Running title: Language and the brain

By, In, Through, and Across: What is it between language and the brain?

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[Abstract]

Contrasting with Saussure's view of language as a primarily social system, Chomsky redefined language as a biological object. The biologism inherent in the Chomskian theory of language resonates with the tradition of investigating "language in the brain". This common prepositional phrase appears innocent, but suggests that language is an object located inside another object. The spatial metaphor has generated important insights from localizationist studies of brain-damaged patients in the footsteps of Paul Broca and Carl Wernicke to the refinement of language mapping in modern functional neuroimaging. However, with this refinement has come the realization that brains are not truly maps and that language cannot be characterized as the inhabitant of an enclosed cortical terrain.

Ontogenetically, this is supported by evidence of plastic changes in the brain organization for language, prompted by maturation, experience, or localized damage. On a *microgenetic* time scale, language processes happen in many brain regions, some of which are known for their roles in perceptual, motor, and other 'non-verbal' functions. It is uncertain whether any of the brain regions involved in language processing fulfill exclusively linguistic functions. Prime examples are 'Broca's area' in the left inferior frontal lobe, and the superior temporal sulcus, which is part of 'Wernicke's area'. Both regions have recently been shown to be multifunctional, with roles in domains that are crucial to language learning and processing, but not specifically linguistic (e.g., imitation, action understanding, perception of biological motion). This implies that language acquisition is built upon and embedded in diverse nonverbal precursor and component functions that emerge from distributed brain networks during the first years of life.

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), which applied behaviorist principles to the question of child language acquisition. Chomsky's review (1959) is remembered for debunking behaviorist linguistics in an uncompromising way. As an alternative, it laid out basic principles of generative grammar, considered to transform linguistics into a true science on a par with mathematics or physics (Chomsky, 1965; Chomsky, 1972a). While the idea of grammar as a set of rules and principles capable of generating an infinite number of sentences would dramatically change the concept of language in the second half of the 20th century, Chomsky's remarks about the biological bases 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 to specific types of learning (ibid.: p.57). In his later writings, Chomsky tied these biological views to Cartesian rationalism (Chomsky, 1966). These forays into dualistic rationalism were strangely blended with and at least partly motivated by Chomsky's political views, which eclectically (and bizarrely) equated empiricism with US imperialism of the Vietnam era and rationalism with progressive enlightenment (Chomsky, 1972b). From the contemporary point of view, Cartesian innatism and dualism may be considered rather strange bedfellows of linguistics as an exact science. This appears to be reflected in the ultimately ambivalent attitude towards linguistic biologism that has characterized Chomsky's work and that of many fellow generative grammarians. While the putatively genetic bases of universal grammar have been a mantra for decades in generative linguistics, actual efforts to identify relevant genes have been modest.

Chomsky's views were not only opposed to behaviorist teachings, which he directly attacked, but also to the Saussurean tradition, which had dominated early 20th century linguistics. While Saussure, arguably the pioneer of structuralist linguistics (Newmeyer, 1986), foreshadowed Chomsky by viewing language ("langue") as a system that could be subjected to "exact" scientific study ("un object de nature concrète"), he considered this object of language as a social entity, "exterior to the individual" (ibid.: 31f.). To Saussure, the core object of linguistics was therefore a social one, whereas the study of "parole", the "grammatical system that exists in every brain" (ibid.: 30), was considered secondary (ibid.: 37). Chomsky reversed these priorities, declaring the language ability (i.e., "universal grammar") as the core object of linguistics, a biological entity that matured in similar ways as other bodily organs (Chomsky, 1976: 10ff.; Chomsky, 1980: ch.5). 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: 56f.).

Given Chomsky's uncompromising 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 similarities" (ibid.: 374), was hard to reconcile with Chomsky's strong views of the autonomy of language vis-à-vis nonverbal cognition (Chomsky, 1957, 1976). Lenneberg (ibid.: 239ff.) 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.: 265). These ideas are surprisingly modern and still capture the gist of neurobiological evidence that has accumulated in the past four decades.

