and less complex subject cleft sentences (“It was the child that enjoyed the juice”). Comparison of the two conditions yielded significant activation solely in Broca’s area, as depicted by a small and lonely activation blob in area 44 (Fig. 2.2a). The presentation is, however, misleading, as at least two additional sites with stronger activation were found in other parts of the brain, but were considered “non-significant”, as they were outside the region of hypothesized activity. The wizardry requires explanation. Functional imaging studies (PET or fMRI) face severe issues of multiple comparisons, as statistics are typically performed separately for each volume element (“voxel”). A whole brain imaging study may include 100,000 voxels or more.⁶ While technical solutions can mitigate the problem (for example,

⁶ Since conventional fMRI statistics test for activation effects separately in each voxel, the large number of voxels creates a need to correct for multiple comparisons. For example, a given voxel shows an effect that is significant at the 95% confidence level (i.e., the probability of obtaining the finding by chance alone is $\leq 5\%$). If comparisons are performed in 10 voxels, the probability

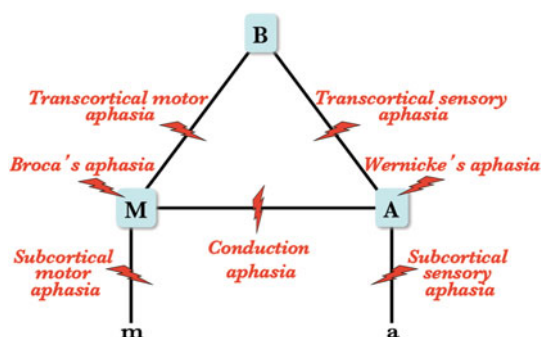


Fig. 2.2 Lichtheim's "house diagram" of the language system. Letters in blue boxes stand for brain centers: *M* motoric language center (Broca's area); *A* auditory language center (Wernicke's area); *B* conceptual center ("Begriffszentrum"). Small letters at the bottom stand for motor and auditory periphery. Exactly seven distinct types of aphasia are predicted from this model, based on lesion sites (indicated by lightning icons) hitting either one of the two language centers (*M*, *A*) or connections between *M* and *A*, with the periphery, or with the conceptual center

based on the fact that true activation tends to occur in clusters; Forman et al. 1995), a more dramatic shortcut is provided by planned comparisons in regions of interest.⁷ Thus in the cited studies by Caplan and colleagues, activity related to syntactic complexity was predicted for Broca's area, for which no correction was performed, but not for any of the remaining brain regions, where signal changes therefore remained below the significance threshold due to multiple comparison correction. A similar "demonstration" of exclusive and modular activation can in principle be construed for just about any task paradigm and any moderately activated part of the brain, based on an *a priori* hypothesis, especially if the study is underpowered due to a small number of participants.

Whether the activation pattern for a given language task appears localized or widely distributed therefore depends relatively little on the task itself, but largely on methodological specifics.⁸ It is thus important to keep in mind that functional imaging evidence from PET or fMRI itself cannot provide direct evidence on how localized a given functional component may be. Ultimately, only reasonable interpretation of

of obtaining the finding by chance increases to 50%. A correction for multiple comparisons is therefore necessary. In its simplest form (the "Bonferroni correction"), the *p*-value is multiplied by the number of comparisons. Such a correction would require that an effect in a single voxel reaches a *p*-value of 0.0000005 in order to "survive" a Bonferroni correction for 100,000 comparisons (assuming that an fMRI study includes this number of brain voxels).

⁷ In technical terms, the region of interest approach drastically reduces the need to correct for multiple comparisons, as only a small part of the brain is considered, thus increasing the probability of a statistically significant finding.

⁸ Among these are statistical power (number of participants), analysis type (whole-brain vs. region of interest), signal to noise ratio (reflecting head motion and other sources of noise), and the investigator's selection of significance thresholds and method of multiple comparison correction.

converging results from many studies, with careful consideration of methodological detail, can provide clues.

2.2.3 *Localizing Syntax and Semantics*

A number of neuroimaging studies have directly compared effects of syntactic and semantic task components. Friederici et al. (2003) found that processing of syntactic violations (e.g., “The blouse was on ironed”) and semantic violations (e.g., “The thunderstorm was ironed”) was associated with activation in large overlapping regions of left perisylvian cortex, the area surrounding the Sylvian fissure (Fig. 2.2b). Specificity, however, was seen in the *degree* of regional activation for the two types of condition. Some regions (the anterior superior temporal gyrus [STG] and the basal ganglia) showed significantly more activation for syntactic violations; others (the middle portion of the STG and the insula, a brain region in the depth of the Sylvian fissure) showed more activation in both the left and right hemispheres) showed more activation for semantic violations. Yet other regions, such as the posterior STG and inferior frontal gyrus (IFG), were activated during both conditions and also when sentences without violations were presented.

These and the findings by Caplan and colleagues described earlier illustrate that interpreting neuroscientific evidence as support for modular localization or holistic organization may be futile, as purely methodological details related to data acquisition, processing, and statistical analysis determine whether imaging results “look” modular, distributed, or holistic. An important additional consideration concerns the specifics of task paradigms. Imaging studies may be presented as comparisons of syntactic and semantic processes, but in reality each study will use a set of specific stimuli and task instructions, which may affect the results and may limit the extent to which findings can be generalized. For example, Kuperberg et al. (2003) used a conceptually similar approach by presenting sentences with syntactic and semantic anomalies, which however occurred in sentences of greater length than those used by Friederici et al. (2003). These and other design differences may have contributed to a rather different pattern of results, with portions of left IFG showing strongest activity for semantic anomalies, but modest activity for syntactic anomalies (which was actually weaker than for sentences without anomalies) in the study by Kuperberg and colleagues.

Note further that the use of sentences with violations implies that the type of violation specifically taxes the corresponding language component (e.g., syntax, semantics). In violation paradigms, the timing of a violation can be pinpointed by the presentation of a single word that creates the violation, which is advantageous in techniques with high temporal resolution (Box 2). It may be reasonable to assume that presentation of syntactically anomalous sentences puts a heavy load on syntactic decoding, but this process may differ from syntactic decoding of sentences without anomalies, as typically encountered in everyday language use.

