Language universals in the brain: How linguistic are they?

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1.   Do language universals need a brain?

Anybody's search for language universals will depend on certain assumptions that are not themselves scientific in the strict sense of the empirical sciences, since they cannot be subjected to experimental testing. These basic assumptions are ontological, as they imply convictions of how those universals might *exist*, and they are epistemological because their mode of existence will determine how one can *find out* about them. Although I do not intend to digress into philosophical questions, it is nonetheless necessary at the outset to clarify certain preconceptions that will characterize this chapter. These are physicalist in nature and therefore the information I will provide in the discussions below will be most relevant to those who believe that minds are organized in certain ways because brains are.

There are alternative positions one could take regarding universals. For example, to Saussure (1915/1972) universal principles of "langue" were communicative in nature, i.e., derived from social interaction, rather than individual minds or brains.[i] In more recent cognitive science, minds have sometimes been likened to software or programs that can be implemented on just about any computational hardware (cf. Fodor, 1976; Gardner, 1987: p78f). The implication of this position would be that some universals of mind may exist without corresponding universals of brain. Conversely, Chomsky − arguably the most prominent thinker in modern linguistics − has insisted that "linguistic universals [are] principles that hold of language quite generally as a matter of biological (not logical) necessity", which is ultimately based on a "genetically determined initial state" (Chomsky, 1980: p232).

The physicalist approach taken in this chapter does not deny the possibility of universal principles of language that are not based on a unique neural architecture. In other words, different speakers (including speakers of different languages) may abide by abstract universal principles, but these principles − though universal descriptively − may be subserved by diverse types of neural processes. This universality could be called *shallow* because it is not found in neurocognitive architecture, but only in the description of linguistic behavior. *Deep universality*, on the contrary, would involve neurofunctional principles shared by all typically developing brains. I will argue below that from a developmental neuroscience point of view, it is not very likely that any deeply universal principles are specifically linguistic. Functional domains that begin to develop before the onset of language acquisition (such as visuomotor coordination, polymodal integration, joint attention, working memory) present us with much more probable roots for linguistic universals.

2.   What is universal in human brains?

When examining human brains, either on a macroscopic level of large anatomical landmarks (e.g., the inferior frontal gyrus; the sylvian fissure; Figure 1) or on a more microscopic level (e.g., the layered architecture of cortex), seeing universality or variability depends on viewpoint in similar ways as seeing a glass half full or half empty. With a human gene "code" that contains probably no more than 35,000 genes (Ewing & Green, 2000), a full a priori specification of the brain's entire architecture (let alone that of other bodily organs) is unlikely. Since development is therefore largely epigenetic in nature the high degree of phenotypic universality, at least within the spectrum of what we call "typical development", is surprising.

As a macroscopic example, every typically developing brain has two almost (but not quite) symmetric hemispheres, each hemisphere in every such brain has a central sulcus (Figure 1), just posterior of which we find cells that increase their firing rates during tactile or somatosensory stimulation. Even more, in every such brain different body parts are organized on this postcentral gyrus in a roughly topographic manner, the face being represented at the bottom and legs and feet at the top, with hands and trunk in between. However, the basic universal blueprint of neuroanatomy is also subject to great individual variability. For example, the precise shape of the central sulcus or the postcentral gyrus will never be the same across individuals. Indeed, this variability of individual brain morphology is one of the insistent problems in functional neuroimaging studies, which rely on our ability to pool brains of individual subjects for statistical group analyses. The process of "spatial normalization" reflects the duality of discernible universality (the brain in "standard space") and observed individual variability (the brain in "native space"; Brett *et al.*, 2002).

For an example of microscopic universality, neocortex in every typically developed human brain examined with suitable methods, such as Golgi or Nissl stains, has been found to consist of six layers with different cell types and specific connectivity patterns for each layer (Amaral, 2000). Although the textbook assumption of six distinct "laminae" defies the true complexity of neocortex (Braitenberg & Schüz, 1991), the principle of layered architecture is universal within the species and it is also universal across different neocortical regions within each individual (Creutzfeldt, 1977). However, with respect to this intraindividual universality, there are interesting variations that correspond to function. Layer IV containing cells that receive axons with sensory inputs from the thalamus is well developed in sensory cortex (e.g., postcentral somatosensory cortex), but virtually nonexistent in primary motor cortex located just anteriorly, in the precentral gyrus.

This difference between primary sensory and motor cortices has obvious functional relevance. It invites the question whether similar functionally relevant differences may exist with regard to more complex cognitive domains, such as language. While language use involves sensory and motor functions (auditory processing of speech; planning and execution of complex movements of the vocal tract etc.), such functions are usually not considered relevant to core language universals because they appear peripheral and shared with other domains (e.g., auditory perception of music; motor execution in playing an instrument). Of greater interest would be species-universal architectural specificity in cortex suspected to play crucial roles in core language components, such as morphosyntax. I will return to this question in detail in section 6 below. Suffice it to emphasize here that in Broca's area in the left inferior frontal gyrus − probably the most obvious candidate for such a "language area − there is indeed some species-universal specificity that distinguishes this cortex from primary sensory or motor areas, but this universal blueprint is again accompanied by substantial individual variability (Amunts et al., 1999).

Universality can be found, not only in the vertical organization of cortex (in the layered architecture described above), but also in its horizontal architecture. This *columnar* organization was first described by Hubel and Wiesel (1968) in their electrophysiological studies of visual cortex in the monkey. Since then, columnar organization has been documented across cerebral cortical regions, not only for unimodal sensorimotor cortices, but also for multimodal association cortices (Mountcastle, 1997). Columns are characterized by intrinsic features (i.e., tight vertical interconnectivity with limited local horizontal connections) and by extrinsic organization (e.g., specific afferents from thalamus; specific efferents to other brain regions). Although this organizational principle appears largely universal across cerebral cortex, there is variability with regard to cell types and connectivity between regions. Whereas the basic blueprint of columnar organization can be considered as ultimately driven by genetic information (but note the caveats in the following section), relatively little is known about individual variability of cytoarchitecture and columnar organization in the human brain that may be based on experiential factors.[ii]

3.   What can genes do for universality in the brain?

As alluded to above, brain organization is unlikely to be fully specified by genes. Nonetheless, it is almost certain that genes play a crucial role in brain anatomical and architectural universality, while being instrumental for neural variability at the same time. In rodents, regulatory genes such as *Emx2* and *Pax6* have been identified that are expressed in graded fashion along the anterior-posterior axis in the developing brain. Mutations of these genes result in distorted proportions of posterior visual cortex versus more anterior somatosensory and auditory cortices (O'Leary & Nakagawa, 2002; Pallas, 2001). Genetic effects on brain morphology have also been demonstrated in humans. Thompson and colleagues (2001) found that monozygotic twins were less different in local gray matter volume compared to dizygotic twins, who in turn showed fewer regional differences than unrelated subjects. Interestingly, the putatively gene-driven similarity between monozygotic twins differed from region to region, with some regions of the brain showing variability similar to what was seen in unrelated subjects. This latter finding suggests the importance of experiential and other non-genetic effects (see below and Section VI).

