



Review

Neuronal basis of speech comprehension

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ABSTRACT

Verbal communication does not rely only on the simple perception of auditory signals. It is rather a parallel and integrative processing of linguistic and non-linguistic information, involving temporal and frontal areas in particular.

This review describes the inherent complexity of auditory speech comprehension from a functional-neuroanatomical perspective. The review is divided into two parts. In the first part, structural and functional asymmetry of language relevant structures will be discussed. The second part of the review will discuss recent neuroimaging studies, which coherently demonstrate that speech comprehension processes rely on a hierarchical network involving the temporal, parietal, and frontal lobes. Further, the results support the dual-stream model for speech comprehension, with a dorsal stream for auditory-motor integration, and a ventral stream for extracting meaning but also the processing of sentences and narratives. Specific patterns of functional asymmetry between the left and right hemisphere can also be demonstrated. The review article concludes with a discussion on interactions between the dorsal and ventral streams, particularly the involvement of motor related areas in speech perception processes, and outlines some remaining unresolved issues.

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1. Introduction

This review article summarises the neuronal basis of speech comprehension in terms of functional-neuroanatomy. Specific aspects include the structural and functional asymmetry in the temporal and frontal lobe, as well as along the proposed ventral stream for auditory speech perception. It is possible only to summarise a fraction of the available literature, and so the review focuses on the underlying anatomical structures. I therefore focus mainly on a review of the fMRI literature, whilst at the same time acknowledging the valuable contribution of electrophysiological studies to this field. The review is divided into two main parts. The first part describes the neuroanatomical basis in terms of functional neuroanatomy, and structural and functional asymmetry. The second part focuses on the well-accepted dual-stream model of the functional anatomy of language (Hickok and Poeppel, 2007). The ventral stream is proposed as the dominant stream for speech comprehension. It interacts closely with the dorsal stream, which plays an important role in speech production.

This review article concludes with a brief summary and an outlook on unresolved issues, related to the current version of the dual-stream model.

1.1. Anatomical basis of the speech and language network

Since the 19th century, it has been established that the left hemisphere is crucial for speech perception, processing, and production. Previous models of speech processing, like the Wernicke–Lichtheim model (Lichtheim, 1885; Wernicke, 1874), have suggested a cortical network comprising Wernicke's area, Broca's area, a third, anatomically less specified area for processing of concepts, and the connections between. Anatomically, Wernicke's area is typically defined as the posterior part of the superior temporal gyrus, including the planum temporale (PT), which is a cortical structure on the superior surface of the superior temporal gyrus, just behind the primary auditory cortex, i.e. Heschl's gyrus (see Fig. 1). Clear anatomical landmarks or cytoarchitectonic descriptions do not circumscribe Wernicke's area, thus there are varying definitions of Wernicke's area. By contrast, Broca's area in the left inferior frontal gyrus (IFG) is clearly defined by the underlying cytoarchitectonic areas, labelled as Brodmann area (BA) 44

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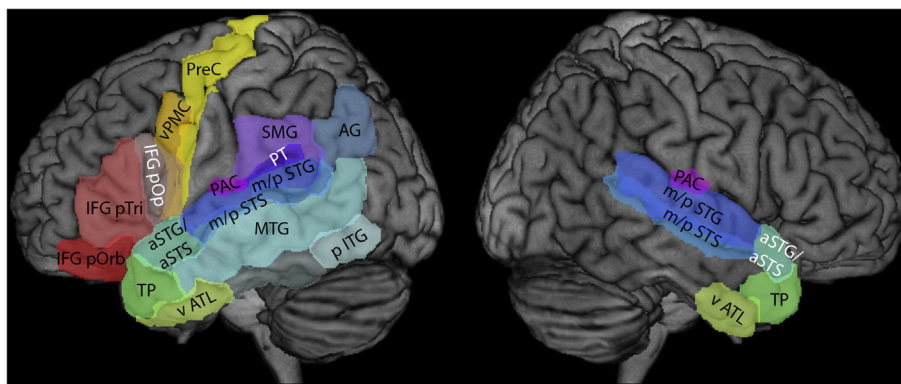


Fig. 1. The figure displays all relevant areas, discussed in this review. These are the primary auditory cortex (PAC, Brodmann area (BA) 41), planum temporale (PT, BA 42/22), supramarginal gyrus (SMG, BA 40), angular gyrus (AG, BA 39), middle and posterior part of the superior temporal gyrus (m/p STG, BA 22), middle and posterior part of the superior temporal sulcus (m/p STG, BA 21/22), middle temporal sulcus (MTG, BA 21), posterior part of the inferior temporal gyrus (pITG, BA 20), anterior part of STG/STS (BA 22), temporal pole (TP, BA 38), the ventral anterior temporal lobe (vATL (comprising anterior MTG and ITG)), inferior frontal gyrus, pars opercularis (IFG pOp, BA 44), inferior frontal gyrus, pars triangularis (IFG pTri, BA 45), inferior frontal gyrus, pars orbitalis (IFG pOrb, BA 47), ventral premotor cortex (vPMC, BA 6), and precentral gyrus (BA 4). Note: Brodmann areas do not always reflect the same anatomical borders as the underlying anatomical structure.

