Comparative primate neurobiology and the evolution of brain language systems
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Human brain specializations supporting language can be identified by comparing human with non-human primate brains. Comparisons with chimpanzees are critical in this endeavor. Human brains are much larger than non-human primate brains, but human language capabilities cannot be entirely explained by brain size. Human brain specializations that potentially support our capacity for language include firstly, wider cortical minicolumns in both Broca’s and Wernicke’s areas compared with great apes; secondly, leftward asymmetries in Broca’s area volume and Wernicke’s area minicolumn width that are not found in great apes; and thirdly, arcuate fasciculus projections beyond Wernicke’s area to a region of expanded association cortex in the middle and inferior temporal cortex involved in processing word meaning.

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Introduction
Language is among the most distinctive attributes of Homo sapiens. Other primate species communicate, but none does so by combining thousands of symbols according to a defined set of rules to generate phrases with a nearly infinite variety of meanings [1,2]. Although chimpanzees raised in human linguistic environments develop limited symbolic abilities, none has eclipsed the language competence of a 2 and 1/2-year old human child [3]. Thus, there must be human brain specializations that support our capacity for language. As discussed below, comparative studies of primate neurobiology have helped to identify some of these specializations. Comparisons with our closest living relative, the chimpanzee, have been crucial in this endeavor, for we cannot conclude that a trait has uniquely evolved in humans unless we also demonstrate its absence in modern chimpanzees [4].

Brain size
The human brain averages 1330 cc in size, a value that far exceeds that for the brain of any other living primate species [5]. Rhesus macaque brains average only 88 cc [6]. Chimpanzee brains average 405 cc and gorilla brains average 500 cc [5]. These numbers suggest the possibility that our unique capacity for language is simply a product of our large brain size. However, evidence from high-functioning human microcephalics, some of whom have brain volumes within the great ape range, suggests otherwise since their linguistic abilities can eclipse those of chimpanzees. Thus, there are apt to be qualitative differences between human and non-human primate brains that support our capacity for language [7].

Language circuitry
In 1970, Geschwind outlined a model of the functional neuroanatomy of human language [8*]. This model is a useful starting point for comparative analysis, however it is important to note that it does not include features that we now know to be important, such as the involvement of the thalamus, basal ganglia and cortical areas beyond Wernicke’s and Broca’s areas in language [9*,10*,11,12]. In this model, Wernicke’s area, the posterior portion of the left superior temporal gyrus, is essential for speech comprehension, and Broca’s area, a region in the left inferior frontal cortex, is responsible for speech production. These two areas are connected by a large white matter fiber tract known as the arcuate fasciculus. Perhaps other primate species lack human language skills because they lack homologues of human Wernicke’s and Broca’s areas [13]. However, when defined based on cytoarchitecture and shared non-linguistic functional properties, such homologues have been identified in non-human primates [14]. This leads to the question of whether there might be microstructural differences within these areas between humans and non-human primates.

Broca’s area
Not only is Broca’s area involved in human speech, it also mediates aspects of communication in non-human primates [15]. Mirror neurons are found in macaque area
F5, part of which is homologous to the posterior part of human Broca’s area (area 44). Mirror neurons ostensibly allow monkeys to improve their understanding of actions they observe in others by mapping those observed actions onto their own motor system and simulating the action in their own brain. Mirror neurons are well known for their response to reaching and grasping movements of both self and others, but they also fire when producing or observing communicative mouth movements [16]. Macaque monkeys communicate extensively with orofacial expressions, so mirror neurons are likely vital to macaque communication.

There is evidence that mirror neuron regions are also involved in orofacial communication in humans [17], however human Broca’s area is also responsible for the grammatical aspects of speech [18,19]. Perhaps, just as Broca’s area is involved in human speech production, Broca’s area homologue in non-human primates is involved in the production of non-human primate vocalizations. However, this does not seem to be the case, since lesioning the monkey homologue of Broca’s area does not impair vocalization [20,21]. Monkey calls instead depend upon the limbic system and brainstem. This neurological difference reflects differences in the nature of human speech and non-human primate vocalizations. In contrast to human speech, monkey calls are largely involuntary expressions of emotional arousal [22], implying that they may not be under voluntary cortical control. On the other hand, there is some evidence that captive chimpanzees will exhibit volitional calls [23], and that Broca’s homologue is involved in their production [24]. This raises the possibility that Broca’s area was recruited for volitional vocal, in addition to orofacial communication, before the divergence of humans and chimpanzees some 5–7 million year ago.