Box 2. Functional imaging techniques can be distinguished in regard to two dimensions of resolution. **Spatial resolution** relates to a technique's ability to pinpoint where in the brain activity occurs. In colloquial terms, images with high spatial resolution are sharp, those with low spatial resolution are blurry. In more technical terms, spatial resolution is largely determined by the size of voxels (3-dimensional pixels). **Temporal resolution** refers to a technique's ability to pinpoint when activation occurs. For example, electrophysiological techniques, such as EEG and MEG (Box 3), have high temporal resolution, with measurements in the millisecond range. PET and fMRI have lower resolution, in the range of seconds to minutes. In fMRI, temporal resolution is largely determined by the repetition time (TR), which is the interval between time points (roughly, how long it takes to acquire a complete 3D image of the brain), typically between 1 and 4 s.

Other groups have therefore used task paradigms, in which syntactic complexity was manipulated (rather than violated). Keller et al. (2001) implemented such a paradigm and additionally used high-frequency (common) or low-frequency (rare) nouns in syntactically simple and complex sentences. They found that effects of syntactic complexity and word frequency interacted in several brain areas (left IFG, STG, and inferior parietal lobe). Greater activation for syntactically complex sentences in these regions was found *only* if sentences included low frequency nouns (e.g., “The pundit that the regent attacked admitted the gaffe at the conclave”), but not for those with high-frequency nouns (e.g., “The writer that the king attacked admitted the mistake at the meeting”). While these results are not easily reconciled with findings from other studies that implemented similar manipulations of syntactic complexity, including the studies by Caplan and colleagues mentioned above, they may partly relate to limited temporal resolution. For example, in the study by Keller et al. (2001), the repetition time (Box 2) was 3 s. The authors correctly caution that any brain site, such as left IFG, may be involved in different aspects of a process at different points in time. Specialization may thus be temporal as well as spatial. Although PET and fMRI have intrinsically limited temporal resolution due to the sluggishness of blood flow increases that accompany neuronal activation, temporal resolution of event-related fMRI (Box 1) can be improved to about 1 s. For example, Ni et al. (2000) were able to identify distinct sequences of activity in response to syntactic or semantic anomalies, modeling blood oxygenation level dependent (BOLD) effects with short latency (a delay time of 4–5 s) and with longer latencies (up to 10 s). Effects for syntactic anomalies occurred in left IFG at mid-latency (about 6 s), while those in right IFG and basal ganglia were seen at long latency.

Whereas fMRI is limited in its capacity to resolve the temporal sequence of language processing (as will be further discussed in Sect. 2.3.2), attempts have been made to increase the spatial resolution of functional results. In particular, a number of studies have explored functional subdivisions within Broca's area. Dapretto and Bookheimer (1999) used a task that required either primarily syntactic or semantic

operations.⁹ Direct comparison yielded stronger effects for syntactic processing in a superior portion of IFG (areas 44/45), whereas stronger effects for the semantic condition were seen in a more inferior portion (area 47). Activation in area 47 has been observed in other semantic studies (Booth et al. 2002; Poldrack et al. 1999; Uchiyama et al. 2008). However, not all types of task conform to this simple model of subdivision. In Friederici et al. (2000a), participants made explicit syntactic (noun or function word?)¹⁰ and semantic judgments (abstract or concrete noun?). While syntax-related activation in the inferior tip of area 44 was expected given the above findings, semantic judgment was unexpectedly associated with more *superior* IFG activation in area 45. This again suggests that simply characterizing a task as “syntactic” or “semantic” may be insufficient and potentially misleading since details of stimulus presentation, comparison condition, and task may affect observed activation patterns.

This raises a further question. Should activity that is localized to a specific site within a “language area”, such as left IFG, be attributed to specifically *linguistic* components of a task [e.g., syntactic transformations and the movement of constituents, as suggested by Grodzinsky (2000)], or rather to components that are shared across functional domains? Broca’s area is located close to premotor cortex and dorsolateral prefrontal cortex (DLPFC), and reasonable candidates of such shared components are therefore the planning motor of complex motor sequences and working memory. Sustained activity, which reflects working memory maintenance, has been observed in animal studies of neurons in DLPFC (Miller and Cohen 2001). Human imaging studies support the crucial role of DLPFC, including IFG, in working memory (Duncan and Owen 2000). Possibly related to this, Fiebach et al. (2005) observed increased activity in Broca’s area associated with greater demand on syntactic working memory, as opposed to syntactic complexity. However, this leaves open the question of specificity. Does syntactic decoding involve a type of working memory that is exclusively specialized for syntactic operations, as opposed to one that is shared with non-syntactic maintenance (e.g., word lists or letter strings)? This question requires some linguistic detail and readers solely interested in the conceptual issues may move on to the next section directly.

Uchiyama and colleagues (2008) directly compared working memory in sentence and non-sentence tasks (matched for working memory load) and found greater activity in parts of left IFG (areas 44 and 45) for the sentence task. A second experiment using garden-path sentences¹¹ identified activation in area 44 overlapping with that from the first experiment. The authors considered these overlapping activations to

⁹ Participants had to judge whether sentences were the same or different. For some sentences, this required syntactic processing (e.g., “The policeman arrested the thief” is the same as “The thief was arrested by the policeman”), whereas in other sentence pairs it required semantic processing (“East of the city is the lake” is different from “East of the city is the river”).

¹⁰ Function words (e.g., “if” or “by”) are primarily grammatical with relatively little meaning, whereas content words (e.g., nouns such as “house” or “love”) are meaningful (semantically rich).

