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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 discus. 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.

This article is part of a Special Issue entitled <Human Auditory Neuroimaging>.

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, whist 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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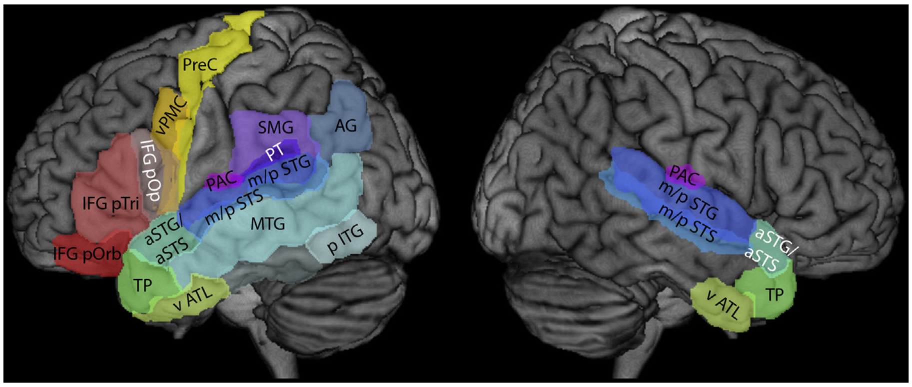

Fig. 1. The figure displays all relevant areas, discussed in this review. These are the primary auditory cortex (PAC, Brodmann area (BA) 41), planum temporale (PT, BA 42/22), supramarginal gyrus (SMG, BA 40), angular gyrus (AG, BA 39), middle and posterior part of the superior temporal gyrus (m/p STG, 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 local volume or concentration of grey matter, or methods that quantify the thickness of the cortex (Fischl and Dale, 2000). Alternatively, the microscopic analysis of post-mortem brains is by far the most precise method for exploring brain structures, and reveals differences within the seven cortical layers. With those cytoarchitectonic measurements, boundaries between brain areas could be identified, which are characterised by changes in the layer-structure of the grey-matter. Those structural boundaries also mark the boundary between two functionally distinct brain areas. The German neurologist and psychiatrist Korbinian Brodmann (1868–1918) was the first to map the complete human brain, defining 43 distinct cytoarchitectonic brain areas in each hemisphere (Zilles and Amunts, 2010). Although it is now proposed that the human brain can be classified into even more cytoarchitectonic substructures, the nomenclature still in use can be traced back to Brodmann. For example, Broca's area in the inferior frontal gyrus consists of Brodmann areas (BA) 44 and 45 (see Fig. 1). While Brodmann did not differentiate between the left and right hemisphere, recent anatomical studies focus on this, using basically the same method – but now with higher resolution and digitized brain sections (Morosan et al., 2001, 2005; Rademacher et al., 2001b). One of the results of relevance here is the investigation of Broca's area, the primary auditory cortex, as well as planum temporale, with the latter two areas being located in the posterior third of the superior temporal gyrus. Broca's area is structurally larger on the left than on the right side. This difference is dominated by a hemispheric difference in BA44, not in BA 45 (Amunts et al., 2010, 1999; Keller et al., 2009) which may develop during aging (Amunts et al., 2003). Any residual asymmetry in BA 45 is functional rather than structural. The functional consequence of this asymmetry is still a matter of debate, since only cytoarchitectonic measures have consistently revealed a structural asymmetry. In vivo structural measurements, like VBM, that can be correlated to behavioural measures, give mixed results with either a leftward or no asymmetry of Broca's area (Keller et al., 2009).

Another highly explored brain region is the posterior superior part of the temporal lobe that comprises the posterior third of the superior temporal gyrus, Heschl's gyrus, and PT (see Fig. 1). This part of the temporal lobe has a very prominent functional and structural asymmetry and constitutes the core of Wernicke's area. Of special interest here is Heschl's Gyrus, which is the primary auditory cortex, and the adjacent planum temporale and, further up towards the posterior lobe, the planum parietale (Shapleske et al., 1999). Anatomical studies of the primary auditory cortex (BA 41) with cytoarchitectonic maps have shown that the cell volume density in sub-region Te1.1 as compared to sub-region Te1.2 is higher in the left, but not in the right hemisphere (Morosan et al., 2001). Although not significantly different between the hemispheres, higher cell volume density has also been found on the left side for the areas Te1.0 and Te1.1 and for Te1.2 for the right side hemisphere (Morosan et al., 2001). Further, cytoarchitectonic measures indicate a leftward asymmetry for the secondary auditory cortex (BA 42), which describes the anterior part of the planum temporale, and the posterior end of the superior temporal gyrus (BA 22), which describes the posterior part of PT (Hutsler, 2003). MR-based methods show that the morphology of the entire PT is larger in the left than in the right hemisphere (Beaton, 1997; Binder et al., 1996; Hugdahl et al., 1998; Santos Sequeira et al., 2006; Steinmetz, 1996). However, the degree of the detected asymmetries depend on the applied methods and anatomical definitions (Westbury et al., 1999). The PT overlaps with Wernicke's area, which was originally seen as an indication that PT is specifically or even exclusively involved in the auditory processing of speech (Geschwind and Levitsky, 1968; Steinmetz, 1996), but more recent models imply speech-independent spectrotemporal analysis functions (Griffiths and Warren, 2002).

The lower boundary of the superior temporal gyrus is the superior temporal sulcus (STS) (see Fig. 1). This area appears to be an important structure for speech comprehension. Interestingly, also this structure demonstrates a left-right asymmetry. It has been demonstrated that the right STS is deeper than its left counterpart, in particular at the base of Heschl's gyrus (Glasel et al., 2011; Ochiai et al., 2004; Van Essen, 2005). This asymmetry seems to be unrelated to the leftward asymmetry of PT, and is already present in infants (Glasel et al., 2011). Furthermore, the depth of the right STS has been shown to be more variable than the depth of the left STS (Im et al., 2010). It is still an open question whether this STS asymmetry has any behavioural correlate and whether this has any relation to speech and language processes.

