

# The Evolution of Broca's Area

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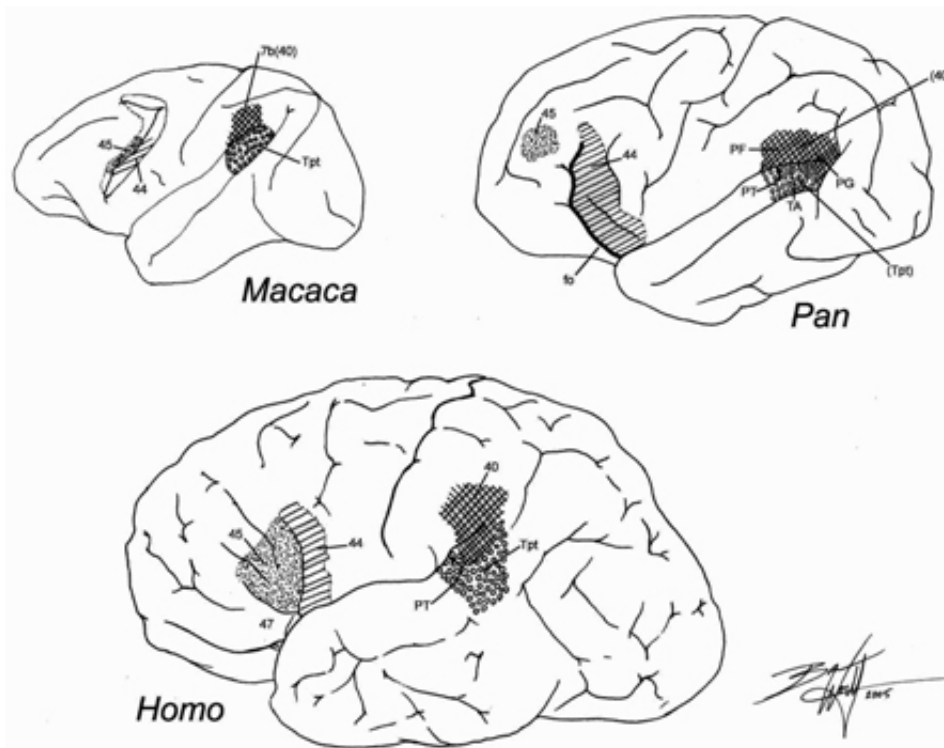
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*Dean Falk*

### Introduction

Discussions about language origins are polarized along two lines of thought. One is based on Chomsky's (1978) premise that the fundamental rules governing human languages are genetically embedded in human brains as a result of rapid mutation(s). According to this view, human language has little, if anything, to do with nonhuman primate vocal communications systems or their neurological underpinnings. The second hypothesis proposes that human language evolved gradually from Darwinian natural selection on primate-like vocalizations and their associated genetic and neurological substrates (Falk 2004a, b; 2007). Assessment of the relative merits of these two views lends itself to hypothesis testing: If the first view is correct, human language areas did not emerge from gradual elaborations of incipient (primitive) cortical areas that subserved vocal communications in their nonhuman primate ancestors, and comparative neurological studies on living primates should confirm the uniqueness of language areas in human brains. If the continuity hypothesis is correct, however, homologous language areas should be present in brains of humans and nonhuman anthropoid primates (Preuss 2000).

Broca's speech area of humans classically consists of Brodmann's areas 44 and 45 (*pars triangularis*) in the left hemispheres, while the receptive language area (Wernicke's area) is traditionally located in that same hemisphere on the planum temporale (PT, located within the depths of the Sylvian fissure), and caudally in area Tpt (temporoparietal) and Brodmann's area 40 (supramarginal gyrus) (Figure 1). (Some workers would also include part of area 37.) Studies on cytoarchitectonics of macaque brains suggest that the inferior limb of the arcuate sulcus contains homologs of areas 44 and 45 (Galaburda and Pandya 1982; Deacon 1992; Preuss 2000), and that regions of the superior temporal and inferior parietal lobes are homologous with human posterior language receptive areas (Galaburda and Pandya 1982; Preuss 2000) (Figure 1). Wernicke's area (narrowly defined) is fundamentally involved with the comprehension of human speech. Furthermore, like humans, macaques are thought to be left-hemisphere dominant for comprehending certain socially meaningful vocalizations (Rauschecker et al. 1995; Petersen et al. 1978, 1984; Heffner and Heffner 1984, 1986).