¹¹ Garden-path sentences have misleading syntactic structure. A classic example is the sentence “The horse raced past the barn fell”, where the final word prompts reanalysis of the initially expected syntactic structure (“The horse raced past the barn”).

reflect verbal working memory. Santi and Grodzinsky (2007) used two types of sentences with filler-gap dependencies, requiring either Binding (“... *the mailman* who [gap] burnt *himself*”) or Movement (“...*the woman* who Kate burnt [gap]”). In addition, they varied working memory load, i.e., the number of noun phrases between the dependent elements (indicated by italics in the examples above). For example, the sentence “Kate loves *the woman* who THE MAILMAN and THE MOTHER of JIM pinched [gap]” requires Movement between two elements (indicated by italics) separated by three noun phrases (indicated by small capitals). Participants performed grammaticality judgments during fMRI scanning. Interestingly, a site in IFG (area 45) showed an interaction effect: Activation increased linearly with working memory load for sentences in the Movement, but not in the Binding condition. The authors interpret this finding as support for a ‘specificist’ view, according to which “Broca’s area is specific to the working memory needs of syntactic Movement rather than general dependency relations” (ibid.: 16). Not considered in this study is the possible impact of other nonverbal task components, such as inhibition. In the example sentence “Kate loves *the woman* who the mailman and the mother of Jim pinched [gap]”, working memory maintenance during syntactic decoding may interact with inhibition of the object “the woman” in the final gap position. Indeed, activation in area 45 of left IFG has been reported in previous studies of response inhibition (Collette et al. 2001; Rubia et al. 2001). Jonides et al. (1998) found that inhibitory activation in left IFG interacted with working memory and was specifically enhanced when words had to be rejected after being maintained in working memory, possibly similar to the sentence requiring Movement cited above (“Kate loves...”). The peak activation effect in the study by Jonides et al. occurred within a few millimeters of the peak observed by Santi and Grodzinsky.

2.2.4 Terminology and Methodology

The debates about functional specificity and neural localization within the language system (syntax vs. semantics) and between language and other systems (e.g., language versus memory or motor planning) highlight open questions regarding the metaphor of “language in the brain”. First, there is the unresolved issue of what exactly those mentalistic concepts are that cognitive neuroscience is supposed to find or locate in the brain. Churchland’s eliminative materialism¹² (1986) was instrumental in debunking the idea that traditional psychological concepts could be directly related to the brain, since “folk psychology may be irreducible with respect to neuroscience—irreducible because dead wrong” (ibid.: 384). Cognitive psychologists and linguists are not immune from this criticism simply because they have invented a highly sophisticated terminology to model human behavior. The assurance that theories are “cognitive” or “mentalistic” surely helped overcome the lim-

¹² Churchland’s eliminative materialism claims that psychology will be eventually replaced by neuroscience (1986).

itations of behaviorist black-box theories, which had ruled out any consideration of mind/brain (Gardner 1987), as mentioned earlier. However, as long as models are constrained solely by behavioral data, the constructs of a cognitive model may still remain inadequate for neuroscientific investigation. The example above from Santi and Grodzinsky (2007) showed that importing the linguistic concept of Movement into a neuroimaging experiment resulted in puzzling findings, arguably because Movement was solely considered as a syntactic operation, ignoring its potential relation to inhibition—a cognitive concept that may translate more directly into the language of neuroscience (Chambers et al. 2009).

As a general conclusion, results from imaging and other cognitive neuroscientific techniques require careful consideration of the methodological fine print. Summarized interpretations will typically resort to cognitive terminology (“syntax”, “working memory”), whereas the actual results depend on the precise implementation of tasks, on the details of data acquisition and processing, and on sample size and statistical significance thresholds. Each well-designed experiment will contribute a small piece to the puzzle (for example towards an understanding of the functional organization of Broca’s area), but pieces may be mislabeled.

The previous sections have shown that language is surely “in the brain”, in the sense that linguistic behavior requires brain function. More specifically, there is overwhelming evidence that certain parts of the brain play crucial roles in language-related functions, in particular the regions of the left hemisphere traditionally known as Broca’s and Wernicke’s areas. However, beyond this bland statement things become less transparent. Imaging and lesion findings have pinpointed a number of additional regions, such as the anterior superior temporal gyrus in syntactic processes (Friederici and Kotz 2003; Friederici et al. 2003), the superior temporal sulcus (STS) in sentence comprehension (Devauchelle et al. 2008; Redcay 2008), and the cerebellum in speech production (Ackermann 2008), language comprehension (Baillieux et al. 2008), and possibly morphosyntactic¹³ abilities (Justus 2004). It is obvious that these brain regions are not exclusively involved in language processing. For example, portions of the STS are considered crucial for the perception of biological motion (Puce and Perrett 2003), as well as social cognition and audiovisual integration (Hein and Knight 2008; Redcay 2008); the cerebellum participates in numerous nonverbal domains, including executive function, working memory, and attention (Baillieux et al. 2008). Some functional links are intuitively appealing; for example, those between biological motion perception, audiovisual integration and speech perception in STS (Redcay 2008), or those between action understanding, imitation, and language in Broca’s area (Nishitani et al. 2005). However, except for rare studies in neurosurgery patients (Duffau 2008; Ojemann 1991), neuroscience techniques avail-

¹³ The grammatical structure of sentences is not fully determined by word order, but also by insertion of small and relatively meaningless grammatical words (such as prepositions), changes in word endings etc. This is reflected in the term “morphosyntax”. For example, interpretation of the sentence “The Rottweiler *was bitten by* the mailman” is not possible based on word order alone, but requires decoding of morphological cues (passive voice indicated by the auxiliary verb “be” and the ending of the verb “bite”, which makes it a participle) and the preposition “by” indicating that “mailman” is the agent of the sentence, i.e. the one who (unexpectedly) does the biting.

able for studies of living humans are limited in their spatial resolution (see Box 2) and are therefore unable to answer questions about the functional specialization of individual neurons or small assemblies of neurons (“minicolumns”).¹⁴

2.2.5 *Variability and Plasticity*

As a tentative conclusion, the existing literature predominantly suggests an integrative organization, with distributed networks for language that partly share neuronal resources with other functional domains. Historically, the schools of localizationist and holistic thinking were thus both partly justified because local functional specialization is accompanied by distributed network organization. However, even if precise evidence were available regarding brain loci specialized in language functions (e.g., some neurons in STS showing increased firing rates only in response to visual stimuli of biological motion, others only in response to speech stimuli), a fundamental question would remain: If such a finding is true for person A, will it equally apply to person B? The question makes little sense when it comes to individual neurons because there is simply no way to identify “the identical neuron” in two human brains. On a more macroscopic level of brain regions and their functional specialization, however, the question is reasonable and can be experimentally tested. Strangely, neuroimaging studies of individual variability are rare. Variability within groups (typically healthy “normal” young adults) is conventionally considered noise. Anatomical variability of the brain is minimized through ‘spatial normalization’, after which (ideally) each image element (voxel) falls onto exactly the same spot in the brain in each individual. If a voxel shows activation for a given task in nine participants out of a group of ten, lack of activity in the tenth individual reduces significance of the group finding, but is otherwise shrugged off as an uninterpretable nuisance.