When considering what in the gross morphology of the brain or the micro-architecture of cortex might be genetically determined, it is important to appreciate that if a feature is "innate" (i.e. present at birth) it is not necessarily driven by genes, for at least two reasons. First, the brain developing in utero is by no means isolated from the external world. Although low-pass filtered and muffled, the fetus can perceive sounds including language stimuli in utero, and some evidence suggests transnatal auditory learning, i.e., postnatal retention of stimuli received in utero (Moon & Fifer, 2000). In one study by Moon and colleagues (1993), infants who were only about two days old showed a preference for native language versus foreign language stimuli, which may be attributed to prenatal experience.

Second, the prenatal brain is highly active and some of the ultimate functional organization of the brain appears to be driven by this activity, rather than by intrinsic information that might directly reflect gene expression. As reviewed by Rakic and colleagues (2004), the differentiation of cerebral cortex into functionally specific areas is driven partly by intrinsic, partly by extrinsic factors, among which afferent activity plays a predominant role. For example, Schlaggar and coworkers (1991) showed that when cortex from the occipital lobe (typically visual cortex) is transplanted into the postcentral region (typically somatosensory cortex) in rat embryos, these rats will develop

almost normal somatosensory barrel fields in the transplanted cortex, i.e., receptive fields for individual sensory hairs (whiskers). This cortical differentiation into barrel fields is presumably determined by afferent activity from somatosensory regions of the thalamus, as opposed to intrinsic information in the transplanted cortex itself, which would have resulted in development of visual specialization.

4.   What can genes do for language?

With regard to the question of 'genes for language', the predominant empirical approach has been similar to the traditional lesion approach in neuropsychology that investigates brain organization based on specific deficits resulting from localized damage (see Section V). Analogously, the focus has been on genetic defects associated with developmental language impairments (Bishop, 2002; Tomblin & Buckwalter, 1994). A series of studies that received much attention was dedicated to familial aggregation of specific language impairment (SLI) in family KE (Gopnik, 1990; Gopnik & Crago, 1991). Speech disorder in this family was later found to be an autosomal-dominant trait involving a single gene on chromosome 7 (Fisher et al., 1998; Lai et al., 2001). The studies by Gopnik and colleagues (1990, 1991) initially suggested a selective linguistic deficit specifically related to aspects of morphosyntax (such as past tense formation). Subsequent testing by Vargha-Khadem and colleagues on a broader battery of tests revealed, however, that deficits in affected family members were by no means exclusively morphosyntactic. For instance, affected family members had significantly lower *nonverbal* IQ scores than unaffected members. They were also affected by orofacial dyspraxia and their phonological working memory was impaired (Vargha-Khadem *et al.*, 1995; Watkins *et al.*, 2002a). Magnetic resonance imaging (MRI) findings in family KE (Watkins et al., 2002b) demonstrating gray matter reduction mostly in motor areas of the brain support the conclusion that basic impairments are non-linguistic and that apparently specific morphosyntactic deficits are in fact secondary to orofacial motor, phonemic, and other impairments.

The findings of impairments beyond the language domain in affected members of family KE serve as a caution to developmental linguists such as Pinker (2001), who has speculated that the genes involved "may have a causal role in the development of the normal brain circuitry that underlies language and speech." As mentioned, in family KE (as well as one unrelated case; Lai et al., 2001) the relevant mutation associated with speech disorder has been located to a region on chromosome 7 (7q31), and specifically to a gene named *FOXP2* (forkhead box P2). This gene belongs to a group of so-called 'forkhead transcription factors', which are involved in the synthesis of ribonucleic acid (RNA) from deoxyribonucleic acid (DNA). Forkhead proteins play a role in various rather general functions related to cellular proliferation and differentiation, as well as signal transduction (Marcus & Fisher, 2003). Since *FOXP2* is expressed, not only in the brain, but also in other body organs, such as the lungs and the heart, it appears unlikely that it could play a specialized role neurocognitive development, let alone a specific function in morphosyntax. Nonetheless, recent work including larger samples of patients with verbal dyspraxia suggests that a specific coding change within the *FOXP2* gene may more specifically affect the developing central nervous system and make it vulnerable to defects in complex and fast orofacial muscular sequencing (MacDermot et al., 2005). This specific genetic abnormality was found in about 6% of patients with verbal dyspraxia. While it is thus unlikely to account for a majority of cases with developmental language impairment, the *FOXP2* gene appears to be one gene that may be importantly involved in the development of orofacial neuromuscular abilities, which may in turn be one of the prerequisite for typical language development (cf. Fisher & Marcus, 2006). From this perspective, *FOXP2* may contribute – in rather indirect ways – to linguistic universality within the spectrum of typically developing children. It is notable, however, that this gene plays a role in precursor functions (orofacial muscular control) that are not per se linguistic. Indeed the link between orofacial dyspraxia and grammatical impairments may appear mysterious, unless one considers that motor functions may serve as precursors to some aspects of language acquisition. I will return to this issue in Section VI.

5.   Where in the brain does language happen?

The previous section highlights how little is known about the genetic bases for language acquisition in typically developing children. The language impairment associated with a single-gene defect in family KE provides probably no more than a tiny fraction of a large set of genes that may be prerequisites for language acquisition through their involvement in brain maturation and developing sensorimotor systems. A comprehensive model of the genes involved in language acquisition that may be responsible for its universality is thus unavailable and will probably remain so for a long time. An alternative and more promising approach to the biological bases of language universality will therefore seek to identify brain areas known to participate in language processing. In this regard, a striking universality can indeed be found among an overwhelming majority of human individuals.