In the brain: Language as a spatial location

History

Chomsky's programmatic critique of Skinner came in the context of what has been described as an anti-behaviorist "cognitive revolution" of the mid-20th century in linguistics, philosophy, psychology, and articificial intelligence (Gardner, 1987). However, the brain was surely not new territory at the time. On the contrary, neurology had an extensive track record studying brain-behavior relationships. Overcoming empirically dubious early attempts (such as medieval ventricular theory or phrenology of the late 18th century; (Clarke and Dewhurst, 1972), modern neurology had accumulated a large database of studies relating localized brain damage to specific profiles of cognitive-behavioral impairment. As neuroimaging techniques identifying local damage *in vivo* were yet unavailable, the link was usually established *post mortem*. Broca's (1861) groundbreaking case of Leborgne, also called "tan-tan" for his stereotypic utterances reflecting severe expressive speech impairment, serves as an ironic example. First, Leborgne conveniently deceased only 6 days after his case had been declared a litmus test of the theory of functional localization at the Paris "Société d'Anthropologie" in 1861 (Harrington, 1987: 42f.). 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, insula, inferior parietal and anterior superior temporal lobe, as well as large portions of the basal ganglia (Dronkers et al., 2007; Signoret et al., 1984). Nonetheless, 150 years later 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. 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. The impaired mind of a lesion patient is considered healthy minus the functional domain of impairment. This latter function is therefore attributed to the site of injury. The logic of this "patho-normal inference" (Müller, 1992) survives in modern cognitive neuropsychology (see Shallice, 1988 for a thorough review).

The case of Leborgne gained such 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. Interestingly, this ultimately scientific debate had political and ideological undertones in mid-19th 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). Yet critics of the localizationist program have made contributions to the debate about brain-behavior relationships that remain topical today. The British neurologists 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 difference in perspective, that contrasts with the common subtractive logic underlying localizationism, as described above. Rather than equating the effect of brain damage as 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 postmorbid condition underscores the importance of postlesional plasticity, which complicates any subtractive patho-normal inference. 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 consider functional *reorganization* triggered by brain damage. Head's conclusion that due to plasticity lesion effects are not simply subtractive remains an important and fundamental insight almost a century later (e.g., see the critique of "residual normality" in developmental disorders by Thomas and Karmiloff-Smith (2002)). Head (1926) adopted the term *diaschisis* from Constantin von Monakow to describe distal effects of brain damage that reflected the more general principle of non-localized postlesional effects. The concept of diaschisis has survived into modern neurology. For example, following localized damage in cerebral cortex, glucose metabolism is often reduced in the contralateral cerebellum. Such 'crossed cerebellar diaschisis' is attributed to contralateral connections between cerebrum and cerebellum and distal effects of damage within cerebro-cerebellar functional networks (Gold and Lauritzen, 2002; Pantano et al., 1986).

Although the skepticism of the subtractive localizationism in the works of Jackson, Head, Marie (1906) and Goldstein (1948) raised many deep and important issues, it did not put an end to localizationism. 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". 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 much of the insights provided by critics of localizationism. 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" (ibid.: xi).

The criticized 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 aphasia, based on lesion sites hitting either Broca's or Wernicke's areas, or connections between these and other nodes of a simple network (Fig. 2). Modern classifications of aphasia (e.g., Broca's, Wernicke's, transcortical sensory and motor, conduction, global) still resemble Lichtheim's taxonomy (e.g., Benson and Ardila, 1996). Most instrumental in reintroducing the serial-connectionist Broca-Wernicke-Lichtheim model to the general community of cognitive psychology and neuroscience was a review by Norman Geschwind in *Science* (1970), which praised the concept of functionally specialized centers for language as "one of the greatest achievements of the last half of the 19th century" (ibid.: 940).