This attitude is based on a convenient fiction (the universality of functional brain organization), which may hamper an adequate understanding of neurofunctional organization. In the few language studies of healthy adults that compared activation findings across individuals, substantial variability was found. Herholz and colleagues (1996) studied seven adults during covert verb generation and found dramatic differences in magnitude and localization of activation in left IFG and in overall patterns of cerebral blood flow changes. However, task compliance could not be monitored in this study because participants were producing words only in their heads (covertly). A second study by Xiong et al. (2000) instead used overt verb generation in a larger sample of 20 young adults. Interestingly, highest consistency of activation was found in motor regions. Areas 44 and 47 in left IFG showed expected groupwise activation, but were not activated in four of the participants. Handedness could affect these find-

¹⁴ A minicolumn includes about 100 neurons with strong excitatory interconnections. These neurons are vertically arranged, giving the impression of a ‘column’. Minicolumns are considered basic functional units of mammalian cortex (Mountcastle 1997).

ings, but was not reported by Xiong and colleagues. Seghier and colleagues (2004) included 30 exclusively right-handed participants in an fMRI study of phonological rhyme judgments and semantic category decisions. Although Broca's area (areas 44, 45, and 47) showed robust groupwise activation and was activated in most participants (88 and 96 % for phonological and semantic tasks, respectively), the individual variability of peak activation loci was high in the left IFG for both tasks.

Quantifying individual variability in neuroimaging is not entirely straightforward, and methodological details such as smoothing (image blurring) and spatial normalization (warping to a standard anatomy) will affect results. However, ample evidence is available from other techniques to appreciate that variability reflects basic principles of functional differentiation (rather than measurement error). Drastic manipulations of brain development in animal models have shown *cross-modal plasticity* in differentiation of the cerebral cortex (O'Leary and Nakagawa 2002; Sur and Leamey 2001). For example, 'rewiring' of connections in deep subcortical regions can transform temporal *auditory* cortex into *visual* cortex, if temporal cortex receives input from visual nuclei in the thalamus during critical developmental periods (Sur et al. 1990). Cortical tissue can also be transplanted during early development and will assume the functional organization of the surrounding 'host' region. Developing occipital cortex will thus assume somatosensory specialization (such as tactile perception), if it is transplanted into the postcentral region and receives input from somatosensory nuclei from the thalamus (Schlaggar and O'Leary 1991). Human imaging studies suggest that similar principles of cross-modal plasticity are at work in people with early loss or congenital absence of one sensory modality. Temporal 'auditory' cortex assumes visual functions in deafness (Finney et al. 2001), and occipital 'visual' cortex takes over tactile functions in congenitally blind people, especially during Braille reading (Sadato et al. 2002).

How is this related to individual variability of language networks? Evidence of cross-modal plasticity can be considered the 'tip of the iceberg' of experience-driven plasticity that is at work in every typically developing brain. Probably the strongest set of evidence for experience-based changes in healthy brain organization comes from studies in professional musicians. Imaging studies have shown effects of musical experience on functional organization in motor (Elbert et al. 1995; Hund-Georgiadis and von Cramon 1999) and auditory cortex (Pantev et al. 1998), as well as on brain anatomy in these regions (Amunts et al. 1997; Hyde et al. 2009; Schlaug et al. 2005). One study using magnetic resonance spectroscopy (Aydin et al. 2005) found that neuronal numbers and function in the left superior temporal gyrus were significantly higher in professional musicians than in non-musicians. It is especially compelling that in all of these studies functional and anatomical plasticity was related to the age of inception of musical practice, which suggests that plasticity reflects the amount of lifetime experience.

Another manifestation of plasticity, i.e., plasticity following brain damage, had been proposed by nineteenth century neurologists, such as Hughlings-Jackson and Head, as discussed in Sect. 2.2.1. With modern neuroimaging techniques, functional reorganization for language can now be experimentally demonstrated. PET and fMRI studies have shown that early-onset damage to the left hemisphere often results in

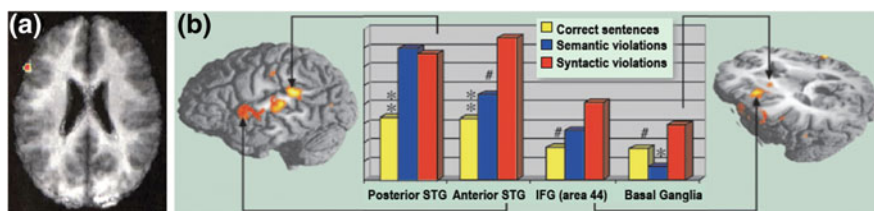


Fig. 2.3 Results from two fMRI studies of syntactic processing, as described in main text. **(a)** Caplan et al. (1999) find only a single and small activation in area 44 of the left hemisphere, based on an *a priori* hypothesis. **(b)** Friederici et al. (2003) observe effects related to syntactic processing in distributed left perisylvian regions. Bars in the center show relative activity in several left-hemisphere regions (posterior and anterior STG; frontal operculum; basal ganglia) color-coded by condition. Pronounced effects for the syntax condition are seen in anterior superior temporal gyrus, inferior frontal operculum, and basal ganglia, but these regions also show some degree of activation for the other two conditions

reorganization of language to the right hemisphere, if the right hemisphere remains intact (Guzzetta et al. 2008; Lidzba et al. 2006; Liégeois et al. 2008; Müller et al. 1999; Staudt et al. 2002; Fig. 2.3).

Greater plasticity in children than in adults can be largely attributed to developmental changes in synaptic density. Early in postnatal development, the number of synapses is extremely high (Bourgeois 2001). During child development, synaptic pruning dramatically reduces the number of synapses (Chugani et al. 1987). The early period of synaptic ‘abundance’ corresponds to greater plasticity, most likely because synaptic pruning is still in process and can be partly suspended, resulting in the emergence of alternative brain networks (Müller 2004; Müller and Courchesne 2000). For example, connections between Broca’s and Wernicke’s area in the left hemisphere may be lost due to early injury. Corresponding connections in the right hemisphere, which in typical development will be mostly pruned away, may now be maintained and strengthened, resulting in atypical right hemisphere dominance for language. The period of intense plasticity roughly corresponds to the ‘critical period for language acquisition’ (Lenneberg 1967), reflected in the easy and apparently automatic acquisition of language(s) in children compared to more effortful and limited acquisition of new languages in adolescents and adults.

