

Tracing the human brain's classical language areas in extant and extinct hominids

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ABSTRACT Language is a cognition that makes us human. It is a function of the structure of the human brain that is made possible by complex wiring of neural networks that evolved over millions of years since humans shared the last common ancestor with the great apes. The human brain accommodates two principle cortical areas that are strongly involved in computing linguistic processes: Broca's and Wernicke's areas. Discovered in the latter half of the 19th century, the regions represent localized but relatively segregated linguistic modules which are linked through connective pathways. Broca's and Wernicke's areas are ancient parts of the primate brain, however, their functional specializations have undergone significant transformations during primate evolution. This chapter will review neurobiological findings concerning the internal make-up and function of the homologous brain areas to Broca's and Wernicke's areas in extant nonhuman primates and discuss relevant knowledge that exists on the brain morphology of extinct hominins. Comparative neurobiology holds the key to understanding how the core language areas have developed their specialized functions in human brains

by offering insights into developments that could have been the driving forces for language during evolutionary history.

KEYWORDS brain, Broca's area, classical language areas, evolution, origins, Wernicke's area

1 **INTRODUCTION**

From so simple a beginning, endless forms most
beautiful and most wonderful have been,
and are being, evolved.
— Darwin, 1859

Throughout history, many societies believed that language was a gift from God to humans. According to the Bible, immediately upon creation Adam received the task from God to give names to all living things and hence develop a language with which he could communicate with Eve. Human society and language are treated as inseparable entities not just by the authors of the Bible, but even more so by modern science that has demonstrated how deeply ingrained language is into our biological and social existence. Contrary to biblical belief, this close relationship is a result of the evolutionary pressures of the ancestral past moulding and shaping the unique human mind as we know it today.

Language is a multifaceted cognitive ability dependent on a complex brain to support it. For humans, communication requires a wide range of different cerebral processes contributing to construct linguistic meaning in the brain. The essence of the neurobiology of language consists of identifying particular linguistic functions and their cerebral control centers to be able to assign functions to specific brain areas. Many contemporary language-brain models are deeply rooted in the premise that two cortical left-hemispheric areas govern the majority of language processes (Price, 2012). This is not to say that no other cerebral regions contribute to linguistic tasks or that the core language areas exclusively compute language. A variety of subcortical structures may be involved in lexical, phonological, syntactic, and/or semantic processes (e.g., Duff

& Brown-Schmidt, 2017; Duffau, Moritz-Gasser, & Mandonnet, 2014; Tiedt et al., 2017). In addition, right-hemispheric structures also make important contributions to language (Silbert, Honey, Simony, Poeppel, & Hasson, 2014). More generally, linguistic processing can build upon and benefit from non-linguistic cognition, such as numerical or spatial processing (see, e.g., de Bruin, Roelofs, Dijkstra, & Fitzpatrick, 2014; Hauser, Chomsky, & Fitch, 2002), which makes the definition of what constitutes a language area difficult. The two core language areas, namely *Broca's* and *Wernicke's areas*, are historically important and well-researched brain regions in terms of linguistic cognition, and a considerable body of research has consolidated their undebated role for language.

This review will discuss the evolutionary development of the core language areas of modern human brains as we know them today. Starting with an historical overview of their discoveries and important findings from early brain-language research of the 19th century, it will continue with a description of which *cytoarchitectonic* studies have contributed to our current knowledge of the language areas and their functions. Neurobiological studies on nonhuman primates will show how equivalent brain regions in monkeys and apes process information related to species-specific communication and how functionality of those areas changed during the evolution of *Homo sapiens*. Lastly, archaic humans – extinct members of the genus *Homo* – which are considered as evolutionary intermediaries between the great apes and humans, will be the focus of discussion. Evidence relating to the existence of the core language areas in the brains of various species of extinct hominins can provide compelling insights into the evolutionary history of neurolinguistic structures of the human brain.

2 THE HUMAN CORE LANGUAGE AREAS

The neurobiological basis of language has traditionally been considered as centered upon two core language areas called Broca's area and Wernicke's area. They are named after their discoverers, the French physician Pierre Paul Broca (1824–1880) and the German neurologist Carl

Wernicke (1848–1905), who were among the first to describe their role in linguistic processing.