Localizationism afresh: Syntax and semantics today

While this revitalized localizationism did not share much scientific heritage with Chomsky's claim of the autonomy of syntax, there is some convergence. For an interesting example, Grodzinsky (1990) reviews Geschwind's "appealing" connectionist model and argues to reject it because it does not provide or 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 the inverse problem. How do we know that a linguistic theory that adequately models empirical facts about language behavior actually relates to the way the brain is organized?[1]

Statements in Grodzinsky's amply commented target article in the high impact journal *Behavioral and Brain Sciences* (2000) illustrate the hazards of the approach. There he writes that Broca's area "is more specialized than previously thought…, handles only intrasentential dependency relations (ibid.: 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…"; 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. There is, of course, no perfect solution to the question of linguistic theory-driven top-down vs. neuroscience data-driven 'bottom-up' approaches, although it appears that extreme positions may hamper progress and only careful consideration of both can advance cognitive neurolinguistics. Note that neuroscience itself is not a discipline of unassorted data, but is guided by theoretical models, which may be usefully applied in cognitive neurolinguistics, as I will discuss later.

How compatible are modular and neo-localizationist views with evidence from cognitive neuroscience? Functional imaging techniques, such as ^{15}O-water positron emission tomography (PET) and functional magnetic resonance tomography (fMRI), 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 (Caplan et al., 1998, 1999; Stromswold et al., 1996) implemented comparisons of sentences at different levels of complexity. Both identified activity in left inferior frontal pars opercularis, presenting prominent figures with exclusive activity in this portion of Broca's area. Closer inspection, however, shows that stronger activation was identified in other parts of the brain, but considered irrelevant as they were outside the region of hypothesized activity. In the 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

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[1] Corresponding issues have been debated in artificial intelligence for decades. Computational models informed by cognitive theories may approximate input-output behavior of a human being, but their internal organization in no way resembles functional brain organization. The model-driven approach in AI (Newell and Simon, 1963) was countered in the 1980s by parallel-distributed ("connectionist") models McClelland & 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 models.

enjoyed the juice"). Comparison of the two conditions yielded significantly increased cerebral blood flow changes (activation) solely in Broca's area, as depicted by a small and lonely activation blob in area 44. The presentation is, however, misleading, as at least two additional activation sites with higher z-scores were found in medial frontal and superior parietal cortex, which were considered "non-significant". The wizardry is simple. 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 with reasonable spatial resolution will include >100,000 voxels. While technical solutions (e.g., based on the fact that true activation tends to occur in clusters (Forman et al., 1995)) can mitigate the problem, a more dramatic shortcut is provided by planned comparisons in regions of interest, which drastically lower correction factors. 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, such as statistical power (number of participants), analysis type (whole-brain vs. region of interest), signal to noise ratio (reflecting head motion and other confounds), and the investigator's selection of significance thresholds and method of multiple comparison correction. 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 converging results from many studies, with careful consideration of methodological detail, can provide an indication.

A number of neuroimaging studies have directly compared effects of morphosyntactic and lexicosemantic 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 in healthy adults. Specificity, however, was seen in the *degree* of regional activation for the two types of condition. The anterior superior temporal gyrus (STG) and the putamen (a part of the basal ganglia) showed significantly more activation for syntactic violations; more activation for semantic violations was seen in the middle portion of the STG and the insula, in both left and right hemispheres. Other regions, such as the left posterior STG and inferior frontal operculum (which is part of Broca's area), 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 (2003) used a conceptually similar approach by presenting sentences with syntactic and pragmatic anomalies, which however occurred in sentences of greater length than those used by Friederici et al. (2003). These and other design differences may have led to a rather different pattern of results, with portions of left inferior frontal gyrus (LIFG) showing strongest activity for pragmatic anomalies, but LIFG activity for syntactic anomalies being weaker than activity for sentences without anomalies.