In conclusion, individual variability of neural networks for language is largely a reflection of brain plasticity. Functional localization (e.g., the existence of Broca’s and Wernicke’s areas) is roughly universal, but a more detailed and microscopic view tends to show variability that is partly experience-driven, partly genetic (see Müller 2009 for review; Thompson et al. 2001). The role of experience, i.e., brain activity in response to and interaction with the environment, and the impact of gene-based brain maturation illustrates that specialized language networks are the product of a dynamic developmental process, rather than a set of stationary locations.

2.3 Through the Brain: Language as a Distributed Process

2.3.1 *Ontogeny*

Studies in infants suggest some degree of early specialization related to language. Near-infrared spectroscopy (NIRS; see Box 3) has recently become a method of choice in the study of infants (Minagawa-Kawai et al. 2008). Differential responses to spoken language in left temporal lobe and visual stimulation in occipital cortex have been reported for infants 6–9 months of age (Bortfeld et al. 2007). Minagawa-Kawai and colleagues (2007) found that changes in vowel length across phonemic category (compared to within-category changes)¹⁵ were associated with greater blood flow response in temporal cortex in 6–7 months old infants. However, a lateralized response (greater in the left than in the right hemisphere) was only seen after 13 months of age.

A similar pattern of change has been observed in event-related potential (ERP) studies (Box 3), which combine EEG with stimulus presentation. Cheour and colleagues used ERP mismatch negativity¹⁶ and showed that newborns were able to learn phonological discriminations during sleep (Cheour et al. 2002) and that phonemic distinctions of the native language emerge in infants before age 12 months (Cheour et al. 1998). Whereas basic phonemic abilities thus seem present early in infancy, word acquisition begins slightly later. Mills et al. (1997) found that words understood by 13–17-month-old children were associated with widespread and bilateral ERP changes (when compared to unknown words). In 20-month-old children, ERP differences between known and unknown words were seen primarily in temporo-parietal regions of the left hemisphere, suggesting increasing localization and lateralization of word meanings.

¹⁵ For an example, consider the length of the vowel /i/ in the word “fit”, which is around 60 ms. With length of > 100 ms, a phonemic boundary will be crossed and the vowel will be perceived as a long /i:/, resulting in the word “feet”. On the other hand, a change in vowel length from 100 to 150 ms will not be perceived as a different phoneme (and the perceived word will remain “feet”). Whereas acoustic length of the vowel can thus vary in graded fashion, some relatively small changes in vowel length around the category boundary will be perceived as distinct phonemes that can change the meaning of a word.

¹⁶ The mismatch negativity (MMN) is an EEG response that follows about 150–250 ms after a deviant stimulus (e.g., a high tone among a series of low tones, or an omitted click in an otherwise regular sequence of clicks; Cheour et al. 2000). It can be reliably measured even in infants and therefore provides a technique for demonstrating perceptual discrimination at an age when verbal responses cannot be obtained. If an infant shows an MMN to stimulus A in a series of presentations of stimulus B, one can infer that the infant brain is able to distinguish A from B.

Box 3. Near-infrared spectroscopy (NIRS) is an optical imaging technique detecting changes in blood oxygenation through the skull. It is non-invasive and relatively insensitive to motion artifacts, which makes it ideal for the study of infants and small children. However, spatial resolution (see Box 2) is low. Two other techniques suitable for the study of small children detect neuronal activity directly (rather than the blood flow changes associated with it). **Event-related potentials (ERPs)** are an adaptation of traditional electroencephalography (EEG) and use microelectrodes on the scalp to detect small changes in electrical currents triggered by a stimulus or task. **Magnetoencephalography (MEG)** relies on the same electromagnetic effects of neuronal “activity, but detects changes in magnetic fields outside the skull in a shielded environment.”

However, neither NIRS nor ERP provide sufficient spatial resolution to pinpoint developmental changes in language organization. FMRI studies of infants remain rare, given the motion sensitivity of this technique. Studying infants 2–3 months of age, Dehaene-Lambertz and colleagues (2002) could show activation in STG in response to speech, which was stronger in the left than in the right hemisphere for both forward and backward speech. In a follow-up study (Dehaene-Lambertz et al. 2006), activation in the STG during presentation of sentences was found to be bilateral in 3-months olds. Interestingly, response in Broca’s area was delayed (occurring several seconds after STG activation) and enhanced when sentences were repeated verbatim (compared to novel sentences). The authors speculate that this finding may reflect “a sentence learning mechanisms” already at work in the left IFG, which they relate to this region’s status as an “integrative node common to perception and production” and the participation of IFG in emerging mirror neuron networks crucial for imitation and action understanding (Nishitani et al. 2005). I will return to this theme in Sect. 2.4.

Imaging and electrophysiological studies in infants suggest *language readiness* of left perisylvian regions (those surrounding the Sylvian fissure, see Fig. 2.4). This is not equivalent to fully established *functional specialization*, but indicates that STG in the left hemisphere tends to have an early advantage in processing complex and fast-changing auditory stimuli (Zaehle et al. 2004). It is less clear, though, whether language readiness in left STG and IFG reflects what Greenough et al. (1987) call *experience-expectant* properties, which primarily apply to evolutionarily old sensorimotor systems.¹⁷ Chomsky’s metaphor of language “growing” in the child similar to a bodily organ (Chomsky and Ronat 1979: 83–84) would imply that plasticity in these regions is experience-expectant. This appears to be supported by studies in congenitally deaf users of sign language showing that left perisylvian cortex is

¹⁷ Greenough et al. (1987, p. 540) define experience-expectant plasticity as “designed to utilize the sort of environmental information that is ubiquitous and has been so throughout much of the evolutionary history of a species.” An example is the development of ocular dominance columns, which are small vertically organized units in visual cortex that respond to information coming from one eye only.