Examining two patients who were unable to speak, Broca discovered that damage to the left inferior frontal gyrus of the cerebral cortex led to language production deficits (so-called *Broca's aphasia* or *non-fluent aphasia*, see Broca, 1861, 1865). Neither claims of location nor left-lateralization of this brain area were entirely new (for a review of the historical debate over the discovery of the lateralized language area known as Broca's area see, e.g., Finger, 2010). However, previous work was rather preliminary and lacking in many of the evidential details that were later provided by Broca, who has thus historically been credited with the discovery of that language area (Cubelli & Montagna, 1994). Traditionally, Broca's area has been described as a productive region concerned with the encoding of vocal signals into meaningful syllables, words (e.g., Indefrey & Levelt, 2004; Papoutsis et al., 2009) and sentences (Embick, Marantz, Miyashita, O'Neil, & Sakai, 2000).

Post-mortem analyses of the brains of both Broca's patients and recent re-examinations with modern neuroimaging techniques revealed their lesions to be more extensive than solely to the posterior part of the left inferior frontal gyrus. They include the insula, anterior parts of the superior temporal lobe and parts of the inferior parietal lobule as well as subcortical parts, such as the claustrum, putamen and globus pallidus (Cabanis, Iba-Zizen, Abelanet, Monod-Broca, & Signoret, 1994; Castaigne, Lhermitte, Signoret, & Abelanet, 1980; Dronkers, Plaisant, Iba-Zizen, & Cabanis, 2007). Based on these findings, it has become clear in the last few decades that the clinical description of Broca's aphasia also involves substantial subcortical and insular damage (Petrides, 2014) and that a localized lesion to solely Broca's area results in a rather mild and reversible language production problem (Mohr et al., 1978; Penfield & Roberts, 1959).

In 1874, Carl Wernicke identified another cortical area whose damage led to language impairment, in this case in the domain of language perception. Disruptions to the posterior portion of the left superior temporal gyrus result in a type of aphasia, which is primarily characterized by poor speech/language comprehension but relatively fluent language output (so-called *Wernicke's aphasia* or *fluent aphasia*, see, e.g., Benson & Ardila, 1996). Wernicke's area is most commonly described as a recep-

tive region for processing and integrating auditory sensory information (Guenther, 2016) and lies immediately posterior to the primary auditory cortex, which is considered crucial for the perceptual processing of speech (Petrides, 2014). Wernicke (1881) suggested that the critical region for auditory language comprehension spans the superior temporal gyrus, including the cortex of the superior temporal sulcus and the adjacent lip of the middle temporal gyrus. He proposed the existence of a larger peri-Sylvian cortical and insular language region in the human brain, including the core language region identified by him. This postulation proved remarkably consistent with the findings of the majority of studies that would follow within the next century, including neuropsychological as well as modern functional neuroimaging studies (e.g., Dronkers, Redfern, & Ludy, 1995; Friederici, 2011; Penfield & Roberts, 1959).

Typical language processing in the human brain is relatively strictly lateralized. Broca's and Wernicke's areas, as well as Heschl's gyrus and the insula, are primarily left-hemispheric regions (Bidula & Króliczak, 2015; but see Keller et al., 2011), whereas a number of right-hemispheric brain regions also play a role, such as the mid part of the superior temporal sulcus (Glasel et al., 2011; Leroy et al., 2015).

After the discoveries of Broca and Wernicke, the German physician Ludwig Lichtheim developed a model of language function that placed both core language areas at the center and attempted to describe how they interact for linguistic computing (Graves, 1997; Lichtheim, 1885). Broca's view of brain language processes corresponded with a mosaic map of specific and separate language function centers, including a *general faculty for languages* and a *specific faculty of articulation* and different input/output pathways (peripheral sensory, motor nerve), between which no connection was described (Broca, 1865). Wernicke, on the other hand, drawing upon his teacher and mentor Theodor Meynert, proposed connective pathways between different language centers and saw all linguistic functions as inter-related in both functional and anatomical terms (Wernicke, 1874, 1881). Based on Wernicke's paradigm, Lichtheim formulated the *Wernicke-Lichtheim Model* of linguistic processing (later modified most notably by Geschwind, 1965) which defines Wernicke's area as the auditory center, Broca's area as the motor output center, and both connected to an (non-localized) *conceptual center* (Lichtheim,