Despite these similarities, there are obvious functional differences between human and chimpanzee Broca’s areas, not just in the motor aspects of speech but also in the involvement of human Broca’s area with syntax [11,25]. These functional differences are likely to be supported by underlying anatomical differences. It is now known that Broca’s area has wider cortical minicolumns in humans than in great apes [26**], whereas minicolumn width does not differ between humans and great apes in primary somatosensory or motor cortex [27]. Cortical minicolumns are vertical columns consisting of approximately 80–100 neurons with strong interconnections that constitute a coherent functional unit. In sensory cortex, for example, neurons within a given minicolumn share a peripheral receptive field. Cortical minicolumns consist of vertically aligned cells separated by vertically defined cell poor spaces where most connections are made. Minicolumns contrast with macrocolumns that consist of many minicolumns bound together by short-range horizontal connections [28]. The larger human minicolumns within Broca’s area are thought to facilitate greater integration of information by providing more space for connections. Finally, Broca’s area is larger in the left cerebral hemisphere of the human brain and this may be related to the strong tendency for many aspects of language function to be lateralized to the left hemisphere. Importantly, this Broca’s area asymmetry is not present in chimpanzees [29].

Wernicke’s area

Whereas production of human and macaque monkey vocalizations depend on different neural substrates, comprehension of species-specific vocalizations seems to depend on similar neural substrates in humans and macaque monkeys [30]. Human speech comprehension depends on the left posterior superior temporal gyrus (i.e. Wernicke’s area) [8**]. Similarly, the left superior temporal gyrus is responsible for discriminating species-specific vocalizations, but not other types of auditory stimuli, in Japanese macaques [31]. Single cell electrophysiology similarly implicates the superior temporal gyrus in processing macaque species-specific calls. Monkey auditory cortex consists of three longitudinal cytoarchitectonic streams in the superior temporal lobe: a core region, a surrounding belt region, and an adjacent parabelt region [32]. Single cell electrophysiology studies have revealed that unlike core areas that respond best to pure tones, lateral belt areas respond best to complex sounds, including species-specific vocalizations [33]. Further evidence for similarity between humans and macaques in the neural substrates for processing species-specific vocalizations comes from a comparative PET neuroimaging study. In a small sample of macaque monkeys, blood flow responses were more pronounced for species-specific calls compared with non-biological sounds within cortical area Tpt as well as the dorsal frontal operculum, presumed homologues of Wernicke’s and Broca’s areas, respectively [34**]. However, it should be noted that another monkey PET study found that the anterior tip of the left superior temporal gyrus, rather than Wernicke’s area homologue, was specialized for processing species-specific calls [35]. The difference could be attributable to the former study measuring blood flow with a temporal resolution of 60 s and the latter measuring glucose metabolism occurring over a period of about 25 min [35].

Like Broca’s area, human Wernicke’s area has functional properties not found in its non-human homologue, such as phonological processing [11]. Are there anatomical differences that support these expanded functional capabilities? A portion of Wernicke’s area known as the planum temporale is leftwardly asymmetric in most humans [36]. However, this same asymmetry is also present in great apes [37,38]. While these findings are consistent with the notion that human brain language systems evolved from pre-existing neural systems present in nonhuman primate ancestors, they also suggest that planum temporale asymmetries are not the neural substrate supporting human-specific linguistic abilities. Nevertheless, potentially
relevant specializations of human Wernicke’s area are apparent at the microstructural level. As with Broca’s area, planum temporale minicolumns are wider in humans compared with chimpanzees, and planum temporale minicolumn width is leftwardly asymmetric (left > right) in humans but not chimpanzees [39**].

Against this backdrop of comprehension-related similarity in brain activation patterns, there is also emerging evidence for differences between humans and macaques. A recent comparative fMRI study showed that whereas both humans and macaques activate the lateral sulcus and superior temporal gyrus (STG) when listening to monkey and human vocalizations, only in humans did the STS also respond to intelligible human utterances. Macaque STS did not respond to monkey calls. Notably, the human STS activations spanned nearly the entire length of the sulcus, and the authors conclude that the evolution of language appears to have recruited most of STS in humans [40*] (see also [41]).

Connections between Wernicke’s and Broca’s areas

Beyond these human specializations within human Broca’s and Wernicke’s areas, there are differences between humans and non-human primates in the white-matter connections that link these two regions. Anterograde and retrograde tracer techniques have been used to describe the connections of Wernicke’s and Broca’s areas homologues in macaque monkeys [42,43,44*,45]. Direct connections between the two regions have been identified, but the pathway is weak [44*,45] and its function unknown. In fact, the dominant frontal connection of Wernicke’s homologue (area Tpt) is not with Broca’s area homologue, but rather with dorsal prefrontal cortex [42]. This auditory ‘where’ pathway is involved with localizing sounds in space [46*]. On the other hand, the dominant connection of Broca’s area homologue is with the cortex of the middle superior temporal gyrus [43] via a ventral pathway known as the extreme capsule that is involved in auditory object recognition [46*].