Another central structure that demonstrates a left-right asymmetry is the arcuate fasciculus. The long direct segment that connects the posterior temporal lobe directly with the inferior frontal cortex (Catani et al., 2007, 2004), tends to be missing or is less well developed in the right hemisphere. The direct segment appears asymmetrical in about 80% of the population (Berthier et al., 2012; Catani et al., 2007), with the proportion of left lateralisation being lower than the degree of left-hemisphere dominance for language. The functional relevance is uncertain but individuals with more symmetrical patterns in the arcuate fasciculus demonstrate a better performance in semantic association task, using the California Verbal Learning Test (CVLT) (Catani et al., 2007). This inter-individual variability of the arcuate fasciculus segments and its behavioural consequences may also partially explain the observed inter-individual variability of repetition impairments in aphasia (Berthier et al., 2012). Conduction aphasia is defined by impaired repetition, and was typically associated with lesions to the left arcuate fasciculus. However, occasional negative cases of impaired repetition without a lesion to this fibre tract as well as cases with lesions to the arcuate fasciculus but unimpaired repetition question this view. These latter cases could be explained by the occasional presence of a long direct segment in the right hemisphere (Berthier et al., 2012). Further work is needed to answer this question. It would also be informative to study whether the observed individual variability of the depth of the right STS (Im et al., 2010) is correlated to the presence and size of the right long direct segment of the arcuate fasciculus.

2.2. *Functional asymmetry in the language network: within auditory cortex*

It is widely accepted that the left and right auditory cortex, comprising the primary and secondary auditory cortex, have different processing capacities with respect to temporal and spectral resolution (Boemio et al., 2005; Obleser et al., 2008; Zatorre et al., 2002), as well as temporal integration windows, as proposed by the "asymmetric sampling in time" (AST) hypothesis (Poeppel, 2003). Both models predict a left hemisphere preference for rapidly changing acoustic cues, and a right hemisphere preference for tonal aspects such as pitch processing. An important anatomical sub-structure is the secondary auditory cortex that overlaps with the anterior portion of the PT. This part of the PT is seen as a computational hub, performing spectrotemporal operations that are important for analysing complex sound structures, like rapidly changing cues (Griffiths and Warren, 2002; Isenberg et al., 2012; Jäncke et al., 2002; Krumbholz et al., 2005). Speech perception relies on a differentiation of those rapidly changing signals, for example for differentiating stop consonants, or different places of articulation. But, PT seems not to be exclusively sensitive to those phonetic signals, and appears to be involved also in early auditory processing of non-verbal stimuli, spatial hearing, as well as auditory imagery (Binder et al., 1996; Isenberg et al., 2012; Obleser et al., 2008; Papathanassiou, 2000; Price, 2012; Specht and Reul, 2003; Specht et al., 2005).

One would predict a higher processing capacity of the left auditory cortex including PT to stop-consonants that are acoustically more complex than vowels. This acoustical complexity of stop-consonants is caused by the release sound following the initial blockage of the airflow during the articulation of the consonant.

A simple behavioural test for probing such a lateralisation of stop-consonant processing is a dichotic listening test. In this test, two consonant-vowel syllables are simultaneously presented to the left and right ears (Asbjornsen and Hugdahl, 1995; Hugdahl et al., 1999, 2009; Voyer and Techentin, 2009). When the participants are asked to repeat what they have heard best or most clearly, they predominantly repeat the syllable, presented to the right ear. This effect is called the 'right ear advantage' (REA). Since the ipsilateral afferent auditory pathways are assumed to be suppressed under dichotic listening situations (Penna et al., 2007), it is widely accepted that the presence of a REA reflects a left-hemisphere dominance for language (Asbjørnsen and Helland, 2006). However, it has to be emphasized that a dichotic listening task does not measure language lateralisation per se. It is more a test of asymmetric processing of phonemes and this asymmetry depends on temporo-spectral characteristic of the stimuli. The strength of the REA varies with the acoustic characteristics of the stimulus, examples include, the voice onset time (VOT), which is the time between the high-frequent release sound of the consonant and the onset of the voice during the vowel articulation (Rimol et al., 2006; Sandmann et al., 2007), and place of articulation, which is the location of the blockage of the airflow during the articulation of the consonant (Voyer and Techentin, 2009). Furthermore, the strength of the REA is influenced by secondary features, for example, saliency of different stimulus pairing, or even priming effects (Sætrevik and Hugdahl, 2007; Sætrevik and Specht, 2009). Interestingly, this varying pattern of ear-dominance is not inborn, but develops over the first five to eight years, parallelled with developing speech and language competences. Consequently, a developmental sex-difference can be observed, with girls developing this pattern earlier than boys (Westerhausen et al., 2010). One reason for this developmental effect in the dichotic listening performance is the still ongoing development of the corpus callosum, which has been shown to influence in particular the perception of the stimuli, presented to the left ear (Westerhausen et al., 2010; Westerhausen and Hugdahl, 2008; Westerhausen et al., 2011).

The absence of a functional asymmetry at the phonemic level can be further linked to developmental speech disorders, like dyslexia, since it has been repeatedly shown that dyslexic subjects can suffer from various other impairments, such as phonological processing, phoneme awareness, but also visual-spatial attention (Heim et al., 2008; Helland et al., 2008; Lallier et al., 2013). Dichotic listening tests have shown that the REA is reduced in subjects with dyslexia, both in children (Asbjørnsen and Helland, 2006; Helland et al., 2008; Helland and Asbjørnsen, 2001; Lallier et al., 2013) as well as in adults (Iliadou et al., 2010; Obrzut and Mahoney, 2011). Such a reduced phonological awareness may cause confusions in the perception of similarly sounding phonemes, which, in turn, causes perceptual difficulties beyond the phoneme level (Helland et al., 2008). Further, a well-developed phonological awareness is assumed to be a prerequisite for learning a mapping between phonology and orthography, i.e. learning to read (Ramus et al., 2003). A diminished functional asymmetry within the auditory system is often accompanied by a reduced structural asymmetry in PT (Heiervang et al., 2000). However, this should not be overgeneralised, since a reduced structural asymmetry is also observed in persons who stutter (Braun et al., 1997; Büchel and Sommer, 2004; Fox et al., 2000; Yairi, 2007), and the results for phonological processing are less consistent (Brady and Berson, 1975; Foundas et al., 2004; Sommers et al., 1975).

Taken together, the functional asymmetry within the auditory system appears to be an important prerequisite for phonological processing in normally developing individuals, but this asymmetry is not inborn and develops over the first decade. Although the underlying mechanisms are still not fully understood, an important contributor appears to be the development of the corpus callosum, facilitating an inter-hemispheric transfer.