Note that the use of sentences with violations implies that the type of violation specifically taxes the corresponding language component. 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, as discussed in the following section. 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.

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 manipulated the frequency of nouns used in conjoined active (simple) and object-relative clause sentences (syntactically complex). They found that syntactic complexity and word frequency effects interacted in LIFG, LSTG and left 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 be partly related to limited temporal resolution. For example, in the study by Keller et al. (2001), the repetition time (i.e., the time during which a set of brain slices for one time point is acquired) was 3 sec. The authors correctly caution that any brain site, such as LIFG, 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 regional blood flow increases accompanying neuronal activation, temporal resolution of event-related fMRI can be improved to about 1 sec. For example, Ni et al.(2000) were able to identify distinct patterns of activity in response to syntactic or semantic anomalies, modeling blood oxygenation level dependent (BOLD) effects with short latency (4-5 sec) and with longer latencies (up to 10 sec). Effects for syntactic anomalies occurred in LIFG at mid-latency (c. 6 sec), while those in anterior cingulate gyrus, basal ganglia and right IFG were seen at long latency.

Whereas fMRI has limited capacity to resolve the temporal sequence of language processing, 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 (LIFG). In a study by Dapretto and Bookheimer (1999), participants judged whether sentence pairs were the same or different. The task was designed so that judgment required either primarily syntactic or semantic operations. Direct comparison yielded stronger effects for syntactic processing in a superior portion of LIFG (areas 44/45), whereas stronger effects for the semantic condition were seen more inferiorly (area 47). Activation of this inferior portion of LIFG (area 47) in semantic tasks has been observed in many other 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?) and semantic judgments (abstract or concrete noun?). While activation in the inferior tip of the frontal operculum (area 44) was expected given the above findings, semantic judgment was associated with more superior activation in pars triangularis of LIFG (area 45), close to the inferior frontal sulcus. This again suggests that characterizing a task as “syntactic” or “semantic” may be misleading since details of stimulus presentation, comparison condition, and task may affect observed activation patterns.

This latter consideration raises the question of whether activity in a "language area", such as LIFG, and the precise locus of activity within such area should be attributed to specifically linguistic components of a task (e.g., syntactic transformations and the movement of constituents, as suggested by Grodzinsky (2000)) as opposed to components that are shared across functional domains. In view of the location of Broca's area in the vicinity of premotor cortex and dorsolateral prefrontal cortex (DLPFC), reasonable candidates of such shared components are sequential processing (as in complex motor planning) and working memory. Sustained activity supporting active maintenance of multimodal representations has been observed in animal studies of neurons in DLPFC (Miller and Cohen, 2001), and human imaging studies support the crucial role of DLPFC, including LIFG, in working memory (Duncan and Owen, 2000). Fiebach et al. (2005) observed increased activity in LIFG (areas 44 and 45) 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 nonsyntactic maintenance (e.g., non-sentential word lists or letters)? Uchiyama and colleagues (2008) directly compared working memory in sentence and non-sentence tasks (matched for working memory load) and found greater activity in portions of LIFG (areas 44, 45) for the sentence task. A second experiment using garden-path sentences[2] identified activation in area 44 overlapping with that from the first experiment. The authors considered this convergent activation to reflect verbal working memory involved in articulatory rehearsal. 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]*") and parametrically manipulated working memory load (i.e., the number of noun phrases between the dependent elements indicated by italics). 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 LIFG (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.: p.16). Not considered in this study is the possible impact of other nonverbal task components, such as inhibition. In the example sentence "Kate loves…" cited above, maintenance during syntactic decoding may interact with inhibition of the object "the woman" in the final gap position. Activation in area 45 of LIFG 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 area 45 of the left hemisphere interacted with working memory and was specifically enhanced when words had to be rejected after being maintained in working memory. The peak effect in this study occurred within a few millimeters of the peak observed in the study by Santi and Grodzinsky.