The tracer methods that have been used to delineate white matter connections in macaque monkeys are invasive, terminal procedures that cannot be used in humans. Instead, human white matter pathways have traditionally been described based on gross dissections of post-mortem brains [47]. However, it is difficult to precisely define cortical terminations of fascicles using these methods. Diffusion tensor imaging provides a non-invasive alternative method that can be applied to humans and non-human primates [48–50]. Although DTI has demonstrated connections between Broca’s and Wernicke’s areas (or their homologues) in humans, chimpanzees, and rhesus macaques, the human pathway bears one major difference from that of the non-human species. In both rhesus macaques and chimpanzees, the posterior terminations of the arcuate are focused on the homologue of Wernicke’s area in the posterior superior temporal gyrus. Humans, however, also possess a massive projection of the arcuate into the middle and inferior temporal gyri, ventral to classic Wernicke’s area [51**].

Figure 1

Potential neurological specializations supporting human language Broca’s area has wider minicolumns in humans compared with great apes, and the volume of human Broca’s area is leftwardly asymmetric, whereas this is not the case in chimpanzees. Wernicke’s area also has wider minicolumns in humans compared with great apes, and there is a leftward asymmetry in the column width in humans that is absent in chimpanzees or macaque monkeys. Finally, the human arcuate fasciculus pathway includes a massive projection to the cortex ventral to classic Wernicke’s area that is involved in lexical-semantic processing and that has markedly expanded in human evolution, displacing adjacent visual cortex in a posterior and medial direction in the process.
The cortex of the middle and inferior temporal gyri appears to have expanded in human evolution. In the process, it displaced nearby extrastriate visual cortex [52,53]. For example, visual motion area MT lies within the superior temporal sulcus (STS) in chimpanzees and rhesus macaques. However, in humans, it lies considerably posterior to STS, and STS instead appears to contain association cortex [54]. The posterior limit of the temporal-lobe arcuate fasciculus terminations in the human brain coincides very closely with the anterior limit of visual motion area MT, consistent with displacement of MT by the highly expanded arcuate pathway.

The region of the middle temporal gyrus that receives arcuate projections has been referred to as an ‘epicenter for lexical-semantic processing’ [55]. Thus, this portion of the arcuate fasciculus may be carrying lexical-semantic information to Broca’s area for further processing. Although some have postulated that the ventral extreme capsule pathway was recruited into the language system during human evolution [44], comparative DTI data suggest that there has been far greater evolutionary expansion of the arcuate fasciculus than there has been of the extreme capsule. These data suggest that the arcuate fasciculus was a more important substrate for human language evolution. Further evidence in support of this claim is the observation that the human arcuate fasciculus is leftwardly asymmetric, in parallel with typical left hemisphere lateralization of language function, whereas the human extreme capsule pathway is not leftwardly asymmetric [56].

Conclusion

In summary, the human brain has multiple anatomical specializations that may be relevant to explaining our capacity for language. First, human brains have wider cortical minicolumns in both Broca’s and Wernicke’s areas compared with great apes. Second, human brains exhibit leftward asymmetries in Broca’s area volume and in the width of planum temporale minicolumns that are not found in great apes. Third, the projections of the human arcuate fasciculus reach beyond Wernicke’s area to a region of expanded association cortex in the middle and inferior temporal cortex that appears to be involved in processing word meaning (Figure 1).

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- **of outstanding interest

This study applied functional MRI to humans and macaque monkeys listening to identical stimuli in order to compare the cortical networks involved in processing vocalizations. Human superior temporal sulcus (STS) was responsive to human speech, but macaque STS was not responsive to macaque species-specific vocalizations.


This study used tracer injections and autoradiography to demonstrate a dorsal connection between the superior temporal sulcus (STS) and Broca's area homologue in macaque monkeys. The authors refer to this minor connection as a simple arcuate fasciculus.


This study combined microelectrode recording and anatomical tract tracing to demonstrate the existence of dorsal and ventral auditory streams in macaque monkeys, involved with spatial and non-spatial aspects of auditory processing, respectively.


This study used diffusion weighted imaging and tractography to show that the arcuate fasciculus pathway connects with Wernicke’s area or its homologue in humans, chimpanzees and rhesus macaques. However, the human arcuate fasciculus has a much greater projection into the middle and inferior temporal gyri, ventral to classic Wernicke’s area.


Reviews comparative fMRI studies of visual system pathways in macaque monkeys and humans to conclude that human early and mid-level visual areas are located more posterior and medially than their corresponding macaque counterparts.