In addition to behavioural measures of asymmetry, functional neuroimaging studies have tried to identify neuronal correlates of these asymmetries within the auditory cortex, focussing in particular on the level of vowel and consonant processing. Consonants are acoustically more complex than vowel sounds and so their perception depends on a higher temporal resolution, engaging left auditory cortex, more so than right auditory cortex (Boemio et al., 2005; Zatorre et al., 2002). Such findings are evidence for a general left dominant processing of those speech specific signals, which forms the central tenet of the asymmetric sampling theory (AST) (Poeppel, 2003). On the other hand, such a left-right dichotomy in temporal resolution may oversimplify the underlying processes, given the acoustic complexity of a speech signal (McGettigan and Scott, 2012).

In order to test the differential processing of vowels in the auditory cortex, Osnes and colleagues applied a sound morphing procedure to gradually change the musical instrument-like sound into a vowel-like sound (Osnes et al., 2011a). The advantage of such a sound morphing procedure is that is separates responses that are equivalent for any sound from those which are sensitive to phonetic features. Osnes found an increasing response in the middle part of the superior temporal gyrus and the anterior part of PT bilaterally, as there were more phonetic features present in the sounds, while there was steady-state response to non-phonetic sounds. However, this research has limited direct applicability to a specialized speech-processing network since vowels are merely steady-state sounds. Stop consonants are more relevant to speech processing and dominated by rapidly changing frequency modulations, either with or without simultaneous voicing (voiced/unvoiced consonant). Rimol and colleagues examined the neuronal responses to unvoiced consonants and consonant-vowel syllables (Rimol et al., 2005). The results demonstrated that, like for vowels, both auditory cortices are involved, but with a clear leftward asymmetry for both consonants as well as consonant-vowel syllables in comparison with a matched noise condition. This leftward asymmetry holds even when consonant-vowel syllables are presented dichotically (van den Noort et al., 2008). These studies together support the AST model of a differential processing between the left and right auditory cortex. The predictions of the AST model for language asymmetry appear to be upheld across tasks requiring different degrees of selective attention (Alho et al., 1998; Zaehle et al., 2009).

Further evidence for the AST model comes from electrophysiological and combined electrophysiological and fMRI studies (Giraud et al., 2007; Giraud and Poeppel, 2012; Giraud et al., 2008; Morillon et al., 2010). By measuring brain oscillations and their neuroanatomical correlates, these studies have confirmed that the left and right auditory cortices respond differently to specific spectro-temporal characteristics of speech sounds. Recent results suggest that the incoming speech signals are transformed into intrinsic oscillations within the auditory cortex (Giraud and Poeppel, 2012). Moreover, oscillations in the theta band (4–8 Hz) and the gamma band (25–35 Hz) are suggested to be the main contributors to this process. Functional asymmetry may arise through more dominant gamma activity in the left auditory cortex and a more dominant theta activity in the right auditory cortex that may sample the high-frequent sounds of stop-consonants and the tonal characteristic of vowels differently (Giraud and Poeppel, 2012).

A functional asymmetry can also be observed for non-phonetic stimuli, like differential processing of intensity and duration of harmonic frequency modulated tones (see, e.g., Angenstein and Brechmann, 2013). Accordingly, a more rightward asymmetry can be observed during the processing of music sounds, due to its tonal characteristic (Zatorre et al., 2007), but all studies demonstrate only a functional asymmetry for the auditory cortex and not a complete lateralised processing. It has also been discussed whether the observed asymmetry in the auditory cortex and beyond may reflect a more categorical perception (Hickok and Poeppel, 2007; Liebenthal, 2005).

In summary, functional asymmetry of auditory processing depends on spectro-temporal features of speech sounds. Furthermore, the behavioural as well as functional imaging studies conclusively indicate that not only both auditory cortices contribute to the perception of phonetic signals, but that the entire temporal lobe of both hemispheres contributes to the processing of speech signals, but their contribution varies with the acoustic features to be processes.

2.3. *Functional asymmetry in the language network: beyond auditory cortex*

Functional asymmetry occurs also beyond the auditory cortex within the ventral stream. According to the dual-stream model (Hickok and Poeppel, 2007), the ventral stream is a processing network that runs from the posterior superior temporal area towards the ventral anterior temporal lobe, and is assumed to map sound to meaning. The ventral stream is the dominating processing network for speech comprehension. Focussing on core processes, such as phonological, lexical, semantic, and syntax processing, a functional asymmetry can be observed within the ventral stream. For example, the left STS is a structure that is particularly involved in processing phonological information (Hickok and Poeppel, 2007; Price, 2012, 2010; Turkeltaub and Coslett, 2010), while the right STS has been identified as an area that is important for voice identification (Belin et al., 2004; Belin and Zatorre, 2003; Ethofer et al., 2013; Latinus and Belin, 2011), as well as the processing of emotional prosody (Buchanan et al., 2000; Jäncke et al., 2001; Price, 2012; Ross and Monnot, 2011; Schirmer and Kotz, 2006; Wittfoth et al., 2010). It should be noted that both left and right STS are response to these sounds, but that the magnitude of the response differs across hemispheres (Turkeltaub and Coslett, 2010). This notion was confirmed by a recent fMRI study, using a sound-morphing paradigm, where sounds gradually changed from white noise into either a consonant-vowel syllable or a respective piano/guitar sound, demonstrated a significant interaction effect between these two morphing sequences exclusively within the left STS (Osnes et al., 2011b; Specht et al., 2009b). Notably, responses were detected in both STS during processing the morphing sequence, but there was a stronger left than right STS response to the increasing intelligibility of the sound as speech sound, while the responses increased similarly on both sides when the sound morphed from white noise into a music sound. A similar observation has been made, using a phonological repetition-suppression paradigm (Vaden et al., 2010). In this study, word lists with low, medium, or high degree of phonological repetition have been presented to the subject with the hypotheses of decreased activation in case of high degree of phonological repetition. Among other areas, this predicted pattern was discovered within the left and right middle STS. Again, a left-right asymmetry was observed, which could reflect either a functional asymmetry towards the left or a more individual activation pattern within the right STS (Vaden et al., 2010). Additional support for the latter notion comes from afore mentioned anatomical studies that demonstrate that the right STS is deeper than its left counterpart (Glasel et al., 2011; Ochiai et al., 2004; Van Essen, 2005), and the depth appears to be more variable for the right STS (Im et al., 2010). Taking up the argument raised by Vaden et al. (2010), a higher variability and thus a less precise registration of the right STS could indeed explain some of the discovered functional asymmetries of the STS, which then may not be real but an artefact when comparisons are made between the left and right STS on a standardized group rather than an individual level.