1885). The model puts strong emphasis on the functional connectivity of cerebral areas and their associative networks, a view that was supported by other researchers at the time who showed fiber tracts linking the core language areas (e.g., Burdach, 1822; Dejerine, 1895). Thanks to the pioneering work by Geschwind (1970), a large fiber tract between Broca's and Wernicke's area, the *arcuate fasciculus*, was identified as a crucial pathway for language processing (see also Marin in this volume). Later research identified additional fiber tracts linking lateral areas of the temporal cortex with the frontal cortex (Petrides & Pandya, 1988; Schmahmann et al., 2007), and a part of the superior longitudinal fasciculus was described as most crucial for language processing (e.g., Schmahmann et al., 2007). In the last ten to fifteen years, numerous studies using *diffusion tensor imaging* (DTI-tractography) have delineated with modern neuroimaging techniques the relationship of language to white matter pathways, such as the arcuate fasciculus, ventral pathway and uncinate fasciculus (Catani & Jones, 2005; Frey, Campbell, Pike, & Petrides, 2008; Saur et al., 2008). Whether the arcuate fasciculus actually plays the role in linguistic processing that Geschwind described has been debated recently (see Dick & Tremblay, 2012, for a review).

Undoubtedly, most researchers agree with the general premise of the *dual-pathway model* of language/speech processing, where a dorsal stream maps auditory speech sounds to articulation and a ventral stream maps auditory speech sounds to meaning (Ungerleider & Haxby, 1994); however, the exact neural connections comprising the system are often considered controversial (Hickok, 2009; Rauschecker, 2011; Rauschecker & Tian, 2000; Saur et al., 2008; Weiller, Bormann, Saur, Musso, & Rijntjes, 2011). Although the extensive degree of connections between the different brain language areas was not known at the end of the 19th century, Wernicke's and Lichtheim's work guided future researchers in the direction that proved to be most useful for finding the neurobiological foundations of language. The *Wernicke-Lichtheim Model* came to be the standard neuropsychological model for language and was elaborated on extensively over the following 100 years (Ben Shalom & Poeppel, 2008; Graves, 1997), spawning many modern descendants (see, e.g., Friederici, 2002; Hickok & Poeppel, 2004; Indefrey & Levelt, 2004; Price, 2000).

Broca's and Wernicke's areas are often inconsistently defined in the literature as both involving large portions of the cortex with relatively

vague boundary markings (Guenther, 2016). In general, there is substantial variation concerning the precise boundaries of the areas among individuals as well as between hemispheres of the same individual (Amuts et al., 1999; Steinmetz & Seitz, 1991). One way to delineate discrete cortical areas more narrowly is to define them on the basis of their cellular organization (i.e., the cytoarchitecture). Cells receive, compute and send out information to other cortical and subcortical structures with which they are linked (Petrides, 2014), and their internal make-up is relevant to understanding their particular functions. The procedure of hardening brains to stain cellular elements of thinly sectioned slices only became possible in the latter part of the 19th century and was pioneered by Carl Wernicke's teacher Theodor Meynert, who was able to demonstrate different cell types and various layers of neurons in different cortical regions (Meynert, 1867). His work was followed by other researchers, including the German neuro-anatomist Korbinian Brodmann who in 1909 published the most famous *cytoarchitectonic map* of the human cerebral cortex, introducing the numerical nomenclature to denote the cortical regions that is still widely used today (i.e., "Brodmann area" or "BA" plus corresponding number of his cytoarchitectonic map). The following two centuries saw a rise in interest in cytoarchitecture due to the development of new methods and techniques (e.g., Economo & Koskinas, 1925; Sarkissov, Filimonoff, Kononowa, Preobraschenskaja, & Kukuev, 1955), and beginning in the 1980s, functional neuroimaging of distinct foci of functional activity in the human brain drew on cytoarchitecture to define cortical regions (e.g., Talairach & Tournoux, 1988).

Both Broca's and Wernicke's areas correspond to more than one Brodmann area. Broca's area includes Brodmann's areas 44 and 45, with area 44 lying on the pars opercularis and area 45 on the pars triangularis of the inferior frontal gyrus (Amuts et al., 2010), while Wernicke's area corresponds to parts of Brodmann's areas 21, 22 (central and posterior superior temporal gyrus), 41 and/or 42 (Ardila, Bernal, & Rosselli, 2016). Even though there are no exact correspondences between the core language areas and their cytoarchitecture, the cytoarchitectonic divisions of the human cortex are particularly useful in cross-species comparisons. Cortical cells, like all other biological structures, change slowly and thus remain highly conserved for a longer evolutionary period (Geschwind &

Rakic, 2013), opening up the possibility of comparative neurobiological studies across related species.