and 45 (Amunts et al., 2010, 1999; Keller et al., 2009; Narr et al., 2007; Rentería, 2012). Both Wernicke's and Broca's areas demonstrate a leftward asymmetry in some of their substructures. However, it should also be noted that the degree of the asymmetry detected depends on the analysis methods applied and the anatomical definitions used (Keller et al., 2009; Rademacher et al., 2001a; Westbury et al., 1999).

With respect to the structural connectivity between Wernicke's and Broca's area, the most important fibre connection appears to be the arcuate fasciculus. This fibre tract is not only more developed in humans than in apes and monkeys, it is also more developed in the left than the right hemisphere (Catani et al., 2007, 2004; Pulvermüller and Fadiga, 2010). As revealed by diffusion tensor imaging (DTI), the arcuate fasciculus is not a single fibre tract. In the left hemisphere, the most dominant fibre tract is the direct segment that runs from the posterior superior temporal gyrus via the parietal lobe to the inferior frontal cortex. A second branch has just recently been described and it is divided into two parts; a posterior and an anterior indirect segment. The posterior indirect segment connects the superior temporal gyrus with the inferior parietal lobe (an area also sometimes called 'Geschwind's area') and the anterior indirect segment connects the Geschwind's area with the inferior frontal cortex (Catani et al., 2007, 2004). This fibre tract also demonstrates a left-right asymmetry.

Already Carl Wernicke's original work proposed an additional ventral connection between the temporal and the frontal lobes. The anatomical correlates for this assumption are the uncinate fasciculus, and a recently described tract along the extreme capsule (Saur et al., 2008; Weiller et al., 2011). Both fibres connect the temporal lobe with the inferior frontal gyrus. The recent tract terminates in the ventral part of the inferior frontal gyrus and thus directly connects language related areas. The uncinate fasciculus connects to limbic structures and thus may not directly contribute to speech and language.

2. Structural and functional asymmetries in the language network

2.1. Structural asymmetry in the language network

Cerebral asymmetry in terms of morphology and function (such as foot or eye preferences, visual-spatial processing) can be found in many vertebrate and invertebrates (Ocklenburg and Güntürkün,

2012), but might vary from one individual animal to another. The occurrence of a cerebral asymmetry is not uniquely human. There is evidence that the occurrence of a population-wide consistent asymmetry, like handedness or hemispheric dominance for language, is more unique for humans (Corballis, 2009; Crow, 2002), while reports on species-specific foot and hand preferences in chimpanzees and other primates are inconsistent (Corballis, 2009). In the human population, 90% show a preference of the right over the left hand for tool use. In general, the development of cerebral asymmetries is controlled by a number of genetic and environmental factors (Concha et al., 2012; Francks et al., 2007; Rentería, 2012), but only some candidate genes have been identified so far (Bishop, 2013; Francks et al., 2007; Ocklenburg et al., 2013). The presence of a structural asymmetry is often assumed to be a prerequisite for the development of a functional asymmetry. However, such a structural predisposition can be override through early childhood experiences or specific learning abilities or disabilities, strengthening or weakening the functional asymmetry (Bishop, 2013; Wada, 2009).

This section focuses on the functional and structural asymmetries in the human brain with respect to speech perception. Functional and structural asymmetries describe the differences of homologous areas of the left and right hemisphere with respect to differences in size of an area, its grey-matter density, cortical thickness, cytoarchitectonic characteristics, or its association to cognitive functions. It is worth mentioning other structural and functional asymmetries in the human brain, related to handedness, eye-preference, vision, spatial processing, memory. These are beyond the scope of this review.

At a first glance the two hemispheres of the brain are almost symmetrical. However, on closer examination, an asymmetry becomes apparent. There is a protrusion of the right frontal lobe beyond the left and of the left occipital lobe beyond the right, known as "petalia" (Narr et al., 2007; Rentería, 2012). Consequently, the left auditory cortex is slightly lower than the right (Rademacher et al., 2001a; Toga and Thompson, 2003). While these gross structural asymmetries do not seem to have an impact on functional asymmetries, small asymmetries of sub-structures do. Therefore, one has to focus on microstructural differences.

Those structural differences could be analysed in two ways. A popular method uses high-resolution anatomical scans analysed using "Voxel-based morphometry" (VBM) (Ashburner and Friston, 2000; Good et al., 2001a, 2001b) that quantifies differences in the

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