The left anterior temporal lobe appears to be more dominant in speech comprehension than its right homologue. This structure is mainly attributed to the conceptual processing of meaningful sentences (Binder and Desai, 2011; Hickok and Poeppel, 2007, 2004; Humphries et al., 2007, 2006; Patterson, 2007; Patterson et al., 2007; Poeppel et al., 2012; Price, 2012; Vigneau et al., 2006). This notion is further supported by lesion studies (Magnusdottir et al., 2013; Schwartz et al., 2009) and studies using direct cortical stimulations (Matsumoto et al., 2011). However, the degree of the functional asymmetry seems to depend on the content and required level of abstraction (Binder et al., 2011). A left-hemispheric dominance in phonological and lexical processes is also found in the inferior frontal gyrus, for both spoken and read words (Heim et al., 2009; Price, 2012; Specht et al., 2005). By contrast, the right homologue seems to play a greater role in processing emotional information such as prosody, rather than speech comprehension per se (Schirmer and Kotz, 2006).

Since Broca's first report, the left inferior frontal gyrus has been known as an important area for speech processing, particularly speech production (Price, 2012). Less evidence exists for speech relevant function of the right hemisphere homologue (Boatman, 2004). While the temporal lobe functions demonstrate only to a certain degree a leftward asymmetry, the language related functions of the inferior frontal gyrus are mainly left lateralised (Hickok and Poeppel, 2007). However, functional imaging studies indicate that right hemisphere homologues of Broca's area, as well as posterior temporal area may be supportive during processing of prosody (Schirmer and Kotz, 2006), but also demanding language tasks (Van Ettinger-Veenstra et al., 2012; van Ettinger-Veenstra et al., 2010), while other studies on effortful listening indicate a stronger left hemisphere contribution, but only in hierarchically higher-order areas (Wild et al., 2012).

In summary, a functional asymmetry emerges along the ventral stream, with strong bilateral contributions in the posterior superior temporal areas and an increasing leftward asymmetry towards the anterior temporal lobe. This forms a kind of laterality gradient along the ventral stream.

3. From a regional approach to hierarchical network models

While the original models of language were mainly based on clinical observations, the simplicity of these early models is obsolete in light of more recent neuroimaging and lesion data. By having only two or three language related areas and connections in between them, the classical models by Wernicke and Lichtheim (1885; Wernicke, 1874), and later on by Geschwind (1965a, 1965b), are far from effective in describing the functional complexity of speech comprehension, or from being able to describe the various symptoms in aphasia. The conceptual models of speech perception in the brain have been readdressed. Current models assume a more hierarchical network structure with dynamic and context dependent interactions between different regions (Hickok and Poeppel, 2007; Poeppel et al., 2012; Price, 2012; Rauschecker and Scott, 2009; Scott and Wise, 2004).

In line with the classical Wernicke-Lichtheim model (Lichtheim, 1885; Wernicke, 1874), speech perception is still upheld to be predominantly mediated by the left temporal lobe, with the left frontal lobe most important for speech production. Perhaps contradictory to the classical model, are the results from functional neuroimaging studies demonstrating speech perception responses to speech sounds in the right temporal lobe (Hickok and Poeppel, 2007). The left temporal lobe as a whole has been identified to be crucially involved in language processes with several functional sub-divisions, and a number of studies have identified language related regions also outside of the classical language areas, i.e. Wernicke's and Broca's area (Price, 2012). Regions that have been implicated in the language processing network include the temporo-parietal junction, supramarginal gyrus (BA 40), angular gyrus (BA 39), basal ganglia, and also their right hemisphere homologues (Catani et al., 2007, 2004; Damasio et al., 2004; Dronkers and Ogar, 2004; Poeppel and Hickok, 2004), or left insular cortex (Ackermann and Riecker, 2004; Dronkers, 1996; Weiller et al., 2011). Recent models propose a hierarchical dual-stream processing network with the ventral and the dorsal streams (Hickok, 2012; Hickok and Poeppel, 2007, 2004; Scott and Wise, 2004). The concept of two distinct streams originated from animal research (Rauschecker and Scott, 2009), and is further supported by afore described fibre tracts that mirror the two functional streams on the neuroanatomical level. The ventral stream, also called "what" stream (Scott and Wise, 2004), is assumed to provide important functions for speech perception, like phonetic decoding, phonological and sub-lexical processing, and speech comprehension, like lexical, combinatorial, and semantic processing (Hickok, 2012; Hickok and Poeppel, 2007). The dorsal stream, also called "how" stream (Scott and Wise, 2004), supports auditory-motor integrations and comprises anatomically the premotor areas and the articulatory network, like Broca's area and the anterior insular cortex (Hickok and Poeppel, 2007). The two streams are assumed to be hierarchically organised where the input to each processing step depends on the computational output of the previous step (Hickok and Poeppel, 2004). The ventral and dorsal stream model claims for different patterns of lateralisation; while the dorsal stream tends to be left lateralised, the posterior part of the ventral stream is said to be symmetrical (Hickok and Poeppel, 2007). The model also suggests that the right temporal lobe has some fundamental speech perception capacities, which is supported by several neuroimaging results (see also (Poeppel and Hickok, 2004)).

Further validation for the dual-stream comes from neurocomputational models. Ueno and colleagues modelled a neuroanatomically constrained dual-stream model, with a dorsal and a ventral stream (Ueno et al., 2011). The dorsal stream provided functions that were important for repetition, and the ventral stream provided functions that were important for the extraction of meaning. They could demonstrate the division of function between the two streams, and that learning to speak requires both streams. Further they were able to demonstrate that a gradual shift from acoustic to semantic processing along the ventral stream improves the performance of the model (Ueno et al., 2011).

3.1. Mapping the ventral and dorsal stream with neuroimaging

Even though researchers broadly agree on the concept of the ventral and dorsal stream, it is still a matter of debate, which anatomical areas should be associated to the ventral and dorsal stream, and where these two streams diverge. In addressing this issue, this section focuses on the ventral stream and on speech comprehension.