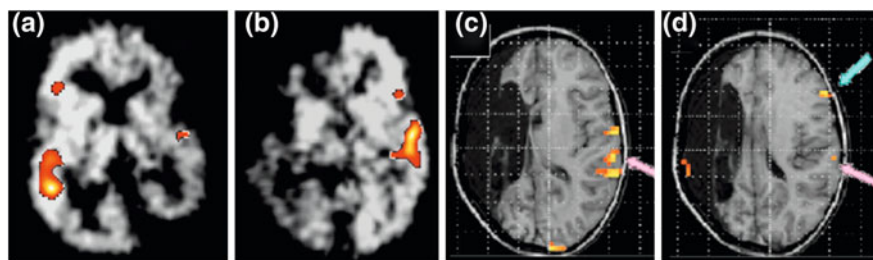


Fig. 2.4 Clinical studies showing effects of developmental plasticity. (a)–(b) PET studies showing activation for listening to sentences in two children with Sturge-Weber syndrome, a congenital condition that results in progressive calcification of one hemisphere, leaving the other intact. (a) A child with calcification and shrinkage of the right hemisphere shows a typical pattern of left hemisphere activation in superior and middle temporal gyri and inferior frontal lobe. (b) A second patient, with damage to the left hemisphere shows almost a mirror image of activity, in inferior frontal and superior/middle temporal gyri of the *right* hemisphere (see Müller et al. 1998 for complete data). The capacity for language to reorganize into the right hemisphere early in life is further illustrated in (c)–(d) by the example of a patient with left hemispherectomy (removal of the left hemisphere). Activations during overt word generation are seen in right IFG (*blue arrow*) and right superior and middle gyri (*magenta arrows*). (c)–(d) adapted from Liégeois et al. (2008)

crucial for language acquisition even when one typical sensory modality of language learning (hearing) is missing (Campbell et al. 2008). Conversely, the finding of language reorganization into the right hemisphere in children with early left hemisphere damage, as described in Sect. 2.2.5, may suggest that plasticity at work in emerging language systems is to some extent *experience-dependent*, i.e., partially dependent on environmental interaction.

While regional proto-specialization or ‘readiness’ for language can thus be observed surprisingly early in the infant brain, imaging studies in older children have shown substantial changes in language networks over time. One finding is the increase in lateralization of language-related activity with age (Brauer and Friederici 2007; Holland et al. 2001; Ressel et al. 2008). Holland and colleagues (2001) found that leftward asymmetry of whole-brain activity during covert verb generation correlated significantly with age in 7–18 year-old children, although a follow-up in a larger sample suggests that age-dependent lateralization is subtle and task-dependent (Holland et al. 2007). Some studies have found age-dependent increase of activation in Broca’s area for verb generation (Holland et al. 2001; Szaflarski et al. 2006) and phonological rhyme judgment (Booth et al. 2004). However, this intuitively appealing finding is not always replicated. For example, Brauer and Friederici (2007) used syntactic and semantic violation tasks (as described earlier) and found left IFG activation in children for all types of sentences (including those without violations), whereas activation in adults was confined to area 44 and only observed for sentences with violations. Conversely, Schlaggar, Petersen, and colleagues (Brown et al. 2005; Schlaggar et al. 2002) identified positive age-dependent effects in left frontal cortex using several overt word generation tasks, which require spoken production of words and are preferable to covert generation (without articulated speech) because

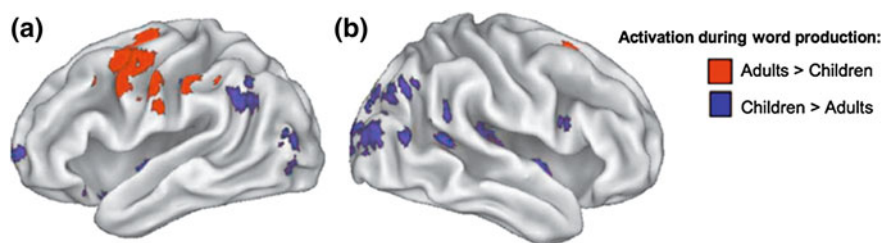


Fig. 2.5 Brain regions showing age-dependent differences in activation during word production, in an fMRI study of children and adults between 7 and 32 years of age. *Red clusters*, mostly in motor and premotor regions of the left hemisphere (a), show greater activation in adults than in children. Conversely, greater activation in children (*blue clusters*) is seen mostly in posterior parts of the brain, in both the left (a) and the right hemispheres (b). Adapted from Brown et al. (2005)

performance can be monitored (Fig. 2.5). The site of age-dependent increase in these studies was not the IFG, however, but premotor area 6, possibly related to motor planning. The overall pattern in these studies suggests greater activity in children on the perceptual side (receiving a word stimulus) and greater activity in adults on the response side (articulating a word). It is unclear whether greater activity in visual cortex, which was very pronounced in children up to age 10 years, but leveled off in older children and adults, represents simply different attention-related strategies of dealing with a verbal stimulus-response task (young children being more input-oriented), or whether it reflects a stronger perceptual dependence of word representations in children.

This brief review¹⁸ suggests substantial developmental changes in language organization during childhood. However, as in previous discussions of language organization in adults, simple generalized conclusions (such as increasing leftward asymmetry or increasing activity in left IFG) are thwarted by complex results and dependence of findings on task designs and methodological detail. For example, Brauer and Friederici (2007), as mentioned, could not find evidence for greater left IFG activity in adults than in children. However, when further inspecting activation in Broca's area in a follow-up study (Brauer et al. 2008), they found that BOLD effects (Box 1) were delayed in children around age 6 years, compared to young adults. Such delay was not seen in auditory cortex in the left temporal lobe, suggesting that it might not be simply explained by a slow blood flow response, but by delayed neuronal activity in Broca's area. This study highlights dynamic changes in language processes on a smaller time scale, i.e., changes observable during a single language-related process, to which I will turn now.

¹⁸ For a more comprehensive review of the literature on developmental change in language networks see Müller and Palmer (2008).

2.3.2 *Microgeny*

Microgeny relates to the unfolding of a cognitive process that typically occurs on a scale of milliseconds to seconds. The term will be used here in analogy to ontogeny (and phylogeny), as a time scale of neurocognitive change, and not as a theory assuming parallels between time scales, as proposed by Brown (1988).