To begin with, the percentage of people who process language predominantly in their left hemispheres is very high, probably around 95% for right-handed adults. Interestingly, this rule does not apply to some individuals (relatively many left-handers, in fact), whose language nonetheless falls within the normal spectrum (Tzourio et al.,

1998). Hemispheric asymmetry on its own can therefore not account for universal principles of language. However, there is more to neuroanatomical universality. Even though either hemisphere may in principle be able to support language (see Section VI), the particular regions within a hemisphere that activate during language processing appear to be very consistent across members of the species.

Historically, most of our knowledge of the brain organization for language originates from studies of lesion patients. Leborgne, Broca's (1861) legendary case, as well as aphasic lesion patients later studied by Wernicke (1874) provided the basis for our current understanding of language areas in perisylvian cortex (cortex surrounding the lateral sulcus) of the left hemisphere. In section 6, I will return to the question of what exactly it means when we talk about a "language area". Although the role of Broca's area in inferior frontal cortex and Wernicke's area in the posterior superior temporal region as "language areas" was originally established based on lesion patients, their important participation in language processing has been more recently confirmed in numerous neuroimaging studies (Cabeza & Nyberg, 2000), including studies using languages other than English, such as Chinese (Mandarin; Chee *et al.*, 2000), Japanese (Homae et al., 2002), Italian (Moro et al., 2001), French (Crozier et al., 1999), German (Friederici et al., 2003), Finnish (Laine et al., 1999), and Dutch (Indefrey et al., 2001). Functional imaging has also identified additional regions frequently activated by language tasks, such as parts of the cerebellum (Fiez & Raichle, 1997) and the middle and inferior temporal gyri (Martin & Chao, 2001; Martin *et al.*, 1995).

This apparent universality of neuroanatomic substrates yields a promising approach to linguistic universality. Maybe these regions contain some special cellular architecture or maybe they are interconnected in ways that are universal within the human species and permit specifically linguistic processing. I will examine this possibility in the following section. However, before doing this it needs to be acknowledged that apparent universality of "language regions" within our species could be an illusory result of conventional statistical procedures in functional neuroimaging.

With very few exceptions, imaging studies of language are based on groupwise analyses of typical adults. As mentioned above, this requires spatial normalization that at least partially removes the pronounced anatomical variability of individual brains. Groupwise analyses that typically employ t-statistics, however, also remove functional variability. Indeed this variability is considered noise, or "error" (Smith, 2001). In view of the thousands of functional neuroimaging papers published every year, surprisingly few have examined individual functional variability for language. In a positron emission tomography (PET) study, Herholz et al. (1996) found consistent activation in left inferior frontal area 45 associated with verb generation in all of their seven right-handed participants. However, there was variability of activation within the inferior frontal lobe, which was only partly accounted for by anatomical variation. Functional variability appeared even more pronounced in other frontal and in temporo-parietal regions. Xiong and colleagues (2000) quantified functional variability in a second PET study of 20 young adults, also using a verb generation paradigm. Interestingly the highest consistency of activation was seen, not in left perisylvian cortex, but in the mediofrontal supplementary motor area. This latter activation was probably related to the presence of a motor response in the experimental, but not the control condition. The finding suggests that motor processing is associated with less functional variability than language processing. When examining larger regions, consistency of activation ≥80% was, however, seen in inferior frontal and superior temporal areas. Nonetheless, it is remarkable that a few subjects did *not* show significant activation in one of these regions, given that they are considered core language areas. Even in subjects with activation in these regions, activation peaks occurred at a mean Euclidian distance of more than 10mm from the peak loci identified in groupwise analyses. This extent of variability in inferior frontal and lateral temporal cortex has more recently been replicated in a functional magnetic resonance imaging (fMRI) study by Seghier and coworkers (2004), who used a phonological rhyme detection and a semantic categorization task in 30 right-handed young adults (see also Burton et al., 2001).

In conclusion, neuroimaging studies suggest − in accordance with the lesion literature − that there are a few perisylvian regions in the inferior frontal lobe and in lateral temporal cortex of the left hemisphere that participate relatively consistently in language tasks such as word retrieval. These areas may be called "language areas", although this denomination requires several important qualifications. First, there is individual variability and some people do not seem to rely on these brain regions in typical ways during language processing. Correspondingly, some patients with damage to these regions do not become aphasic (Alexander & Annett, 1996; Hund-Georgiadis *et al.*, 2001). Second, the precise loci of activity within these large "language areas" vary substantially between individuals. Third, individual subjects will typically show activation in many sites outside these regions and these sites will be characterized by great variability. Fourth, the finding of activity related to a language task will depend very much on the precise nature of the chosen task. Studies of individual variability have focused mostly on simple lexical retrieval tasks, whereas little is known about variability for morphosyntactic and other language functions. All this, however, leaves open the theoretical possibility of some special processing architecture within language areas that is universal across the species, although it may be anatomically organized in slightly varying loci. In the following section, I will examine more closely what it might mean for a brain region to qualify as a "language area" and what a developmental account of a language area implies with regard to universality.

6.   What's in a "language area"?

The exemplary part of the brain selected for this discussion will be Broca's area. The term originated as a misnomer related to Paul Broca's reports on patient Leborgne, who suffered from severe expressive (or non-fluent) aphasia – uttering nothing but his legendary "tan-tan" and a curse word left discreetly undisclosed by Broca (1861, 1866). Postmortem examination showed a large lesion that Broca himself identified as primarily left inferior frontal. Later study of the preserved brain, ironically, showed that the damage went far beyond "Broca's area" (i.e., inferior frontal cortex; Signoret *et al.*, 1984). Nonetheless, the term is still widely used almost a century and a half later, although there is no complete consensus on its precise anatomical meaning. While it certainly includes the pars opercularis of the inferior frontal gyrus (roughly corresponding to Brodmann area 44), many will also consider the pars triangularis (area 45; e.g., Amunts et al., 1999; Caplan *et al.*, 2000; Dronkers *et al.*, 2000; Friederici, 2002) and possibly the more inferior area 47 as part of Broca's area (e.g., Cooke et al., 2002; Keller et al., 2001).