The debates about functional specificity and neural localization within the language system (syntax vs. semantics) and between language and other systems (e.g., language vs. memory or motor planning) highlight open questions regarding the metaphor of "language in the brain". First, there is the

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[2] Garden-path sentences have misleading syntactic structure. A classic example is the sentence "The horse raced past the barn fell", where the final word requires reanalysis of the initially expected syntactic structure ("The horse raced past the barn").

unresolved issue of what exactly those mentalistic concepts are that cognitive neuroscience is supposed to find or locate in the brain. Churchland's eliminative materialism (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" was surely crucial in overcoming the limitations of behaviorist black-box theories, which had ruled out any consideration of mind/brain because techniques of direct observation of mind/brain were unavailable (Gardner, 1987). However, as long as models are constrained entirely 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.

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 minutiae of data acquisition and processing, and on statistical power and 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.

Language is thus 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 are crucially involved in language-related functions, in particular perisylvian 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 in sentence comprehension (Devauchelle et al., 2008; Redcay, 2008), and the cerebellum in speech production (Ackermann, 2008), receptive language functions (Baillieux et al., 2008), and possibly morphosyntactic abilities (Justus, 2004). These brain regions are clearly 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 (theory of mind) and audiovisual integration (Hein and Knight, 2008; Redcay, 2008); the cerebellum appears to participate in nonverbal domains too numerous to list (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 available for human *in vivo* studies never achieve the spatial resolution sufficient for answering questions about the functional specialization of individual neurons or functional units such as minicolumns (Mountcastle, 1997).

Variability and plasticity

As a tentative conclusion, the extant 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 was 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, does it equally apply to person B? The question is absurd in regard to individual neurons because there is simply no way to find "the identical neuron" in two different 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 via '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 will reduce significance of the group finding, but is otherwise shrugged off as uninterpretable nuisance.

This attitude is based on a convenient fiction (universality of functional brain organization), which may hamper an adequate understanding of neurofunctional organization. In the few language studies of healthy adults that have examined intraindividual activation findings, variability appeared substantial. Herholz and colleagues (1996) studied seven adults during covert verb generation and found dramatic differences in magnitude and localization of activation in LIFG and in overall patterns of cerebral blood flow changes. However, task compliance could not be monitored in this study. 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 4 and 6). Areas 44 and 47 in LIFG showed expected groupwise activation, but were not activated in 4 participants. While handedness, which could be a confound, was not reported by Xiong et al., 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 in LIFG) 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 LIFG for both tasks (with standard deviations of 6-11mm on each axis).

Quantifying individual variability in neuroimaging is non-trivial, as preprocessing (e.g., spatial smoothing and normalization) will impact results. However, ample evidence is available from other techniques to appreciate that variability reflects basic principles of functional differentiation (rather than noise). Drastic manipulations of brain development in animal models have shown *cross-modal plasticity* in cerebral cortical differentiation (O'Leary and Nakagawa, 2002; Sur and Leamey, 2001). For example, 'rewiring' of subcortical connectivity 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 region. Developing occipital cortex will thus assume somatosensory specialization, if it is transplanted into the postcentral region and receives input from thalamic somatosensory nuclei (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 early 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. The probably 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; Bangert and Schlaug, 2006; Schlaug et al., 2005). One study using magnetic resonance spectroscopy (Aydin et al., 2005) found that neuronal numbers and function in the left STG, as detected by N-acetyl-aspartate, 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 reflection of plasticity, i.e., plasticity following brain damage had been proposed by 19th century neurologists, such as Hughlings-Jackson and Head. 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 reorganization of language to the right hemisphere, if the right hemisphere remains intact (Guzzetta et al., 2008; Lidzba et al., 2006; Liegeois et al., 2008; Müller et al., 1999; Staudt et al., 2002).