3 **HOMOLOGUES OF BROCA'S AND WERNICKE'S AREAS IN NONHUMAN PRIMATES**

Primates first appeared in the fossil record around 55 million years ago (Seiffert, Perry, Simons, & Boyer, 2009), with the evolutionary lineage leading to modern humans splitting from the great ape lineage about seven to eight million years ago (Langergraber et al., 2012). The diverse order of primates includes prosimians, such as lemurs and tarsiers, and a multitude of simian species, for instance marmosets, capuchins, macaques and apes. The great apes (*Hominidae*) are the closest living relatives of humans and share over 97% of genes with them (Locke et al., 2011). Macaque monkeys are, after humans, the most widespread primate genus and share about 93% of their genes with humans (Gibbs et al., 2007). Research pertaining to the evolution of human behavior is often focused on chimpanzees, but neuroscience widely uses macaques to model functions of the human brain.

During human evolution, there was substantial neurological rewiring and reorganization of the cortex, wherein some areas increased in size (e.g., the anterior prefrontal cortex) while others decreased (e.g., parts of the insular cortex, see Semendeferi, Armstrong, Schleicher, Zilles, & Van Hoesen, 1998, 2001). The increase in white matter volume of the precentral cortex indicates that the frontal lobes in humans have increased in neurological complexity as compared to those in great apes (Schoenemann, Sheehan, & Glotzer, 2005). The human brain is not just an enlarged version of the chimpanzee brain but differs with regard to form and function (Rilling, 2006).

Cytoarchitectonic studies have helped trace the nonhuman origins of specific human brain regions to draw conclusions as to their evolutionary development. Cortical regions homologous (in cell make-up) to Broca's and Wernicke's areas have been identified in macaque monkeys (Galaburda & Pandya, 1982; Preuss, 2000) as well as in all great apes (Cantalupo & Hopkins, 2001; Spocter et al., 2010), and those areas seem

to be involved specifically in the processing of species-specific vocal and gestural communication signals (Gil-da-Costa et al., 2006; Petrides, Cadoret, & Mackey, 2005; Tagliabata, Russell, Schaeffer, & Hopkins, 2008). The function of Broca's area in humans may thus be a specialization of more ancient brain functions related to vocal and gestural communication in Old World primates (Schenker et al., 2010).

The macaque homologue of Broca's area has gained fame with the discovery of *mirror neurons*, which are a class of neurons that represent meanings of actions (in the sense of an *action vocabulary*) accessible through auditory stimuli (Kohler et al., 2002). Therefore, the link between motor action and speech is not new to the human Broca's area but has an evolutionary precedent, a fact that has fed various hypotheses on language origins (e.g., Gallese, 2008).

While Broca's area is lateralized to the left cortical hemisphere in most humans (Toga & Thompson, 2003), the degree of lateralization of homologous regions in nonhuman primates is still unclear. Allometric measurements of the homologue of Broca's area in chimpanzees are not in agreement over hemispheric specialization (Cantalupo & Hopkins, 2001; Schenker et al., 2010). Human brains are characterized by the so-called *Broca's cap*, a bulge at the level of the temporal pole that includes a part of Broca's area, namely Brodmann area 45 (see Falk, 2014). A similar structure in chimpanzees, called the *orbital cap* (which does not exactly correspond to Broca's cap, see Falk, 2014), may or may not show size difference between the two hemispheres (Cantalupo & Hopkins, 2001; Schenker et al., 2010; Sherwood, Broadfield, Holloway, Gannon, & Hof, 2003). Nevertheless, behavioral studies suggest a certain degree of lateralization of communicative functions in nonhuman primates (Vauclair, 2004). Chimpanzees have been shown to possess a tendency to process species-specific sounds primarily in the inferior frontal gyrus of the left hemisphere (Tagliabata et al., 2008; Wilson & Petkov, 2011). In macaques, stimulation of the left Broca's area homologue elicits orofacial movements (Petrides et al., 2005), and orofacial asymmetries were shown to be associated with the production of species-specific calls in marmosets, macaques and chimpanzees (Fernández-Carriba, Loeches, Morcillo, & Hopkins, 2002; Hook-Costigan & Roger, 1998; Schenker et al., 2010). Due to the fact that chimpanzees tend to produce asymmetric orofacial movements during the production of (learned) calls, it has been