3.2. The ventral stream

In general, speech comprehension is a complex, multi-functional task that does not only require processing of auditory information; it requires attention, working memory, and integrative processes in order to understand not only single words but also sentences and narratives. In this respect, the ventral stream is the dominant processing network for speech comprehension and provides functions such as lexical, semantic, and syntactical processing (Hickok, 2012; Hickok and Poeppel, 2007). Along this path, the ventral stream appears to become more and more left lateralised, forming a kind of 'lateralisation gradient' from the posterior superior temporal lobe towards the anterior temporal lobe (Peelle, 2012; Specht, 2013). The ventral stream is hierarchically organized with processing steps, where the input to one level depends on the output of the previous one. The proposed lateralisation gradient mirrors also the increasing linguistic complexity of the performed processes, with auditory perception in the posterior superior temporal area and semantic and syntactic processing mainly in the anterior temporal lobe. Thereby, the ventral stream hosts the important functions for both speech perception and speech comprehension. However, it should be emphasized that this processing hierarchy is not assumed to be linear and unidirectional, but characterized and influenced by inter-hemispheric interaction, feed-forward and feedback connections as well as higher-order processes, such as attention and expectancy. Further, speech perception and speech comprehension are two distinct functions within the ventral stream. While the perception process is mainly an automated processing of auditory signals, speech comprehension requires a certain level of attention and awareness (Davis et al., 2007).

3.3. The ventral stream – posterior superior temporal areas

According to the dual-stream model, the posterior superior temporal lobe, including the primary and secondary auditory cortex, belongs neither to the ventral nor to the dorsal stream, as it provides general auditory processing capacities, which is important for both streams (Hickok and Poeppel, 2007). The primary and secondary auditory cortex is assumed to send output to the middle and posterior STS, from where the two streams may originate (Hickok and Poeppel, 2007; Turkeltaub and Coslett, 2010). Accordingly, neuroimaging data consistently demonstrate that speech perception is mainly mediated through temporal lobe structures, confirming the "ventral stream" model, with mainly auditory and phonetic processing in the posterior temporal lobe and semantic and sentence processing in more anteriorly located areas of the temporal lobe (Price, 2012, 2010).

Besides general auditory processing as a prerequisite for auditory speech comprehension, the posterior temporal area of the left and right hemispheres have been directly associated to speech comprehension abilities as well as narrative comprehension. For example, a lesion study in aphasic patients revealed that a structural integrity of the left posterior superior temporal area predicts auditory short-term memory capacity, which in turn affects speech comprehension (Leff et al., 2009). A longitudinal study on children and adolescents demonstrated an increasing fMRI signal during narrative comprehension as a function of age within the posterior superior temporal area of both hemispheres (Szaflarski et al., 2012). Interestingly, this bilateral pattern was not seen when the same cohort of children was investigated with a verb-generation task (Szaflarski et al., 2006), indicating a maturation process that supports narrative comprehension (Szaflarski et al., 2012), or perhaps short-term memory, taking the afore mentioned lesion study into account.

In conclusion, the posterior temporal area is an area where the ventral and dorsal stream may diverge. Developmental studies underlie the importance of posterior superior temporal structures of both hemispheres in developing narrative comprehension competence. The connection to verbal short-term memory capacity, attention, and intelligibility of speech sounds indicate an interconnection with higher-order processes that become in particular dominant during processing of sentences and narratives, but that may be not seen or detected by studies, probing simple auditory processing functions.

3.4. *The ventral stream – middle and posterior superior temporal sulcus (STS)*

The middle and posterior part of the STS has been identified as an important anatomical structure within the speech comprehension network. Functional imaging studies using speech sounds of variable intelligibility have indicated an increasing sensitivity to speech sounds along a posterior-anterior axes within the left superior temporal gyrus and sulcus (Davis and Johnsrude, 2003; Hervais-Adelman et al., 2012; Peelle et al., 2010; Scott et al., 2000; Specht et al., 2009b). While posterior STS responds to speech and complex sounds, the more anteriorly adjacent middle portion of the STS processes mainly phonological and sub-lexical information (Belin et al., 2000; Jäncke et al., 2002; Price, 2012, 2010; Scott et al., 2000; Specht et al., 2009b; Specht and Reul, 2003).

Besides a general functional asymmetry of the STS, there is also evidence for a division of labour between the left and right STS, indicating that they process distinct aspects of the speech signal. A recent meta-analysis on fMRI data demonstrated a high sensitivity of the left STS to phonetic and phonological information (Turkeltaub and Coslett, 2010). On the other hand, the right STS has been identified as the temporal voice area, which is an area that responses almost uniquely to vocal sounds (Belin et al., 2004; Belin and Zatorre, 2003; Ethofer et al., 2013; Latinus and Belin, 2011). Further, the right hemisphere, and in particular the right STS is also often discussed in connection with processing of emotional prosody (Buchanan et al., 2000; Jäncke et al., 2001; Price, 2012; Ross and Monnot, 2011; Wittfoth et al., 2010). This notion is further supported by lesion data that demonstrate a disturbed processing of affect prosody after right brain damage (Ross and Monnot, 2008). However, neuroimaging studies are not giving a coherent picture of a pure right lateralised processing of emotional prosody (Kotz et al., 2003), but studies broadly agree on a general involvement of right but also left STS in prosodic processing.

It should be emphasized that these specific results for the left and right STS only indicate a higher sensitivity to phonological and vocal signals, but this does not necessarily imply that this is a speech specific area. Moreover, a meta-analysis by Hein and Knight indicated that the STS of the left and right hemisphere apparently is involved in several different processes, involving not only phonological processing, but also theory of mind, audio-visual integration, or face perception (Hein and Knight, 2008).

In conclusion, the middle and posterior part of the STS of the left and right hemisphere is an important contributor to the perception of auditory speech signals where the left and right STS process different aspects of a speech signal. The posterior and middle portion of the left STS has repeatedly been reported as an important area for phonological and sub-lexical processing, while the right STS is important for voice identification and prosodic processing. However, studies have also demonstrated that the same areas are involved in processing of non-phonetic sounds, but also other, non-linguistic functions, like theory of mind.