Since there is no consensus as to its precise anatomical substrate, it is not surprising that there is also considerable debate about the functional role of the region. Among the strongest recent proposals is Grodzinsky's (2000), according to which area 44 exclusively specializes in syntactic transformations. This hypothesis is related to earlier work in linguistics and neurolinguistics, particularly in the study of agrammatism, which was originally considered a selective loss of grammatical functors and morphemes with retained lexicosemantic knowledge (Friedmann & Grodzinsky, 1997; Kean, 1985). In some functional neuroimaging studies pursuing this hypothesis (e.g., Caplan et al., 2000; Indefrey et al., 2004; Stromswold et al., 1996) apparently 'modular' activation foci in the left inferior frontal gyrus have indeed been found to be associated with syntactic complexity.

Cellular architecture. As mentioned earlier, apparent functional specificity could reflect a distinct type of cortical architecture specifically tuned to morphosyntactic processing. Such architecture in left inferior frontal cortex could be universal within the species (i.e., identical in every individual), possibly based on intrinsic genetic information. Unfortunately, the literature on cytoarchitecture in Broca's area is small. Simonds and Scheibel (1989) studied 17 brains of deceased infants and young children (3-72 months of age), examining dendritic complexity. They found that the homologue to Broca's area in the right hemisphere had an early advantage in dendritic development, with pronounced left inferior frontal development kicking in at the beginning of the second year. In brains of 4 to 6-year olds, Broca's area in the left hemisphere showed greater dendritic length compared to its homologue and adjacent premotor cortex in both hemispheres. These findings could reflect intrinsically driven cytoarchitectonic developments specifically enabling left inferior frontal cortex to assume morphosyntactic functions. Amunts and colleagues more recently showed that there is substantial individual variability in the cytoarchitecture and the boundaries of cytoarchitectonic fields within inferior frontal cortex (Amunts et al., 1999). Area 44, often considered the "core" or exclusive site of Broca area (see above), is 'dysgranular', containing only a very thin layer of granular cells in layer IV. Interestingly, this feature is shared with motor cortex and makes area 44 an unlikely candidate for a substrate specifically involved in morphosyntactic or any other kind of non-motor linguistic processing. This finding is consistent with dendritic complexity in area 44, which on most parameters (such as dendritic spine density) resembles premotor cortex more than it resembles prefrontal association cortex (Jacobs *et al.*, 2001).

Amunts et al. (2003) also examined developmental changes in the cytoarchitecture of inferior frontal fields, focusing on the gray level index (GLI; i.e., the fraction of cortical volume taken up by neuronal cell bodies). One finding was that GLI asymmetries in area 44 (but not 45) were leftward in the first decade of life – roughly corresponding with the 'critical period' for language acquisition – but reversed in early adulthood, turning robustly rightward in people aged 50 years and older. However, the GLI may not be a precise enough measure to illuminate developmental changes in specific processing capacities that may be related to language acquisition. Indeed, it remains unclear whether the results from these developmental studies, including those from Scheibel's group mentioned above, reflect intrinsic cytoarchitectonic changes that are causative of Broca's area's capacity to play an important role in language acquisition – as opposed to changes that are secondary *results* of this area's language involvement. This causality conundrum is quite common in developmental cognitive neuroscience because it is known that, while brain structure affords function, function in turn affects structure. In other words, there is reciprocal or circular causality in the interaction between neuroanatomy and functional physiology that makes it almost impossible to determine the 'root cause' of a developmental outcome.

Plasticity. Studies on the cellular architecture of Broca's area are thus inconclusive with regard to the question of universal processing specificity. However, the question can be addressed in a more indirect way using a more traditional neuropsychological approach, i.e., the study of lesion patients. It is known that in adults left inferior frontal lesion usually results in nonfluent aphasia (Caplan et al., 1996; Pedersen et al., 1995), which may be consistent with universal specificity (aside from the caveat raised earlier in this section). The same is not true for lesion effects in children. As a most striking example, left hemispherectomy (i.e., resection or complete disconnection of the entire left hemisphere) following early-onset lesion is often associated with good long-term language outcome if the right hemisphere remains intact (Mariotti *et al.*, 1998; Vanlancker-Sidtis, 2004; Vargha-Khadem *et al.*, 1997;

Vargha-Khadem & Mishkin, 1997), although underlying etiology affects the specifics of language outcome (Curtiss et al., 2001).

The above clinical behavioral studies have been more recently complemented by neuroimaging work demonstrating the readiness of the right hemisphere to assume language functions following early left hemisphere injury. Some studies in typically developing children shed light indirectly on the relevant developmental plasticity, suggesting that the participation of Broca's area of the left hemisphere in word generation gradually increases between ages 7 and 18 years (Holland et al., 2001), which may be incompatible with the idea of an innately predetermined specifically linguistic and species-universal architecture in left inferior frontal cortex. However, the findings reported by Holland and colleagues were based on only 17 subjects and apparent age-related effects may have been confounded by differences in behavior, which was unmonitored in a covert word generation paradigm. A more recent study including 95 right-handed children and adults between the ages of 7 and 32 years (Brown et al., 2005) in several overt word generation tasks found that activation for several lexical tasks in Broca's area was age-independent, whereas activity in more superior portions of premotor cortex increased with age. The location of these effects suggests that they may be related to speech articulatory development rather than core language components, such as morpho-syntax.

Functional neuroimaging of clinical patients yields evidence that is even more telling with regard to the search for a potential innately prespecified and species-universal language-related functional architecture in Broca's area. Consistent with the behavioral studies described above, imaging studies in children with early-onset damage to the left hemisphere demonstrate a significantly greater potential for reorganization of language functions into homotopic right hemisphere areas, such as right inferior frontal cortex (Müller *et al.*, 1999a; Müller *et al.*, 1999b). More recent fMRI studies in children with early-onset left hemisphere lesions (Liegeois et al., 2004) and in adult patients with a history of pre- or perinatal left hemisphere lesions (Staudt et al., 2002) confirm the readiness of right-hemisphere cortex homotopic to typical left hemisphere perisylvian language cortex to assume language functions early in development. Indeed, this potential for reorganization appears to be greater in the language domain than it is for motor control. This effect could be shown statistically in a study of a group of 9 pediatric patients with early onset unilateral left hemisphere damage (Müller *et al.*, 1998a), but can be illustrated more easily in single case examples (Figure 2). Bearing in mind that group statistical approaches to the study of brain damaged patients are always limited by variance related to numerous clinical and demographic parameters, these results suggest that the cortical architecture subserving language functions in Broca's area is less "hard-wired" than the architecture in precentral cortex subserving motor control.