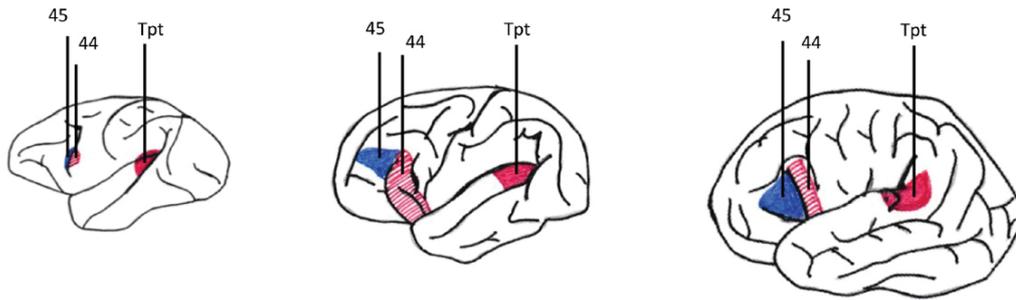


Figure 1. Schematic drawing of macaque (left), chimpanzee (mid) and human (right) brains (left hemispheres) with Brodmann areas 44/45 and temporo-parietal areas (*Tpt*) indicated (based on Amuts et al., 2010; Frey, Mackey, & Petrides, 2014; Gannon, Holloway, Broadfield, & Braun, 1998; Schenker et al., 2008; Spocter et al., 2010). Images are not to scale.

suggested that both tasks are functionally lateralized to the left hemisphere (Losin, Russell, Freeman, Meguerditchian, & Hopkins, 2008).

While lateralization of the nonhuman homologue to Broca's area is still contested, more agreement exists concerning asymmetry in the chimpanzee homologue of Wernicke's area (Hopkins et al., 2016; Spocter et al., 2010). In humans, the planum temporale at the core of Wernicke's area is significantly enlarged in the left hemisphere, with the left-hemispheric area being approximately ten times larger in size than the right one (Geschwind & Levitsky, 1968). The nonhuman homologue area of Brodmann area 22, comprising the largest part of Wernicke's area, is called the temporo-parietal area (*Tpt*) and has been localized in macaques, galagos (Gannon, Kheck, & Hof, 2008; Preuss & Goldman-Rakic, 1991) and all great apes (Hopkins, Marino, Rilling, & MacGregor, 1998, see Figure 1). The human-like lateral asymmetry is already evident in baboons and great apes (Hopkins et al., 1998; Hopkins & Nir, 2011; Marie et al., 2017), indicating that the planum temporale asymmetry dates back to a common ancestor of catarrhine primates (Sherwood, Subiaul, & Zawidzki, 2008).

A number of behavioral studies suggested that perception of species-specific vocalization may be lateralized to the left cerebral hemisphere in macaques (e.g., Ghazanfar, Smith-Rohrberg, & Hauser, 2001; Hauser & Anderson, 1994; Petersen, Beecher, Zoloth, Moody, & Stebbins, 1978). Neurobiological studies confirmed some of these findings and, additionally, identified the left *Tpt* area in macaques to be specifically in-

volved in the processing of conspecific calls (Heffner & Heffner, 1986; Poremba et al., 2004). Rauschecker et al. (1995) demonstrated that pure tones are processed at the core region of the superior temporal cortex in macaques, whereas complex, species-specific vocalizations are processed in more lateral regions.

A neuroimaging study measuring planum temporale activity of chimpanzees during the perception of species-specific vocalizations confirmed that the planum temporale region of the chimpanzee brain is functionally specialized for the processing of species-specific vocal signals, though no evidence was found for a lateralization effect (Tagliatela, Russell, Schaeffer, & Hopkins, 2009). The majority of studies on nonhuman primates corroborate the fact that the temporal region of the primate brain, including humans, is home to a voice recognition system that is specialized in processing communication signals from conspecifics (see, e.g., Belin, Zatorre, Lafaille, Ahad, & Pike, 2000; Petkov et al., 2008; Spocter et al., 2010).

There is ample evidence indicating that species-specific communication signals of great apes are lateralized to the left cerebral hemisphere, although the exact brain regions involved may be yet unclear. Studies that directly measure neurological processes during communication tasks are scarce (e.g., Tagliatela et al., 2009), but numerous behavioral studies have revealed a trend of left-lateralization. Manual gestures in most great apes seem to be governed by left-hemispheric structures (e.g., *chimpanzees*: Hobaiter & Byrne, 2013; Hopkins & Leavens, 1998; *bonobos*: Hopkins & Vauclair, 2012) and the laterality effect may be even stronger when vocalizations accompany these gestures (Hopkins & Cantero, 2003; Tagliatela, Russell, Schaeffer, & Hopkins, 2011). Both Broca's and Wernicke's areas have been implicated in those communicative processes. Hopkins and Nir (2011) and Spocter et al. (2010) identified a correlation between the degree of asymmetry of the planum temporale and the propensity for right-handedness of gestures in chimpanzees (Hopkins & Nir, 2011; Spocter et al., 2010). Tagliatela et al. (2006) described the same correlation for gesture handedness and size of the inferior frontal gyrus. As shown by Meguerditchian et al. (2012), both the planum temporale and inferior frontal gyral surface asymmetry are correlated with communicative gesture in chimpanzees. At the moment it is unclear which of the two brain regions is more closely linked to communication.