**Figure 1:** Gross language areas in humans and their proposed homologs in macaques and common chimpanzees. In the left hemispheres of humans, Brodmann's areas 45 (*pars triangularis*) and 44 comprise Broca's speech area, while areas Tpt (temporoparietal), PT (planum temporale, buried within the floor of the Sylvian fissure and located behind Heschl's gyrus), and Brodmann's area 40 are parts of Wernicke's receptive language area. Human area 40, macaque area 7b, and chimpanzee area PF/PG are proposed homologs, as are human and macaque areas Tpt and chimpanzee area TA; *fo*, fronto-orbital sulcus of chimpanzee. Identifications are based on cytoarchitectonic and functional similarities and should be viewed as tentative. Data from Preuss (2000); Amunts et al. (1999); Gannon et al. (1998); Aboitz and García (1997); Galaburda and Pandya (1982); Crosby, Humphrey and Lauer (1962); Jackson et al. (1969); Bailey et al. (1950); von Bonin (1949). (Figure reproduced from Falk 2007: Fig. 9.4.)

Although less experimental work has been done on chimpanzees, early comparative anatomists speculated about how a chimpanzee-like frontal lobe in human ancestors could have evolved into Broca's area. As discussed elsewhere (Falk 2007), these efforts were hampered by a lack of consensus about the identities of homologous gyri and sulci in apes and humans, which were often proposed on the basis of relative positions of sulci rather than on cytoarchitectonic grounds. A distinguishing feature of chimpanzee (and other great ape) brains is the fronto-orbital sulcus (*fo*), which incises the lateral border of the dorsal frontal lobe and then courses caudally on the orbital surface to the temporal pole (Connolly 1950). The lower portion of *fo* provides the anterior limiting sulcus of the insula, which can be seen peeking out near the rostral end of the Sylvian fissure in many specimens (because chimpanzees usually lack all but the rudiment of a frontal opercula (Connolly 1950)). The bulge delimited by *fo* in chimpanzees (Figure 1), or orbital cap, represents Brodmann's area 44 (Bailey 1948; Bailey et al. 1950; Connolly 1950; Jackson et al. 1969) (Figure 1) and may incorporate part of area 45 (Sherwood et al. 2003). Some workers have suggested that, as discussed below for humans (Amunts et al. 1999), area 44 is larger in the left than the right hemisphere of chimpanzees (Cantalupo and Hopkins 2001), but this hypothesis has recently been challenged (Sherwood et al. 2003). In any event, it is important for paleoneurologists to realize that the bulge that appears at the level of the temporal pole in humans, the so-called "Broca's cap", is not homologous to the orbital cap of chimpanzees because the human cap contains areas 45 and 47 rather than areas 44 (Connolly 1950) and sometimes part of 45 (Sherwood et al. 2003) (Figure 1). With respect to chimpanzee homologs of Wernicke's area, on the other hand, the planum temporale is reported to be larger on the left than the right in

chimpanzees (Gannon et al. 1998), as is well known to be the case for humans (Geschwind and Levitsky 1968; Amunts et al. 1999).

Wernicke's area has been interpreted as a more ancient structure than Broca's area (Aboitiz and García 1997), in part, because area Tpt appears in some prosimians (Preuss and Goldman-Rakic 1991). Aboitiz and García propose that Tpt first differentiated in primates as a bottleneck where cross-modal associations acquired phonological correlates, and that Wernicke's area eventually "originated as a place in which multimodal representations or concepts obtained a linguistic dimension by being mapped into simple phonological sequences" (Aboitiz and García 1997:390). According to the authors, during primate evolution area Tpt became increasingly connected with inferoparietal regions and these contributed to a link between the auditory system and a parieto-premotor circuit with incipient Broca's area. A second parallel pathway may also have evolved directly between the precursor of Wernicke's area and prefrontal cortex. Hypothetically, Broca's area developed, in part, as a phonological rehearsal device entailed in generating complex vocalizations. Eventually, an evolving parieto-premotor circuit contributed to the origin of a lexicon (perhaps at the level mastered by apes schooled in American Sign Language). Syntax and the generation of discourse, however, emerged only later in conjunction with further elaboration of these circuits (Aboitiz and García 1997). Because Aboitiz and García's model is well-reasoned and based on comparative and experimental evidence, their observations warrant serious consideration.

The anatomical arrangement of the language areas fits this large-scale cortico-cortico network and can be described as part of it. In this sense, the neural architecture involved in language is embedded in a complex system of large-scale connectivity that is the hallmark of the primate brain, and therefore should not be considered as an isolated system working independently of similarly organized cortico-cortico networks (Aboitiz and García 1997:388).

### **The evolution of Broca's area**

The inferior frontal convolution consists of cytoarchitectonic areas located in the *pars opercularis* (area 44), *pars triangularis* (area 45) and *pars orbitalis* (area 47) (Brodmann 1909). These areas are referred to as the frontal operculum ('cover') because (along with the parietal and temporal operculum) they form the walls of the anterior Sylvian fissure that cover the insula (Crosby et al. 1962:344). Broca's pioneering work on brains of aphasics (Broca 1861) revealed that areas 44 and 45 on the left side of the brain are involved in the articulatory aspects of language – hence the name "Broca's speech area" or "Broca's area". Neurons in Broca's area are activated by simple movements of the mouth and hands, and similar movements in monkeys activate the ventral premotor cortex (Colebatch et al. 1991; Gallese et al 1996; Petersen et al. 1988, Rizzolatti et al. 1996). These activated neurons are called 'mirror neurons' because they also discharge when similar actions are observed in others (Rizzolatti et al. 1996). Mirror neurons are hypothesized to be part of an action-perception network that facilitates gestural (manual and orofacial) communication in apes and humans as well as linguistic communication in the latter (discussed in Falk 2004c).