Connectivity. As mentioned above, neuroimaging studies of morphosyntactic processing have quite consistently reported activation in left inferior frontal gyrus. However, when considering the entire neuroimaging literature relevant to Broca's area, any exclusive syntactic specialization of area 44 begins to appear rather improbable (Duncan & Owen, 2000). In particular, left inferior frontal activation has been reported for non-syntactic language processing as, for example, in lexicosemantic and phonological tasks (see review in Heim, 2005). More intriguingly, such activity is also found associated with tasks that are traditionally considered as non-linguistic, such as imitation (Buccino et al., 2004; Iacoboni et al., 1999), motor imagery (Binkofski et al., 2000; Gerardin et al., 2000), object manipulation (Binkofski et al., 1999), motor preparation and complex motor planning (Fincham et al., 2002; Krams et al., 1998), digit sequence learning (Haslinger et al., 2002; Toni et al., 1999), working memory (Chen & Desmond, 2005; Goldberg *et al.*, 1996), rule shifting (Konishi et al., 1998), response selection (Thompson-Schill et al., 1997), and response inhibition (Kemmotsu et al., 2005; Rubia et al., 2001).

Some of these findings are probably related to monkey studies that have demonstrated the existence of neurons in area F5 – arguably homologous to area 44 in humans (see below) – that display increased firing rates, not only when a monkey performs a specific action, but also when the monkey *observes* another monkey perform the same action, or even when the monkey looks at an object (such as a tool) that is typically associated with this action (Fadiga et al., 2000; Ferrari et al., 2005). These functional characteristics of inferior frontal neurons have been attributed to a 'mirror neuron system' (Rizzolatti et al., 2002). Since mirror neurons show increased spiking rates during observation of actions, they have been hypothesized to be crucial for the meaningful interpretation of actions performed by others and the ability in monkeys (and presumably in humans) to relate an observed action to similar action performed by themselves. Mirror neurons may thus be instrumental for action understanding (Rizzolatti & Craighero, 2004) and possibly for 'mind reading' or 'theory of mind' (Gallese, 2003).

However, it appears misleading to attribute such functional role to a set of neurons in a small anatomical location (such as F5 in the monkey or Broca's area in the human). Instead, it is certain that inferior frontal mirror neurons can display the described firing patterns only based on their connectivity with distributed brain regions of a mirror-neuron circuit. Aside from inferior frontal cortex, crucial regions within this circuit are the superior temporal sulcus, whose role in the perception of biological motion is known (Puce & Perrett, 2003), and a rostral portion of the inferior parietal lobe (area PF in the monkey brain; Rizzolatti & Craighero, 2004). The mirror neuron system can be considered part of what has been traditionally called the dorsal stream of visual perception (Rizzolatti & Matelli, 2003). Originally described as a visuospatial pathway, the dorsal system has been more recently characterized as a

system of "vision for action", additionally incorporating portions of prefrontal cortex (Goodale & Westwood, 2004). While primary functions of the mirror neuron system relate to visuomotor and audiomotor (Kohler et al., 2002) coordination, it has been argued that this system plays a pivotal role in language development, both phylogenetically and in child language acquisition (Rizzolatti & Arbib, 1998).

A number of functional neuroimaging studies have examined the suggestion of Broca's area being a homologue of area F5 in the monkey and thus the site of mirror neurons (Grèzes & Decety, 2001; Nishitani *et al.*, 2005; Rizzolatti & Arbib, 1998). These studies have confirmed the participation of left inferior frontal cortex in functions attributed to the mirror neuron system, such as action imitation (Iacoboni et al., 1999), motor imagery (Binkofski et al., 2000), action observation and recognition (Buccino et al., 2001; Buccino et al., 2004), and observation and imitation of lip movements (Nishitani & Hari, 2002).

A few functional imaging studies have attempted to relate mirror neuron functions directly to linguistic processing. Tettamanti and colleagues (2005) found a significant effect in the pars opercularis of left inferior frontal gyrus when comparing comprehension of action-related sentences to comprehension of abstract sentences (not referring to any body movement), which were matched for syntactic complexity. The results suggest that mirror neuron activity can be prompted, not only by observation and imagery of actions as previously shown, but also by listening to corresponding linguistic stimuli. Based on the design in this study, it cannot be ruled out that these stimuli simply evoked action imagery, which in turn activated inferior frontal cortex. However, given the intimate proximity of activity identified in the study by Tettamanti and colleagues and inferior frontal activity observed for syntactic decoding of sentences in many other studies (e.g., Friederici et al., 2003; Indefrey et al., 2004), it would appear that cortical resources may be shared between functions attributed to the mirror neuron system and linguistic functions.

One fMRI study by Hamzei and coworkers (2003) directly compared linguistic and mirror-neuron-related effects in a small sample of healthy adults. In a conjunction analysis, the investigators found three sites of convergent activity for action recognition, action imitation, and covert verb generation. These were in parietal cortex (possibly homologous with area PF in the monkey brain, as described above), on the border of inferior frontal and premotor cortex, and in pars opercularis of inferior frontal cortex (Broca's area), all in the left hemisphere. When inspecting statistical maps in individual subjects, Hamzei and colleagues found that activity for action recognition was always immediately adjacent to and often overlapping with activity for verb generation, but no consistent spatial relation between the two could be identified. Although it is beyond the spatial resolution of fMRI to isolate the function of individual 'mirror neurons' or even small sets of these, the spatial proximity of effects suggests that mirror neuron and language-related functions share cortical resources in inferior frontal cortex.

The evidence of developmental neurofunctional plasticity and of inferior frontal participation in the mirror neuron circuit laid out above underscores the need for cautious interpretation of clinical and imaging results. It is true that most adult patients with left inferior frontal damage will experience speech impairment and grammatical deficits; and it is true that most functional imaging studies manipulating morphosyntactic complexity (or a variety of other language-related variables) will identify left inferior frontal activation; and indeed it is true that whenever researchers have bothered to examine activation maps intraindividually, they have found that virtually every right-handed adult shows such language-related activation in left inferior frontal cortex, albeit in slightly varying loci. But does this imply that Broca's area is a piece of human cortical tissue uniquely and universally prespecified to process language functions, be they morphosyntactic or other? A view from an adult perspective that ignores development may suggest confirmation. However, the discussion and evidence presented above should have elucidated why such an 'adults-only' approach to explaining the functional organization of the brain is gravely misleading. A truly explanatory model of a brain region's function requires an account of the interaction of intrinsic information (based on genes and gene expression) with extrinsic information. The latter has many meanings and implications. For instance, as discussed in Section III, the functional differentiation of developing neocortex is largely determined by input activity. If thalamic input activity is driven by visual stimuli, the receiving cortex will assume visual functions, regardless of its location and intrinsic information.