Given the low temporal resolution of PET and fMRI, the technique of choice for microgenetic studies of language has been ERP (Box 3). At least four distinct electrophysiological components have been attributed to different language subprocesses (reviewed by Friederici and Kotz 2003). An early negative component (N100) corresponding to phonological analysis is followed by an early left anterior negativity (ELAN) at about 150–200 ms after stimulus presentation, which reflects first-pass syntactic decoding (cf. also Neville et al. 1991). This is followed at about 400 ms by a semantic component (N400), and finally in some cases of reanalysis or repair (e.g., for sentences with complex structure or violations) by a positive component (P600). While these ERP components can be indirectly related to imaging and lesion findings for clues on anatomical sources, magnetoencephalography (MEG; Box 3) provides an improved combination of high temporal resolution and better spatial resolution, as signals are less distorted by the skull in MEG than in EEG (Wheless et al. 2004).

Magnetic fields corresponding to the N100 and associated with phonological processing can expectedly be localized to sources from the posterior STG, near the primary auditory cortex (as reviewed in Salmelin 2007). MEG components corresponding to the syntactic ELAN have been identified less consistently (Knösche et al. 1999; Kubota et al. 2005; Kwon et al. 2005). This may relate to differences between EEG and MEG. Signals predominantly originate from neurons at the top (“crest”) of a gyrus in ERP, but from neurons buried in the sulci in MEG. As a consequence, ERP and MEG data may not always coincide. Friederici et al. (2000b) therefore used fMRI to localize brain activity that was the source of magnetic fields and were thus able to identify an MEG component that peaked around 150 ms after presentation of a syntactic violation (e.g., “The fish was in *caught*”). Interestingly, the sources were located in STG (just anterior to the primary auditory cortex) and IFG of *both* hemispheres. This is surprising given the overwhelming lesion and imaging evidence of left-hemisphere lateralization for syntax (discussed in previous sections). However, a few imaging studies have also reported right hemisphere effects related to syntactic complexity (Just et al. 1996), syntactic violations (Newman et al. 2001), and repair¹⁹ of such violations (Meyer et al. 2000). Relatively early morphosyntactic effects (with a latency of around 200 ms) have also been shown in frontal and tempo-

¹⁹ Meyer and colleagues (2000) instructed some of their participants to repair sentence violations. For example, when presented with the sentence “The spy was in the caught”, participants would not only indicate that the sentence was ungrammatical, but also covertly fix the violation, generating “The spy was caught” in their minds (without speaking). Activation for this repair condition was particularly strong in right IFG and STG.

ral regions for grammatical gender decisions in an MEG study with German speakers (Härle et al. 2002).²⁰

Maess and colleagues (2006) used MEG for more accurate localization of the N400 that has been reported for semantic violations in numerous ERP studies over the past 30 years (Kutas and Hillyard 1984). Corresponding magnetic evoked fields (MEFs) were found in distributed frontal and temporal regions (areas 45 and 47 in IFG, STG, and inferior temporal gyrus). While effects were more robust in the left hemisphere, most corresponding (homotopic) regions in the right hemisphere also showed effects of semantic violation. MEFs with long latencies (≥ 400 ms) have also been found for sentence and word stimuli in meaningful contexts, without violations (reviewed in Salmelin 2007).

The findings described above seem to suggest that syntactic processes happen generally before semantic ones. However, this simplification is not entirely correct. Some MEG studies have detected semantic MEFs at earlier stages. Shtyrov and Pulvermüller 2007 used word pairs, such as “ball-kick”. MEFs related to semantic mismatch (e.g., “ball-eat”) peaked in left temporal cortex at ~ 115 ms latency, followed by a weaker MEF in the inferior frontal lobe 16 ms later. On the other hand, both semantic *and syntactic* anomalies have also been found to be associated with prolonged effects, often occurring at > 500 ms latency. Kwon et al. (2005) used Korean stimuli with sentence-final morphosyntactic or semantic violations. Both violation types were associated with MEFs in left temporal lobe peaking at a latency of 600 ms.

2.4 Across the Brain: Language Connected

Overall, the neuroscientific evidence on language suggests a picture that differs from what Chomsky may have imagined when he declared language to be a gene-based biological object. Although it cannot be entirely ruled out that a neural architecture uniquely specialized for language and genes that specify this architecture might yet be discovered (cf. Fisher and Marcus 2006), the prospect of such innately predetermined autonomy (or modularity) of language is faint. The findings reviewed above show that several brain regions are quite consistently involved, mostly in the left perisylvian cortex. Some of them, such as left IFG and STG, correspond to Broca’s and Wernicke’s areas that have been considered ‘language areas’ since early studies of aphasic patients. However, the closer one inspects the functional characteristics of these ‘language areas’ from a cognitive neuroscience perspective (rather than a narrow neurolinguistic view), the more these areas appear to assume ‘multiple personalities’. Broca’s area is called by the name of “syntax” in some studies (Caplan

²⁰ Unlike English, German morphosyntax (cf. Footnote 13) relies heavily on grammatical gender since every noun has one of three genders (feminine, masculine, neuter) and articles and pronouns change in agreement with the gender of the corresponding noun. For example, in “Die Tüte riss und ihr Inhalt fiel heraus” (“The bag tore and its contents fell down”), the article “die” and the pronoun “ihr” have the feminine form, in agreement with the grammatical gender of “Tüte”.

et al. 1999; Heim et al. 2003), “semantics” in another (Homae et al. 2002), and “phonology” in yet another (Fiez et al. 1993). Then the plot thickens and we hear the same persona called “imitation” (Heiser et al. 2003), “motor preparation” (Krams et al. 1998), “planning” (Fincham et al. 2002) and “imagery” (Binkofski et al. 2000), “action understanding” (Buccino et al. 2004; Hamzei et al. 2003), “visuomotor coordination” (Müller and Basho 2004), “sequence learning” (Haslinger et al. 2002), “tonal discrimination” (Müller et al. 2001), “artificial grammar learning” (Bahlmann et al. 2008), “working memory” (Nystrom et al. 1998), “rule shifting” (Konishi 1998), “response selection” (Thompson-Schill et al. 1997), “response inhibition” (Collette et al. 2001) and so on. As there is no technique allowing neuroscientists to probe for functional preferences of individual neurons in the healthy human brain, it remains theoretically possible that each of these specializations is entirely separate from linguistic specializations, and that the left IFG consists of a large array of functionally discrete modules. One may invoke the known columnar organization of cortex (Mountcastle 1997; cf. Sect. 2.3) and speculate that neighboring columns might have distinct and unrelated functions.