3.5. *The ventral stream – posterior middle and inferior temporal gyrus*

According to the dual-stream model by Hickok and Poeppel (2004, 2007), the posterior middle (BA 21) and inferior temporal (BA 20) areas serve as a lexico–semantic interface. Multiple evidences exist for a modality independent processing system in this part of the left temporal lobe. Studies on visual as well as auditory lexical decision tasks have repeatedly indicated that the inferior temporal gyrus is part of a lexical system, together with inferior frontal areas (Binder et al., 1997; Heim et al., 2009; Hickok and Poeppel, 2007; Noppeney and Price, 2002; Price, 2010; Zahn et al., 2000). A meta-analysis by Binder identified that in fact the entire middle-temporal gyrus should be considered to be as part of the semantic system, in addition to angular gyrus, prefrontal areas, posterior cingulate gyrus, as well as fusiform and parahippocampal gyrus (Binder et al., 2009). This interpretation is supported by further, more recent neuroimaging studies (Chao et al., 1999; Visser et al., 2012) and lesion studies (Bates et al., 2003). In addition, at the border of the posterior inferior temporal gyrus to the occipital lobe, two distinct language related areas are adjacent, whereof one area within the occipito–temporal sulcus is broadly known as the “visual word form area” and responds only to visual stimuli, while the anteriorly adjacent area within the posterior inferior temporal gyrus is modality independent, and responds during both, auditory and visual orthographic and phonological task (Cohen et al., 2004). Among other areas, this multimodal area is also remarkably close to an area that has repeatedly been demonstrated to be affected in dyslexic subjects (Raschle et al., 2012; Richlan et al., 2009; Silani, 2005; Specht et al., 2009a). Note, dyslexia is not a pure reading problem, since dyslexic subjects also demonstrate impairments in phonological processing, phoneme awareness, or visual-spatial attention (Heim et al., 2008; Helland et al., 2008; Lallier et al., 2013). It has been further suggested, that phonological awareness is a prerequisite for learning a mapping between phonology and orthography (Ramus et al., 2003), which, in turn, may relay on a functional integrity and connectivity of the posterior inferior temporal gyrus and the adjacent visual word form area.

In summary, the posterior middle and inferior temporal areas are mainly modality independent areas and are involved in both lexical as well as semantic processing. They are an important part within the semantic network that comprises also, among other areas, the angular gyrus, inferior frontal gyrus, and further prefrontal areas of the left hemisphere (Binder et al., 2009).

3.6. *The ventral stream – anterior temporal lobe*

A typical finding in neuroimaging studies of speech comprehension and sentence processing is an extension from the posterior superior temporal areas towards the left temporal pole, forming the ventral stream (Scott et al., 2000). This posterior-anterior extension reflects the hierarchical organisation of the ventral stream and may reflect an increasing abstraction from the original input signal (Davis and Johnsrude, 2007). In other words, the more linguistically complex the processing, the greater degree of integration of information is required thus placing greater demands on lexical and semantic processing during sentence comprehension. For fMRI studies, the consequence is a greater spread of activation into anterior parts of the left temporal lobe, extending into the inferior frontal gyrus and inferior temporal gyrus. The anterior temporal lobe, particularly the temporal pole, is typically associated with sentence processing (Price, 2012). The posterior middle and inferior temporal areas and angular gyrus, are also associated with the syntactic and semantic aspects of sentence processing (Binder and Desai, 2011; Hickok and Poeppel, 2007, 2004; Humphries et al., 2007, 2006; Patterson, 2007; Patterson et al., 2007; Poeppel et al., 2012; Price, 2012; Vigneau et al., 2006). This is further supported by a study, using direct cortical stimulation of the anterior superior temporal gyrus and sulcus, causing auditory sentence comprehension deficits (Matsumoto et al., 2011). Unlike auditory and linguistic functions, sentence processing and lexical and semantic retrieval are assumed to be strongly left lateralised. Evidence for this comes from functional neuroimaging (Ferstl et al., 2008; Humphries et al., 2007; Price, 2012; Specht et al., 2008)but also from studies using voxel-based lesion symptom mapping (Magnusdottir et al., 2013; Schwartz et al., 2009) and studies in patients suffering from "primary progressive aphasia", which is caused by neuronal degeneration (Grossman, 2002; Mesulam et al., 2009; Patterson, 2007; Wilson et al., 2009; Zahn et al., 2005). In particular, the clinical phenotype of semantic dementia is associated with grey matter atrophy (Adlam et al., 2006; Mesulam et al., 2009; Mummery et al., 2000) and white matter damage (Galantucci et al., 2011) of the left anterior temporal lobe.

Comprehension of spoken narratives requires multilingual skills. It goes beyond simple sentence and syntax processing, and narrative comprehension has to be seen as an interplay of various cognitive processes, involving speech perception, lexical and semantic processing, syntax processing as well as combinatorial processing and working memory. Other structures in addition to the left anterior temporal lobe are of crucial importance, as well. Although, auditory narrative comprehension has been investigated only by a few neuroimaging studies, evidence exists that the posterior superior temporal lobe is of crucial importance (Crinion et al., 2003; Wilson et al., 2008) in concert with the angular gyrus (Golestani et al., 2013; Jang et al., 2013). Furthermore, contributions of the default mode network, which is a brain network mainly active during rest (Raichle and Snyder, 2007), and premotor cortex have been reported (Wilson et al., 2008).

However, it should be noted that fMRI studies suffer from susceptibility artefacts within the ventral anterior temporal area (Visser et al., 2012, 2010), which may cause that the contribution of this area is underestimated. Accordingly, studies, using a distortion corrected imaging technique are able to demonstrate are more graded contribution of both, the left and right ventral anterior temporal lobe to semantic processing, with bilateral contribution to pictures and environmental sounds and more left lateralised responses to speech sounds (Visser and Lambon Ralph, 2011).

In conclusion, the anterior temporal area is an important part in both multimodal semantic processing but also processing of sentences and narratives. It is in particular left lateralised for auditory speech comprehension and recruits right hemisphere homologues for non-verbal semantic processing. However, caution should be applied here as neuroimaging are lacking sufficient signals from this area and thus, the full picture may not emerge.

3.7. The ventral stream — (ventral) inferior frontal gyrus

The current concept of the dual-stream model proposes that the ventral and dorsal streams both terminate in the inferior frontal gyrus, but not necessarily within the same portion of this structure (Saur et al., 2008). Thus, the inferior frontal gyrus is not necessarily considered as part of the ventral stream as it serves in particular functions for speech production rather then perception. Nevertheless, the inferior frontal gyrus has been repeatedly demonstrated to be involved in modality independent phonological and lexical processing. Evidence comes, for example, from functional neuroimaging studies (Heim et al., 2009; Price, 2012; Specht et al., 2005), but also from studies, using direct electrocortical stimulation (Boatman, 2004). These studies mainly refer to the pars triangularis of the inferior frontal gyrus, which is also the area where the fibre connection through the extreme capsule terminates (Saur et al., 2008) that connects the anterior temporal lobe with the ventral inferior frontal gyrus and thus may indicate the endpoint of the ventral stream within the inferior frontal gyrus.