This approach to understanding a cortical region's functional role, however, yields more intricate answers when it comes to complex functional domains such as language that are not driven by a single sensory modality and are governed by principles that appear modality-independent. Nonetheless, a developmental approach strongly constrains the set of potential models that are reasonable from a neuroscientific perspective. The functional specificity of Broca's area is unlikely to be fully determined by thalamic or other subcortico-cortical afferents. The evidence on the mirror neuron circuit discussed above suggests that the functional role of Broca's area is in part determined by cortico-cortical connectivity. In view of this evidence, the linguistic role of Broca's area can be understood in two ways: either as coincidental vis-à-vis its involvement in the mirror neuron circuit; or as meaningful from the developmental perspective. In-depth discussion is beyond the scope of this chapter, but developmental neuroscience shows that nothing is coincidental in functional brain organization (because, for example, organization reflects activity, which in turn is a prerequisite for trophic supply and thus survival of neurons; Jessell & Sanes, 2000). Before completing the picture of developmental specification in Broca's area, it is important to note that this region

is likely to participate in many circuits besides the mirror neuron circuit. The role of the arcuate fasciculus in connecting posterior and anterior perisylvian regions has been established for a long time (for recent evidence from diffusion-tensor MRI, see Catani et al., 2005). More important is the connectivity with brain regions that provide access to meaningful object representation.[iii]

It was mentioned above that evidence for a mirror neuron circuit is in part related to what has been more traditionally known as the dorsal stream of visual processing (Rizzolatti & Matelli, 2003). The dorsal stream plays a crucial role in both visuospatial processing ("where") and in visuomotor coordination ("how"), whereas the ventral stream is instrumental for the perception and meaningful interpretation of visual objects ("what"; Goodale, 2004; "what"; Ungerleider & Mishkin, 1982). An analogous organization of the auditory system into "where" and "what" pathways has been recently documented based on monkey and human neuroimaging data (Arnott *et al.*, 2004; Rauschecker & Tian, 2000). Indeed, a study by Kohler and colleagues (2002) demonstrated the existence of audiovisual mirror neurons with increased firing rates for specific actions, regardless of whether they are heard, seen, or performed by a monkey.

Interestingly, tracer studies in the monkey show that visual association cortex in anterior temporal cortex, involved in complex object recognition along the visual ventral stream, and auditory association cortex in the superior temporal gyrus involved in complex auditory processing along the auditory ventral stream, both connect to inferior frontal cortex (areas 47 and 45; Romanski *et al.*, 1999). This suggests that Broca's area is a site of converging connectivity from dorsal stream, including the mirror neuron circuit, and the ventral stream. This convergence would gather within a small cortical territory afferent information that can be considered crucial to a child's capacity for language acquisition.

Returning to the findings of apparently non-linguistic activation in Broca's area listed above, what initially appeared puzzling can be demystified from a developmental neuroscience point of view that takes adequate account of the mechanisms involved in the functional differentiation of cortex and the importance of interregional connectivity. The participation of Broca's area in a wide variety of functions (from imitation, to action understanding to working memory and response inhibition), rather than being coincidental or mysterious, is *explanatory*, i.e., it accounts for its capacity to assume language-related functions in the young child's brain. This of course cannot imply that all of the mentioned non-linguistic functions are fully developed precursors by the time language acquisition begins (say, around one year of age). Rather, some basic domain-specific functions (of imitation, working memory, inhibition, etc.) precede language acquisition, but development in these domains continues alongside language acquisition and throughout childhood. These non-linguistic domains therefore provide 'ingredients' of language acquisition, rather than strictly speaking precursors.[iv] From this perspective, ingredient domains – while traditionally considered 'non-linguistic' – are in fact intimately linked to language acquisition.

7.   Conclusion

The search for potential linguistic universals first leads to genes. A simple biological account of universality would be based on species-universal genes, defects of which result in specific language impairment. Despite some intriguing findings, as those related to coding changes in the *FOXP2* gene, it is certain that such an account is not just too simple, but in fact misleading. Neural specificity for complex cognitive domains such as language can only be understood from a developmental perspective that takes into account the interplay between intrinsic and extrinsic information, and between structure and function. Rather than being intrinsically (genetically) predetermined, local architecture (e.g. in Broca's area) is largely an *outcome* of function and activity. Specificity is shaped by afferent and efferent connectivity. It is therefore not surprising that studies of the cellular architecture in Broca's area have not identified any signs of a special processor that might be uniquely endowed to perform morphosyntactic or other specifically linguistic operations. A much more likely account of the unique and grossly universal functional characteristics of Broca's area relates to its pivotal position in functional networks, in particular the dorsal pathways of visual and auditory perception, which are instrumental for sensorimotor integration and include mirror neuron circuits crucial for action understanding, and the ventral visual stream, which provides access to meaningful object interpretation and thus to semantic representations.

The most promising neurobiological approach to language universals is thus *non-linguistic*, referring to processing domains that begin to develop even before the child starts learning words and grammar. Some of these 'language ingredient functions' are related to the participation of Broca's area in the sensorimotor circuits mentioned above. Other functional characteristics, such as working memory and response inhibition rely on additional network participation that could not be discussed in this chapter (cf. Kemmotsu et al., 2005; Lenartowicz & McIntosh, 2005). Convergence of these networks in inferior frontal cortex provides Broca's area with an array of inputs (information) that is crucial for language acquisition. Since input-output connectivity in Broca's area is unique within the brain, it assumes linguistic functions universally, i.e., in every typically developing brain. Even in many atypically developing brains with early-onset damage to Broca's area in the left hemisphere, functional reallocation will favor the homologue in inferior frontal cortex of the right-hemisphere.