In conclusion, individual variability of neural networks for language is a reflection of brain plasticity. Functional localization (e.g., 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 (cf. 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 developmental process, a dynamic sequence of events, rather than a stationary location.

Through the brain: Language as a distributed process

Ontogeny

A comprehensive review of the literature on ontogenetic change in language networks is beyond the scope of this chapter (see Müller and Palmer, 2008). Studies in infants suggest some degree of early specialization related to language. Near-infrared spectroscopy (NIRS), an optical imaging technique detecting changes in blood oxygenation through the skull, has recently become a method of choice in the study of infants because it is non-invasive and relatively insensitive to motion artifacts (Minagawa-Kawai et al., 2008). Differential response to spoken language in left temporal lobe and visual stimulation in occipital cortex has 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) were associated with greater hemodynamic response in temporal cortex in 6-7 month old infants. However, a lateralized response (left > right hemisphere) was only seen after age 13 months.

A similar pattern of change has been observed in event-related potential (ERP) studies, which combine EEG with stimulus presentation. Cheour and colleagues used ERP mismatch negativity (MMN), which indicates perceptual differentiation between auditory stimuli, and showed that neonates 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 (compared to unknown words). In 20 month-old children, ERP differences between known and unknown words were seen primarily in temporoparietal regions of the left hemisphere, suggesting increasing localization and lateralization of word meanings.

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 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 (Dehaene-Lambertz et al., 2002). In a follow-up study (Dehaene-Lambertz et al., 2006), activation in STG during presentation of sentences was found to be bilateral in 3-month olds. Interestingly, response in Broca's area was delayed (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 mechanism" already at work in LIFG, 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).

Imaging and electrophysiological studies in infants suggest *language readiness* of left perisylvian regions. 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. Chomsky's metaphor of language "growing" in the child similar to a bodily organ (Chomsky and Ronat, 1979: p.83-4) would imply that plasticity in these regions is experience-expectant. This is supported by studies in congenitally deaf users of sign language showing that left perisylvian cortex is 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 mentioned above, 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 LIFG (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 paradigms (as described earlier) and found LIFG activation in children for all types (including sentences without violations), whereas activation in adults was confined to the frontal operculum 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 paradigms, which are preferable to covert generation because performance can be monitored. The site of age-dependent increase, however, was not IFG, 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 extrastriate visual cortex, which was very pronounced in children up to age 10 years, but leveled off in older children and adults, represents simply different attentional strategies of dealing with a verbal stimulus-response task (young children being more input-oriented), or whether it reflects a stronger perceptual dependence of lexical representations in children.

This very abbreviated review 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 LIFG) 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 LIFG 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 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 hemodynamic latency, 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.

Microgeny

Microgeny relates to the unfolding of a cognitive process and thus typically occurs on a scale of milliseconds to seconds. According to Brown's (1988) microgenetic theory, a microgenetic process is a "recapitulation in cognition, of patterns laid down during phylo-ontogeny" (ibid.: p.3). This idea of ontogenetic and microgenetic processes reflecting phylogenetic change is thought-provoking (cf. Brown, 1994; Schweiger and Brown, 2000), but has generated few testable hypotheses in neurolinguistics. The term *microgeny* is therefore used here in analogy to ontogeny (and phylogeny), as a time scale of neurocognitive change, not as a theory assuming parallels between levels.

Given the low temporal resolution of PET and fMRI, the technique of choice for microgenetic studies of language has been ERP. At least 4 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) provides an improved combination of high temporal resolution and better spatial resolution, as signals are distorted by the skull in EEG, but not MEG (Wheless et al., 2004).