However, neuroscientists who have learned their trade beyond the confines of linguistics will tend to find such conjectures far-fetched. One reason is that cortical connections are predominantly local (Braitenberg 1991) and that neighboring sites therefore tend to participate in similar (though subtly specialized) functions. While one may cling to historical ideas of innate specialization, autonomy of language and modularity, the neuroscience of ‘language areas’ provides a unique opportunity for a deeper understanding of how children develop the ability to understand and produce words and string them together in phrases and sentences. Imaging and other neuroscience techniques provide a complex picture of the brain regions involved in language. By learning what else these regions are also involved in, we obtain clues as to what the cognitive and sensorimotor components and precursor functions may be that support and guide language acquisition (for detailed review see Müller 2009).

Our understanding of how relatively elementary functional specializations come together in support of more complex higher cognitive functions has been boosted by recent developments in the study of white matter, which contains axons connecting different parts of the brain. In particular, diffusion tensor imaging, an MRI technique that can be used for mapping out fiber tracts in the brain (Le Bihan 2003), has been applied to language-related connections. Traditional notions of the main pathway connecting Broca’s and Wernicke’s areas, known as the arcuate fasciculus, had to be modified recently based on evidence from diffusion tensor imaging (Catani et al. 2005; Fig. 2.6).

The study of connectivity is crucial because it helps overcome the idea of intrinsic local specialization that seems tied to the localizationist tradition. Each cortical neuron is connected to thousands or tens of thousands of other neurons (Abeles 1991). The functional “specialization” of each neuron can therefore be defined by its connectivity pattern, rather than as an intrinsic property (Passingham et al. 2002). This is

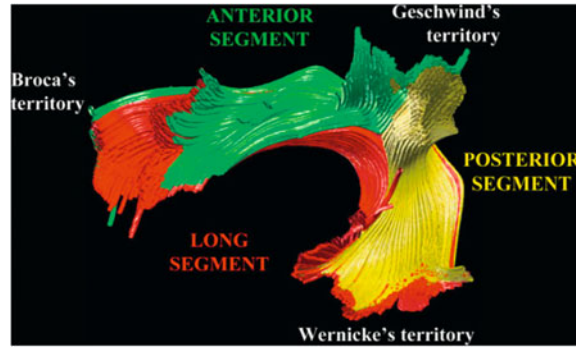


Fig. 2.6 Reconstruction of white matter fibers corresponding connecting Broca's and Wernicke's areas, by means of diffusion tensor imaging (DTI). This study, which was performed in vivo in eleven healthy right-handed men, shows that there are two pathways, a direct pathway connecting Broca's and Wernicke's area, and an indirect pathway via the inferior parietal lobe ("Geschwind's territory"). From Catani et al. (2005)

a principle of simple Hebbian logic,²¹ as synaptic connections are strengthened from simultaneous firing of pre- and postsynaptic neurons, and thus simultaneous firing will reflect shared sensorimotor or cognitive representations (Kandel et al. 2000). Applying such neuroscientific truisms to a 'language area', such as Broca's area, we obtain a glimpse of this region's true colors by considering the complex connectivity of IFG (Anwander et al. 2007; Friederici et al. 2009). This includes connectivity with inferior parietal and lateral temporal regions in posterior perisylvian cortex via the arcuate fasciculus (Fig. 2.6), as well as connectivity along the dorsal stream, which is crucial for visuospatial processing and visuomotor coordination (Goodale and Westwood 2004); the mirror neuron system (Rizzolatti and Craighero 2004), considered to be involved in imitation, action understanding, and possibly some aspects of social cognition (Pineda 2008; see Chap. 3); and the ventral stream (Rilling et al. 2008; Saur et al. 2008), known to provide meaningful interpretation of visual and auditory stimuli (Grill-Spector and Malach 2004). The best available hypothesis on why Broca's area is also a 'language area' is that this terrain of cortex has the ideal connectivity patterns bringing together information that a child needs to acquire language. A similar argument has been made for posterior perisylvian cortex, such as STS (Redcay 2008).

²¹ Donald Hebb (1949) hypothesized that a synapse is strengthened as a result of synchronous firing of the two neurons the synapse connects. This idea, popularized in the phrase "What fires together wires together", has proven basically accurate.

2.5 Final Note

In the localizationist tradition, which has been boosted by the advent of modern techniques of functional “mapping” (such as fMRI), language tends to be regarded as a location (or a set of locations) in the brain. However, functional brain organization is characterized by plasticity throughout life. Experience and activity are associated with continuous change, which may be anywhere between subtle and dramatic (as in professional musicians or the congenitally blind). Plasticity is particularly pronounced during child development and in response to injury. On a smaller time scale, links between language and the brain are also characterized by constant change. A language process (e.g., comprehending an utterance and responding to it) involves a large number of brain regions far beyond the classic language areas of Broca and Wernicke. Anatomical evidence and imaging of fiber tracts suggests that many of these regions are tightly connected, allowing them to cooperate functionally. In view of the functional characteristics of regions participating in language networks, it appears likely that language emerges from processes shared with numerous functional domains traditionally considered nonverbal. Electrophysiological evidence further suggests that the profile of regional activity changes on a millisecond by millisecond basis. Today it is not fully understood what the ‘neural code’ of language processing may be. Single neurons are unlikely to possess complex intrinsic representational capacities. For example, there will be no neuron (or small set of neurons) fully representing the meaning of the word “cat”. However, it is possible that the complex connectivity of neurons relates more directly to their representational capacity. The synchronous activity of a distributed set of well-connected neurons in several areas of the brain (e.g., IFG and visual, auditory, somatosensory, and premotor cortices) may more fully represent the meaning of the word “cat” (what it looks like, what sounds it makes, what it feels like, how one can interact with it; Martin 2007; McClelland and Rogers 2003; Hwang et al. 2009). If this model is true, the question remains of how exactly distributed sets of neurons are transiently tied together to form a representation or cognitive state. Animal studies suggest that synchronous firing patterns play an important role, especially phase-locked oscillations in the gamma band (around 40 Hz; Singer 2001), or in even higher frequency domains (Canolty et al. 2007). However, correlated distributed activity within language networks can also be seen in very low frequency domains (below 0.1 Hz, Hampson et al. 2002) and it remains possible that many different frequency bands of neuronal communication contribute in a complex hierarchical organization (Lakatos et al. 2008) to language representations and processing.

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