Handedness, in general, has been described to be strongly associated with language in modern humans, with the majority of right-handed people demonstrating left-hemispheric specialization for language function (Knecht et al., 2000). A study of hand preference in chimpanzees, however, has shown that the neurobiological correlates of handedness in chimpanzees do not seem to be related to the language areas (Hopkins & Cantalupo, 2004). Handedness may have co-evolved with language only during human evolution (Corballis, 2003), and the connection between the two is possibly related to gestural communication or tool use (see, e.g., Hopkins, Russell, & Cantalupo, 2007; Meguerditchian, Vauclair, & Hopkins, 2013).

Broca's and Wernicke's areas and their nonhuman homologues are not only different in size and situated in different cortical locations across species, but are also characterized by differences in their internal cell-makeup. Broca's area and the temporal plane in humans display wider cortical *minicolumns*, and this is particularly pronounced in the left hemisphere (Rilling & Stout, 2014). Moreover, notable differences between the association networks of the language areas have been described, with human Broca's areas displaying more extensive connections to the temporal gyrus than the homologue in nonhuman primates' brains. Concerning white matter pathways, comparable frontal connections can be found in humans and nonhuman primates, including the superior longitudinal fasciculus, the uncinate fasciculus, the cingulum, the arcuate fasciculus and the inferior fronto-occipital fasciculus (de Schotten, Dell'Acqua, Valabregue, & Catani, 2012; Makris & Pandya, 2009; Rilling, Glasser, Jbabdi, Andersson, & Preuss, 2011). While some of these pathways have been relatively preserved during the evolution of great apes and humans, others were substantially reorganized. The trajectory of the arcuate fasciculus, for instance, has been strongly modified in human brains, linking the left frontal cortex to the middle and inferior frontal gyri and parts of Broca's and Wernicke's areas (de Schotten et al., 2012). In contrast, in macaques the terminal connection of the arcuate fasciculus leads to areas of the visual cortex, whereas in chimpanzees connections with the inferior parietal lobe (supramarginal and angular gyri) are dominant (Rilling et al., 2008). This suggests that the cortical organization and connections of the arcuate fasciculus have undergone significant changes during human evolution by establishing connections

to and from the core language areas, supposedly subserving linguistic functions in the human brain.

In summary, the existing literature on the neurobiology of Broca's and Wernicke's areas and their connections in human and nonhuman primates notes a number of similarities as well as differences between the species. One of the key questions that now emerges is when the human-typical adaptations arose during human evolution.

4 **PALEONEUROLOGY: LANGUAGE AREAS IN THE BRAINS OF ARCHAIC HUMANS**

As language is ubiquitous to all modern humans, it must at least date back to before 200,000 years ago when all modern humans shared a common ancestor (Cann, 2012). In line with evolutionary theory, language could have been formed through gradual adaptations within the existing gene pool of variation and without any extreme mutations prevailing to spread to future generations (Bickerton, 2002).

Because of a lack of data, no definite evidence exists that could tell us about the presumed communication systems of the extinct members of the *hominin group* (i.e., the genus *Homo*) or the neurobiological correlates of their linguistic ability. However, indirect evidence can be gathered by studying brain morphology of archaic humans. This is possible with skull imprints, so-called *endocranial casts* (or *endocasts*, see Figure 2) that show the indentations of the former brain and blood vessels on the inside of the skull (Holloway, Broadfield, & Yuan, 2004). By using this method, particular brain regions can be identified and analyzed in terms of their size. Endocast studies are a standard methodology of *pa-leoneurology*, but unfortunately, researchers are often confronted with the problem of incomplete and fractured skulls from which sulcal indentations can be difficult to determine. Therefore, a certain degree of uncertainty is imminent to this method. Nonetheless, endocast models are valuable and crucial tools for understanding hominin brain evolution when very little direct evidence is available.

The immediate ancestors of humans, the *Australopithecines*, likely did not appear until four million years ago during the Pliocene in East Africa



Figure 2. Endocasts from Sambungmacan *Homo erectus* from Indonesia. Broca's area is enlarged in the left hemisphere in comparison to the right one (reprinted from *The Anatomical Record*, Vol. 262, Broadfield et al., Endocast of Sambungmacan 3, p. 375, Copyright (2001) with permission from Wiley).