The right hemisphere homologue is less consistently described in the neuroimaging literature on speech comprehension in healthy subjects, but indicate possible supportive functions during processing of prosody (Schirmer and Kotz, 2006), and demanding language tasks (Van Ettinger-Veenstra et al., 2012; van Ettinger-Veenstra et al., 2010).

3.8. The ventral stream — additional areas, related to speech comprehension

A number of additional areas have been identified by fMRI above and beyond those originally proposed by Hickok and Poeppel (2007). For example, a meta-analysis of neuroimaging data has made a strong link of the supramarginal gyrus to speech perception processes, mainly categorical perception (Turkeltaub and Coslett, 2010), which would indicate that this area belongs or at least has connections to both the dorsal and ventral streams. Further, this categorical perception indicates that the supramarginal gyrus receives its input from areas that perform phonological processing (Obleser and Eisner, 2009). However, other explanations include functions, like attention, phonological working memory processes, or general categorization functions, that are not exclusively linked to speech perception (Price, 2012). In the same vein are the discussions on the angular gyrus. Already Geschwind included the angular gyrus in his model on reading (Geschwind, 1965a), but this structure appears to be supra-modal, given the reports of angular gyrus involvement in studies on phonological decision, demanding semantic tasks, semantic retrieval, and tasks requiring the retrieval of concepts (Binder et al., 2009; Chao et al., 1999; Golestani et al., 2013; Price, 2012). Further, the intelligibility of the speech information in a higher-order semantic task influences the activation within the angular gyrus (Golestani et al., 2013). Although using written material, Martín-Loeches and co-workers identified the angular gyrus as an important area for understanding the global coherence of a narrative (Martín-Loeches et al., 2008). Furthermore, the angular gyrus overlaps also with the proposed "Geschwind's territory" that is connected through the indirect anterior segment of the arcuate fasciculus with Broca's area as well as the indirect posterior segment of the arcuate fasciculus with the posterior temporal lobe (Catani et al., 2004). Other studies report angular gyrus involvements in number processing and finger tasks, like finger counting (see, e.g., Rusconi et al., 2005), but also as a part of the default mode network (Raichle et al., 2001). In addition, direct cortical stimulation revealed involvement in finger recognition, writing, and finger recognition (Roux et al., 2003), reading aloud (see, e.g., Roux et al., 2004), but also controlling of arm muscles (Kombos et al., 2008). The involvement of the angular gyrus in multiple task and across sensory boundaries, including semantic processing during speech comprehension, reflects that this structure has multiple inputs and may act as a cross-modal hub that integrates and combines the different sensory inputs (Seghier, 2013). Meta-analyses have also revealed that the angular gyrus may have at least three functional subdivisions that differentially contribute to the retrieval and processing of semantic information and concepts (Price, 2012; Seghier, 2013; Seghier et al., 2010). In this respect, the angular gyrus is not only important for speech comprehension but for the entire perceptual system as such.

Another area that appears to be involved in speech comprehension processes is the basal ganglia. This subcortical structure is, among other functions, tied to processing of emotional prosody, as, for example, demonstrated by studies in Parkinson's disease

(Schröder et al., 2010) and basal ganglia infarcts (Paulmann et al., 2009). Besides of the basal ganglia, also other subcortical areas but also the cerebellum contributes to the processing of auditory events (Kotz and Schwartze, 2010).

The original model by Hickok and Poeppel (2007) does not specifically include the supramarginal gyrus, angular gyrus, or subcortical and cerebellar structures. However, given the evidence that these areas support speech comprehension, it would be reasonable to argue that their role in speech comprehension warrants their inclusion in a model on speech comprehension. On the other hand, functions provided by the supramarginal and angular gyrus are not exclusively linked to speech comprehension per se but they appear to deliver important supporting functions.

3.9. The dorsal stream

While the described ventral stream is the dominating processing network for speech perception and speech comprehension, the function of the dorsal stream is less understood in this respect. Undoubtedly, the dorsal stream has an important function in linking speech sounds with the motor system in order to reproduce the sounds with the vocal tract. The dorsal stream is the dominating network for repetition, particularly sub-lexical repetition, like the repetition of pseudowords (Saur et al., 2008). Hence, the dorsal stream is important in infants during the development of speech abilities, as it enables motor programs through auditory-motor integration (Hickok, 2012; Ueno et al., 2011).

Hickok recently discussed the concept of predictive coding in relation to his dual stream framework (Hickok, 2012). In general, predictive coding appears to be a general concept and describes a set of brain processes that match actions with potential outcomes. Predictive coding was originally developed as a descriptive model for the retina (Srinivasan et al., 1982) and later extended to the visual system (Rao and Ballard, 1999), but has been further generalised and applied to other modalities and functions over the last years. In the most generalised view, predictive coding includes both, performed action, in terms of a feedback loop, but also perceived actions, which connects this concept to the mirror neuron system (Friston et al., 2010; Hickok, 2012; Kilner et al., 2007; Kotz and Schwartze, 2010). The mirror neuron system, in short, are neurons that respond to the observation of an action and may also predict the outcome of an action (Iacoboni and Dapretto, 2006; Rizzolatti and Craighero, 2004; Rizzolatti and Sinigaglia, 2010). Therefore, they may, or may not contribute to action understanding (see also (Hickok, 2013)).

There are ongoing discussions whether this system is also involved in auditory speech perception processes and to which extent this involvement is important for speech comprehension.

3.10. The dorsal stream — premotor involvement during sub-lexical speech perception

Recently, a controversial discussion around the involvement of premotor areas in speech perception re-emerged. On the one hand, there is clear evidence that premotor areas are involved in speech perception, especially in the perception of degraded speech (Meister et al., 2007; Osnes et al., 2011b; Price, 2010; Wilson, 2009; Wilson et al., 2004). Further, transcranial magnetic stimulation (TMS) studies demonstrate that stimulation of motor areas influences speech perception abilities, like categorical perception (Möttönen and Watkins, 2009), discrimination of specific place of articulations (Möttönen and Watkins, 2012), or discriminating stop-consonants (Meister et al., 2007). Further, a recent study combined TMS and EEG and measured the effect of TMS stimulation of the lip and hand representations of the left motor cortex on the mismatch-negativity (MMN) response. The authors detected a reduced MMN response after TMS stimulation of the lips but not of the hand representation (Möttönen et al., 2013). This clearly indicates that disturbances within the articulatory network can cause perturb automatic processes, like speech sound discrimination. On the other hand, TMS studies and lesion data demonstrate at the same time that a disturbed motor cortex has only minor or even no effects on general speech perception and speech comprehension abilities (Hickok, 2012, 2009; Hickok et al., 2009; Lotto et al., 2009; Rogalsky et al., 2011), that is speech discrimination abilities are disturbed but not vanished after a disruption within the articulatory network. Together, there is general agreement that speech comprehension does not rely on the dorsal stream and the motor system, since only perception deficits are observed but no general comprehension deficits (Hickok et al., 2009), where comprehension refers to higher-level linguistic processes like lexical, semantic and syntax processing. Thus, an ongoing discussion has emerged on the functional importance of motor and pre-motor areas for speech perception processes, whether they facilitate speech and categorical perception, “mirror” the articulatory process, or are just by-products of low conceptual importance.