Magnetic fields corresponding to the N100 and associated with phonological processing can expectedly be localized to sources from posterior STG (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). Signals predominantly originate from neurons at the crest of a gyrus in

ERP, but from neurons with perpendicular orientation in the sulci in MEG. ERP and MEG data are therefore by definition incomplete and may not always coincide. Friederici et al. (2000b) derived seeds for dipole fitting (i.e., for localizing the source of magnetic fields) from a pilot fMRI study and were able to identify effects peaking around 150 ms after presenting a syntactic violation (e.g., "The fish was in *caught*"). Interestingly, their sources were located in the temporal planum polare (just anterior of primary auditory cortex) and inferior frontal cortex of *both* hemispheres. While this was surprising given the overwhelming lesion and imaging evidence of left-hemisphere lateralization for syntax (discussed in previous sections), a few imaging studies have reported right hemisphere effects related to syntactic complexity (Just et al., 1996) and repair of syntactic violations (Meyer et al., 2000). Relatively early morphosyntactic effects with a latency of around 200 ms have also been shown in frontotemporal regions for grammatic gender decisions in an MEG study with German speakers (Härle et al., 2002).

Maess and colleagues (2006) used MEG for more accurate localization of the N400 that has been reported for semantic violations in numerous ERP studies going back several decades (Kutas and Hillyard, 1984). Corresponding magnetic evoked fields (MEFs) were found in distributed fronto-temporal regions (areas 45 and 47 in IFG, STG, and inferior temporal gyrus). While effects were more robust in the left hemisphere, most homotopic regions in the right also showed effects of semantic violation. MEFs with ≥400 ms latencies have also been found for sentence and word stimuli in meaningful contexts, without violations (reviewed in Salmelin, 2007). Other MEG studies of semantic processing have detected MEFs at earlier stages. Shtyrov and Pulvermüller (2007) examined semantic incongruency in a nonsentential context (word pairs such as "ball-kick" and "ball-eat"). MEFs related to semantic mismatch peaked in left temporal cortex at ~115 ms latency, followed by a weaker MEF in 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.

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 prespecifying 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 left perisylvian cortex. Some of them, such as LIFG and LSTG, correspond to Broca's and Wernicke's areas that have been considered 'language areas' since the early days of modern aphasiology. 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 one study (Caplan et al., 1999; Heim et al., 2003), "semantics" in another (Homae et al., 2002), "phonology" in yet another (Fiez et al., 1993). Then the plot thickens and we hear the identical 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 et al., 2003), "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 et al., 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 living human being, it remains theoretically possible that each of these specializations is entirely separate from linguistic specializations, and that LIFG consists of a large array of functionally discrete modules. One may invoke the known columnar organization of cortex (Mountcastle, 1997) 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. 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 indicating what else these regions are also involved in, they give us 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. 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 architecture of the arcuate fasciculus had to be modified based on recent DTI evidence (Catani et al., 2005).

The study of connectivity is crucial because it helps in overcoming 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 is therefore defined by its connectivity pattern, rather than as an intrinsic property. This is a principle of simple Hebbian logic, 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 get a glimpse of this region's true colors by considering the complex connectivity of IFG. This includes, not only connectivity with inferior parietal and lateral temporal regions in posterior perisylvian cortex via the arcuate fasciculus, but also 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); and the ventral stream, 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. Analogous hypotheses have been proposed for posterior perisylvian cortex, such as STS (Redcay, 2008).

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 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 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. Concordant activity of a distributed set of well-connected neurons in LIFG 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). If this model is true, the question of how exactly distributed sets of neurons are transiently tied together to form a representation or cognitive state remains. Animal studies suggest that synchronous firing patterns play an important role, especially phase-locked oscillations in the gamma band (around 40Hz 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 (<0.1Hz, Hampson et al., 2002) and it remains possible that many different frequency bands of neuronal communication contribute in complex hierarchical organization (Lakatos et al., 2008) to language representations and processing.