(see Figure 3; Leakey, Feibel, McDougall, Ward, & Walker, 1998). Their cranial capacity was about 400–450 cubic centimeters (which is comparable to large chimpanzee brains) and tentative evidence suggests an occipital asymmetry (Holloway, 1983). Concerning the language regions, it is disputed whether Broca's area is clearly defined on Australopithecine endocasts (Holloway, 1983). Falk (1980), for instance, sees enough evidence for the argument that the Australopithecine Broca's area resembles that of great apes. For Wernicke's area, only tentative evidence exists. The assumed increase in the posterior parietal association cortex of Australopithecine brains could have resulted in reorganization of certain temporal regions, including Wernicke's area, by around three million years ago (Holloway, 1983; Spocter et al., 2010).

With the advent of the genus *Homo*, evidence for the core language areas becomes clearer on endocasts. When exactly the first archaic human emerged has been a matter of discussion, though it is assumed that by 1.9 million years ago *Homo rudolfensis* had appeared in East Africa (Antón, Potts, & Aiello, 2014). Those bipedal, terrestrial creatures possessed a brain the size of around 530 cubic centimeters, and the endocast of a famous skull from the Turkana Basin (KNM-ER 1470) shows clear imprints of an asymmetric Broca's area similar to that of modern humans (Holloway, 2015). Contemporary species to *H. rudolfensis* may have in-

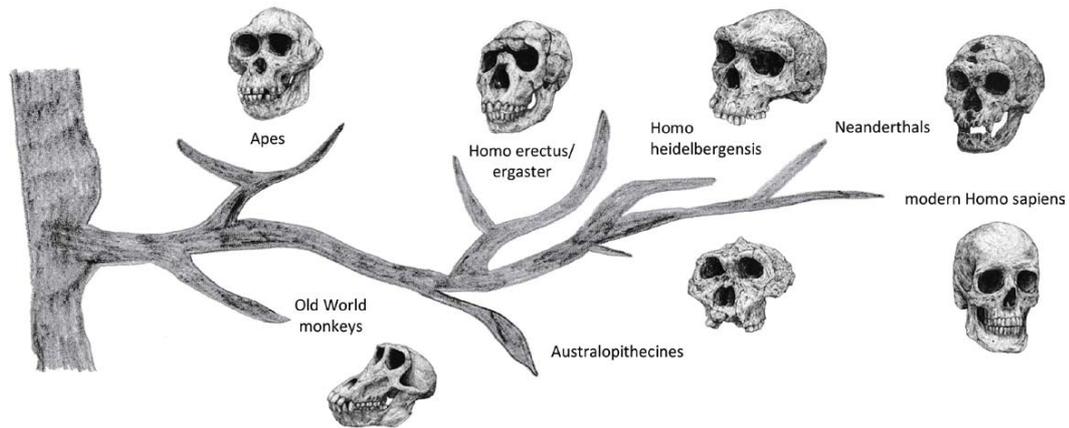


Figure 3. Human family tree.

cluded *H. habilis* and *H. erectus/ergaster* (Boyd & Silk, 2015), and endocasts of specimens of both species seem to demonstrate an asymmetric enlargement in Broca's area (Harris, 1998; Tobias, 1998). Wernicke's area is assumed to have resulted from the general growth of the superior temporal areas (see, e.g., Oubre, 1997). *H. erectus*, the first human to expand beyond Africa and a direct ancestor of modern humans (e.g., Sept, 2015), had evolved larger brains (approximately 1,000 cubic centimeters) with a clear left-occipital-right-frontal asymmetry and a pronounced Broca's cap, as is characteristic for modern humans (Wu, Holloway, Schepartz, & Xing, 2011). Wynn (1998) suggests that both Broca's and Wernicke's areas in *H. erectus* were distinctly human-like.

Approximately 600,000 years ago, a new species appeared in Europe, *Homo heidelbergensis*, which was only a bit smaller-brained (approximately 1,200 cubic centimeters) than modern humans (which is around 1,250 cubic centimeters, see, e.g., Boyd & Silk, 2015). Endocast prints show that their brains were left-occipital-right-frontal asymmetric and showed a prominent bulge in the left hemisphere over Broca's area (Holloway et al., 2004). By 300,000 years ago, the evolutionary transition began that would lead to *Homo neanderthalensis* in Europe. Neanderthals had a brain larger than those of modern humans (approximately 1,500 cubic centimeters) and displayed a clear asymmetry in Broca's area (Holloway, 2015; Jerison, 1997). According to Holloway (1985), Broca's area is as developed on Neanderthal endocasts as it is in those of modern humans. *Homo sapiens altai* (or *Homo sapiens ssp. Denisova*, or simply

Denisovans), close relatives of Neanderthals and modern humans whose fossils were recently discovered in Russia and China, had the largest brains of all archaic humans known today (approximately 1,800 cubic centimeters, Li et al., 2017). At present not much is known about Broca's and Wernicke's areas in this species.