Although much of the above discussions focused on the role of Broca's area as a generally agreed upon neural substrate for language processing, the conclusions that can be drawn from the investigation of developing functional specificity and universality in Broca's area will probably apply to any other brain region participating in language processes, such as superior and middle temporal gyri, inferior parietal lobes, or cerebellar cortex. This general conclusion implies that universal principles of language cannot be intrinsically specified (by genetically encoded specific architecture), but emerge from developmental embedding in and interaction with multiple non-linguistic functional networks that provide crucial ingredient functions to language acquisition.

The linguistic reader, who is used to very specific claims regarding innate principles of universal grammar, will surely be disappointed by the lack of such specific proposals in this chapter. This reader may accept some of the claims regarding developmental embedding in ingredient function, but will wonder what those universal principles are that would result from such embedding. For example, recursive properties and hierarchical organization are considered key characteristics of human language. While there have been computational proposals, such as 'neurally inspired' connectionist approaches to recursion in language (e.g., Voegtlin & Dominey 2005), neuroscience itself does not currently offer conclusive models. Indeed, it appears too early to even pinpoint what level of neuroscientific research one would have to target. Could it be cellular architecture or specific connectivity patterns (as discussed above in Section 6), or the organizational properties typically found in the left hemisphere (cf. Semenza et al., 2006)? As an alternative, the developmental cognitive neuroscientist may trust the linguistic community to identify such principles. Once such 'shallow universals' (as defined in Section I) are identified based on satisfactory consensus in the linguistic community, a neurodevelopmental account needs to be sought that can establish 'deep' (i.e., biologically meaningful) universals. As concluded from the review above, such a neurodevelopmental account is most likely to be founded on the organization and interplay of non-linguistic 'ingredient processes'.

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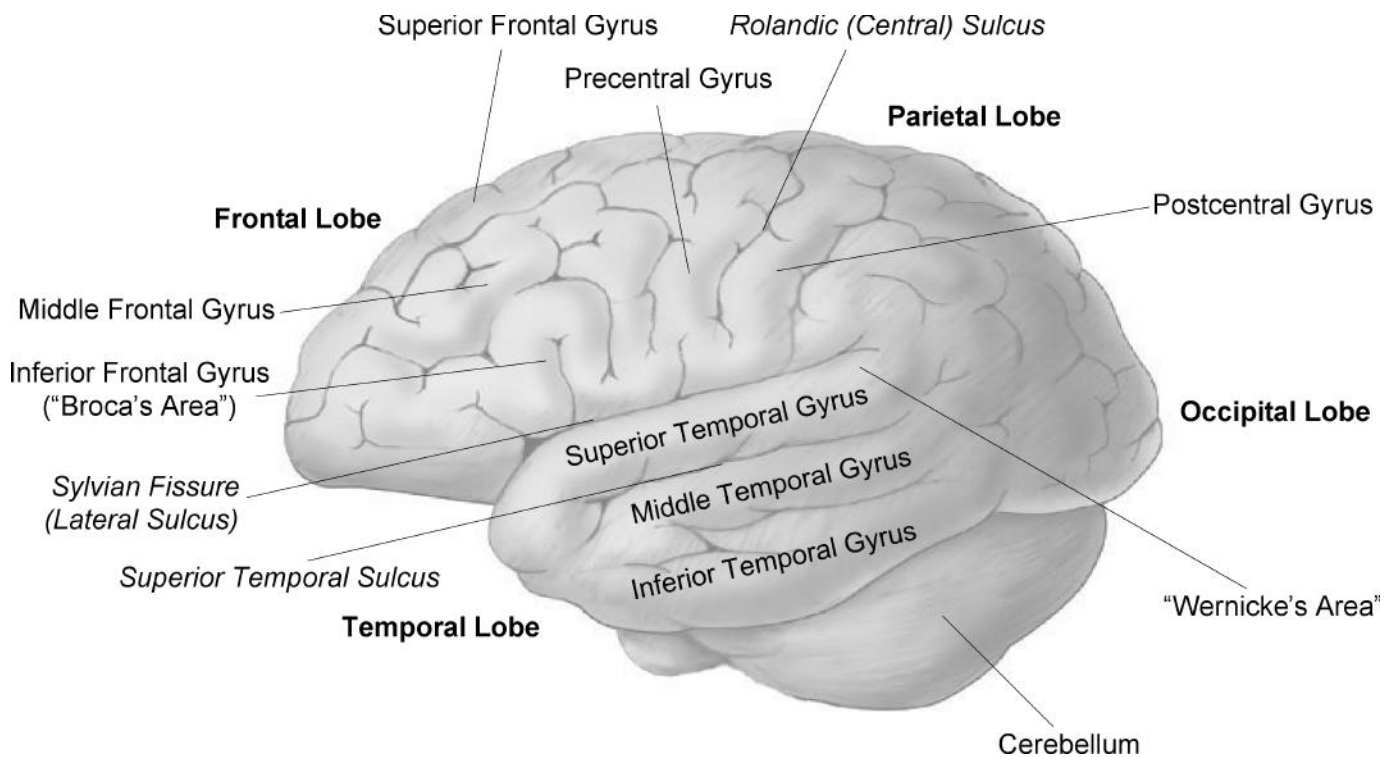
Figures