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Figures

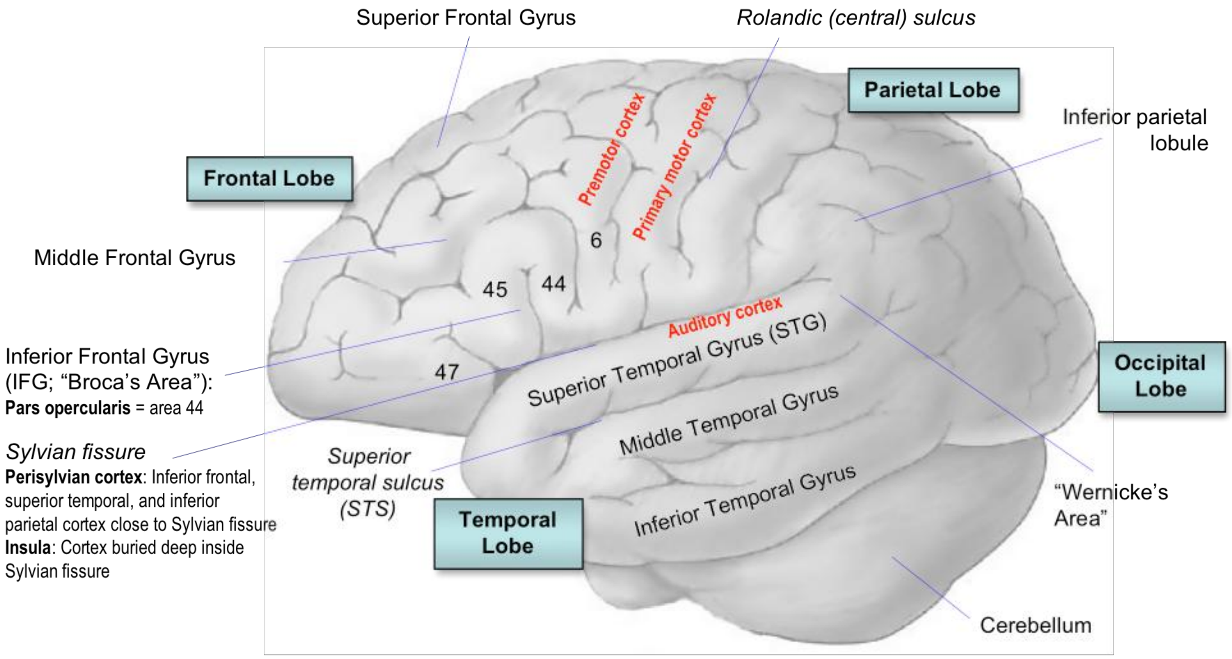

Figure 1. Outline of left hemisphere with anatomical terms used in text.

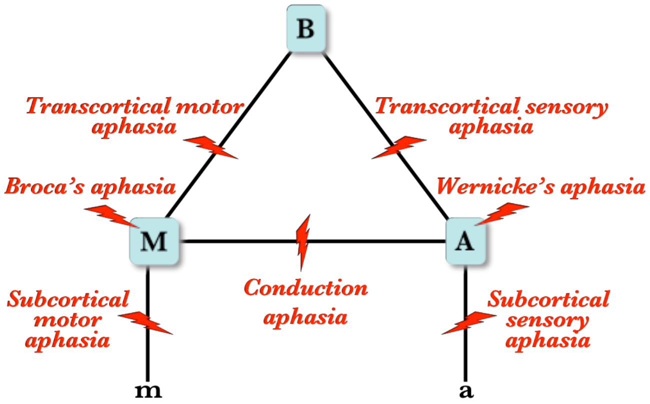

Figure 2. Lichtheim's "house diagram" of the language system. Letters in blue boxes stand for brain centers: M, motoric language center (Broca's area); A, auditory language center (Wernicke's area); B, conceptual center ("Begriffszentrum"). Small letters at the bottom stand for motor and auditory periphery. Exactly seven distinct types of aphasia are predicted from this model, based on lesion sites (indicated by lightening 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.

Figure 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 (yellow: correct sentences; blue: semantic violations; red: syntactic violations). 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.