While left-hemispheric asymmetry is well established in archaic humans, its relation to language function is unclear. In an attempt to put together more puzzle pieces to supplement the scarce data that exists on the neurobiology of archaic humans' language capabilities, researchers have started to include additional information from fossils that could be relatable to linguistic function, such as hand preference (Steele & Uomini, 2009). The archeological record can provide evidence for hand preference of a species through material culture (tools, artefacts) as well as through skeletal asymmetries resulting from preferential use of one limb. Even though right-hand preference is suggested to date back as far as 1.9 million years ago (Toth, 1985), the evidence becomes substantial with *H. heidelbergensis* (Lozano, Mosquera, Bermudez de Castro, Arsuaga, & Carbonell, 2009) and the Neanderthals (Frayer et al., 2012; Uomini, 2011). Whether language and handedness evolved in tandem in archaic hominins is difficult to answer based on the current data, and the exact nature of the concatenation of language and handedness in hominins remains unknown at present.

The existence of the modern core language areas in the brains of archaic humans is certainly tantalizing for research into language origins, though the evidence is mostly uncertain or even highly speculative at times. An enlarged Broca's cap, for instance, may also appear on endocasts of large chimpanzees, indicating that language does not need be the driving force behind its increase (Holloway, 1983). More generally, there is no evidence that these areas in archaic humans functioned as speech/language centers. Without additional evidence regarding respiratory control and vocal tract anatomy of a species, it is difficult to ascertain solely from neuropaleontological data whether a species possessed the abilities to develop a verbal form of *proto-language* (Deacon, 1997; however see Fitch, De Boer, Mathur, & Ghazanfar, 2016). Anthropological research often has to draw on circumstantial evidence to construct a case for language in archaic hominins, connecting, for instance, the production of art or tools to symbolic language.

A new research avenue that has recently opened up is the inclusion of genetics into the question of the origins of human language. Advances in molecular technology have made it possible to start to relate specific brain regions to a set of underlying genes, whose expression directly influences the development of that region. Relevant findings concerning the neurobiology of language have resulted from this research and the forkhead box protein p2 (known as *FOXP2*) has been suggested to play a role in the functioning of Broca's and Wernicke's areas (Liégeois et al., 2003). The gene has also been identified in Neanderthals (Krause et al., 2007) and Denisovans (Meyer et al., 2012), which has spurred hypotheses on language abilities in those close relatives of modern humans. Another recent gene discovery could make important contributions to the genetics of language: *GPR56* is strongly linked to the Sylvian fissure language region, including Broca's area (Bae et al., 2014). New emerging hypotheses on the genetics of language should take into account what role the gene might have played during human evolution.

The field of language evolution has naturally suffered from paucity of data, due to the fact that cognitive abilities do not fossilize, and one way forward can be seen in modern *neurogenetics*. Through the identification of particular sets of genes that are crucial for the development of relevant language areas in the human brain and by comparing those data to genetic information gathered from extant nonhuman primates and extinct hominins, new insights will be possible. The field of *paleogenetics* is only just emerging as a key player in the evolution of language, but it may well turn out to be the missing link between primatology, paleoanthropology and modern linguistics that can move the field of language evolution forward in the 21st century.

5 CONCLUSION

In modern humans, Broca's and Wernicke's areas are complex cerebral regions mediating a versatile range of functions related to language. In terms of their evolutionary history, it can be assumed that the new linguistic functions of *Homo sapiens* brains arose most likely through the modification of existing brain circuitry that was present in the last an-

cestor of humans. The neurobiological correlates of today's linguistic abilities were built on pre-existing neural structures that subserved different cognitive abilities in primate history. It is the most likely evolutionary scenario that Broca's and Wernicke's areas originally processed information in ways that happened to be useful to language: Broca's area may have evolved to extract and analyze sequential and motor patterns while Wernicke's area may have evolved out of a more general ability to analyze species-specific calls. Both of these skills make a useful substrate for language to utilize and their neural connectivity and behavioral interplay could have provided the crucial impetus for the development of the linguistic mind.

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