Recent imaging studies have more precisely delineated specific functions that are facilitated in and around classical Broca's area. Thus, area 44 tends to be activated during phonetic and phonological tasks that entail coordination of lip and tongue movements, but these do not necessarily entail speech per se. For example, area 44 is recruited during rehearsal strategies that rely on silent 'inner speech,' which is consistent with the 'motor' theory of speech perception (Gabrieli et al. 1998; Démonet et al. 1996; Lieberman and Mattingly 1985). Area 44 is also involved in nonlinguistic sequencing of orofacial and tongue movements, while the more rostrally located area 47 facilitates semantic aspects of speech and is recruited during verb generation tasks (Petersen et al. 1988; Démonet and Thierry 2001). Parts of Broca's area are also involved in nonlinguistic tasks such as observation and imitation of finger movements (Binkofski et al 2000; Heiser et al 2003) and recognition of manual gestures (Rizzolatti & Arbib 1998). Because the activated neurons discharge when similar actions are observed in others, they are called 'mirror neurons' (Rizzolatti et al 1996). Thus, more than a century after Broca's area was identified, we

recognize that it has certain nonlinguistic functions and that the act of speech activates wider areas of the cerebral cortex (Falk 2007). Nevertheless, the importance of this area for speech cannot be denied and the question of its phylogenetic development with respect to language evolution remains important (Sherwood et al 2003; Holloway et al. 2004).

Amunts et al. (1999) mapped areas 44 and 45 in ten human brains in order to establish more precise cytoarchitectonic borders and relationships to neighboring sulci (Amunts et al. 1999). Intersubject variability was high for the volumes and cytoarchitecture of both areas, although areas 44 and 45 tended to resemble each other within individuals. Unfortunately for those who interpret hominin endocasts, borders of the two areas failed to coincide consistently with superficial sulci or locations buried within their walls. For example, in some brains area 45 extended beyond the *pars triangularis* onto the orbital surface, or spilled over caudally behind the anterior ascending branch of the Sylvian fissure. Despite these reservations, however, the authors concluded that the *free surface* of the human triangular and opercular parts of the inferior frontal gyrus are highly likely to represent areas 45 and 44 respectively. The relationship of sulci to cytoarchitectural areas 44 and 45 was recently explored in brains from five adult chimpanzees (Sherwood et al. 2003). Just as the border between cytoarchitectonic areas 44 and 45 of humans may not correspond precisely with the anterior ascending branch of the Sylvian fissure (Amunts et al. 1999), the border between the two areas in chimpanzees does not always coincide with the surface of the fronto-orbital sulcus. As is true for humans, intersubject variability is high for chimpanzees and area 45 may spill over caudally into the presumed domain of area 44 (Sherwood et al. 2003).

Amunts et al. also found that the volume of area 44 was larger on the left in all ten brains (but the favored direction of volumetric asymmetry of area 45 varied from brain to brain), and eight of the ten brains also had higher cell densities on the left side. Other workers have observed a similar volumetric asymmetry favoring the left *pars triangularis* in patients who were known to be left-hemisphere dominant for speech and language (Foundas et al. 1996), and Amunts et al. suggest that the morphological asymmetries in area 44 provide a basis for functional lateralization of speech. The take-home message is that humans have a unique sulcal pattern in the region of Broca's area which appears to correlate with speech functions. In other words, if a hominin endocast reproduces a *pars triangularis* and general humanlike shape of the orbital and frontal opercular cortex in contrast to the simpler morphology seen in chimpanzees, one may reasonably conclude that cortical reorganization had, at least to some degree, occurred in the inferior prefrontal cortex of that individual (Holloway et al. 2004).

What remains mysterious in the comparative study of the inferior frontal convolution is the rostral extent of area 45 in chimpanzees and details about area 47 in both species. Because area 47 is important for processing the semantic aspects of human speech, more research would be desirable on this area.

Area 47 is located ventral to areas 44 and 45. However, area 47 does not seem to be homogeneous because it consists of several sub-areas. These sub-areas are arranged in a latero-orbital sequence (Koonin, 1935). By contrast, Economo and Koskinas (1925) found a series of cytoarchitectonic areas and their transitional forms in this region to be arranged in a caudorostral sequence. The mapping of the ventral-orbital surface outside Broca's region clearly needs further attention (Amunts et al. 1999:325-327).

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