Figure 1. The location of some basic anatomical loci referred to in this chapter is indicated on the left hemisphere. The four lobes of the brain are shown in bold, sulci are shown in italics.
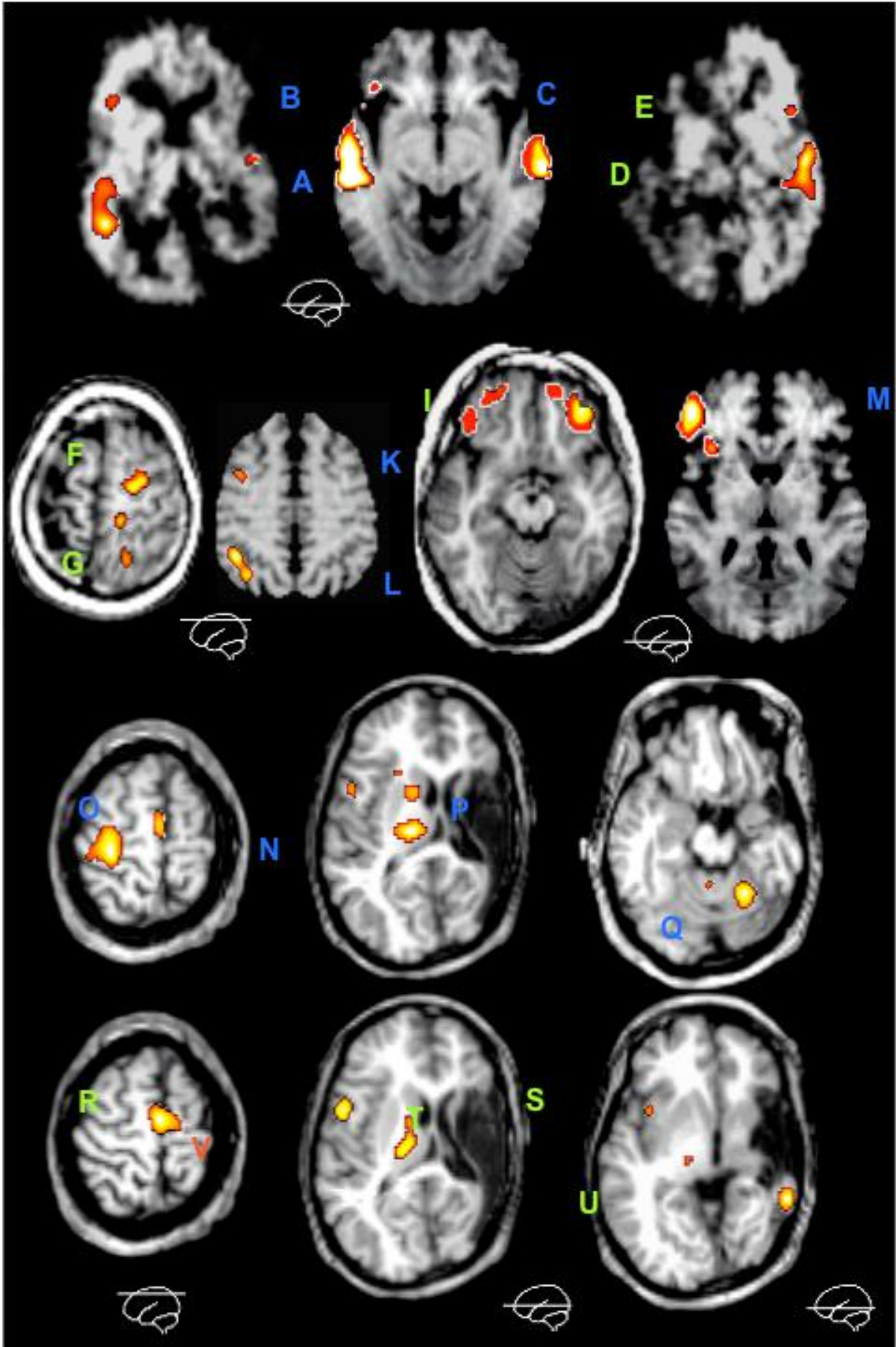
Figure 2. Results from single-case positron emission tomography (PET) activation studies. All images are axial (horizontal) slices of the brain at locations roughly indicated by the lines across the small brain icons underneath the corresponding images. In each image, task-related activations (blood flow increases) are superimposed in red to yellow scale onto brain anatomy in gray, except for two images on the left and on the right of the top row where the grayscale images represent resting blood flow. Inserted caption letters are color-coded: blue for typical activation foci, green for foci suggesting reorganization, and red for absence of typical activation. Note that images are shown in radiological convention (i.e., the left side of each image represents the right hemisphere and vice versa).

   In the top row, a patient with congenital Sturge Weber syndrome, which leads to progressive calcification and shrinkage in only one hemisphere (here: the right hemisphere), shows a pattern of left-hemisphere activation in temporal (A) and inferior frontal regions (B) during listening to sentences, which is similar to the pattern seen in healthy control subjects (C). In a second patient with the same disorder, this time affecting the left hemisphere, right hemisphere activation in temporal (D) and inferior frontal regions (E) is almost a mirror image of the typical pattern. This can be interpreted as homotopic interhemispheric reorganization. In the second row, activation patterns for an expressive language paradigm are seen, in which subjects generate sentences based on an input sentence and a prompt word ("He listened to the radio − *Television*", with the expected response: "He watched television"). Blood flow increases are shown for the comparison with simple sentence repetition. A third patient with unilateral calcification (of the left hemisphere) caused by Sturge Weber syndrome shows right-hemispheric activations in prefrontal (F), inferior parietal (G), and inferior frontal regions (I), that are homotopic to corresponding activations seen in healthy control subjects (K-M). The bottom two rows show activations associated with finger tapping (compared to rest) in a young adult with a history of perinatal right middle cerebral artery stroke. Activations during finger movement with the unaffected right hand show a normal pattern, with foci in primary motor cortex (N), supplementary motor area (O), thalamus and basal ganglia (P) of the left hemisphere, as well as in the ipsilateral cerebellum (Q). For the weak left hand, activity patterns are very different, with focus on the supplementary motor area (R), inferior premotor cortex (S), and thalamus ipsilateral to the movement (T), as well as an activation in what appears to be temporal cortex in the vicinity of the damaged area (U). Remarkably, there is no activation in ipsilateral primary motor cortex (V), suggesting that interhemispheric reorganization in the motor domain is primarily non-homotopic (see Müller et al., 1998a, 1998b).

Endnotes

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[i] "…la langue… [est] à la fois un produit social de la faculté du langage et un ensemble de conventions necessaires…" [Language is a social product of the language faculty and at the same time a set of necessary conventions; ibid.: p25].

[ii] For a review of animal studies suggesting substantial experiential impact, see Buonomano and Merzenich (1998). A single case human postmortem study by Amunts and colleagues (2004) found unusual cytoarchitecture in inferior frontal areas 44 and 45 in an individual with exceptional language abilities, who was fluent in 60 languages; a group study by Jacobs et al. (1993) suggests experiential effects on dendritic complexity in Wernicke's area.

[iii] The argument here is related to a critique of the assumption of 'residual normality' in the study of developmental disorders by Thomas & Karmiloff-Smith (2002).

[iv] Note that this use of the term ingredient does not relate to subcomponents of language (such as phonology, morphology, syntax, etc.), but to functional domains not conventionally considered to belong to language.