The interest in exploring motor areas during speech perception processes dates back to the ‘motor theory of speech perception’ by Alvin Liberman (Liberman and Mattingly, 1985; Liberman and Whalen, 2000). In the 1950th, Alvin Liberman and his colleagues from the Haskins Laboratories studied the perception of synthetic speech and discovered a context dependent modification of acoustic patterns in order to create an appropriate phonetic perception, which resulted in a new way of thinking by seeing speech as acoustic gestures. This idea was then more systematically formulated in their proposed motor theory of speech perception (Liberman and Mattingly, 1985). This was in fact not the only motor theory on speech perception, but perhaps that one that finally became most prominent. However, Liberman's theory and its possible connection to the mirror neuron system is still questionable (Lotto et al., 2009). The controversial character of this issue is further highlighted by a recent discussion between Hickok and Wilson (see (Hickok, 2009; Wilson, 2009)). They discuss two different models, where (i) premotor areas are either involved in speech perception, but perhaps not necessary for understanding speech, or (ii) speech perception is crucially dependent on premotor areas. These two different perspectives are further visible in recent network models on speech perception, where motor areas are either connected unidirectionally from the temporal lobe (Hickok and Poeppel, 2007, 2004; Kotz and Schwartze, 2010) or further connected to frontal areas (Rauschecker and Scott, 2009).

In this context, the observed activation in the premotor area in the earlier described sound-morphing study by Osnes (Osnes et al., 2011b; Specht et al., 2009b) gives new experimental evidence to the original view of Liberman. Premotor cortex involvement was only seen as an intermediate step of the morphing sequence and the activation of left mid-STS stopped increasing after this condition (Osnes et al., 2011b). Accordingly, an independent behavioural study confirmed that participants started to perceive the distorted sounds as speech from the fifth manipulation step (Osnes et al., 2011b). This was further tested with a dynamic causal modelling approach (Osnes et al., 2011b). Although the results could not answer whether premotor areas are an important contributor in the perception process, the dynamic causal modelling results clearly indicated that premotor areas were only connected to the ventral stream when phonological information had to be processed, but it was disconnected from the ventral stream during the processing of non-verbal information approach (Osnes et al., 2011b). Therefore, the additional involvement of premotor areas at the breaking point between perceiving a sound as noise or speech may

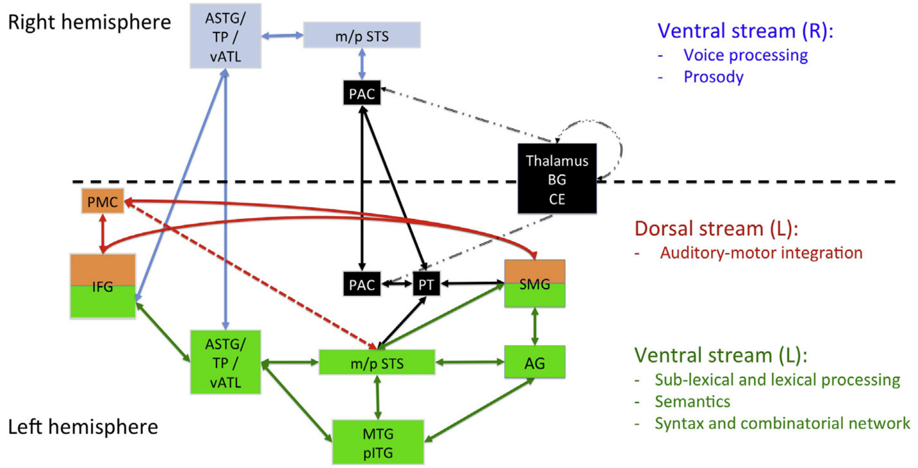

Fig. 2. Schematic representation of an extended dual-stream model for speech comprehension that reflects subcortical contributions of the thalamus, basal ganglia (BG) and cerebellum (CE) (see, for example, Kotz and Schwartze (2010) for more details), as well as extend the cortical model through the inclusion of the supramarginal gyrus (SMG) and angular gyrus, and propose two distinct ventral streams. Note: anatomical abbreviations are listed in Fig. 1.

indicate a functional interaction between the dorsal stream and the ventral stream, which may support Liberman's motor theory of speech perception (Liberman and Mattingly, 1985; Liberman and Whalen, 2000). Note that also Liberman used synthetic speech for his experiments. In fact, premotor activity was also seen in other studies. The afore mentioned study by Rimol et al. (2005) reports the results of an fMRI study on sub-syllabic speech processing. Although not further discussed in his article, premotor activity was seen in both the perception of consonants, as well as consonant–vowel syllables, but not during matched noise. Beyond the phonemic level, the processing of noise-vocoded words activates not only the motor cortex, but also left anterior insula and prefrontal cortex, when subjects were trained in the comprehension of noise-vocoded words (Hervais-Adelman et al., 2012). Interestingly, the anterior insular cortex has also been associated with the control of the vocal tract (Ackermann and Riecker, 2004; Borovsky et al., 2007; Dronkers, 1996). Further, differential activations within the left and right anterior insular cortex have been observed in preschool children at risk for dyslexia (Specht et al., 2009a), confirming, again, a close link between disturbed phonological processing and development of dyslexia.

However, a different view on the connection between the dorsal and the ventral stream that may result in premotor activation comes from studies where the expectancy and the prior knowledge of the participants are manipulated (e.g., Dufor et al., 2007; Osnes et al., 2012). In general, subjects' expectancy has been shown to be an important modulating factor. Thus, many of the here reported studies were performed as passive listening studies, where subjects were performing an arbitrary and irrelevant task (see, e.g., Osnes et al., 2011a; Specht et al., 2009b; Specht and Reul, 2003). This may also explain why the often observed frontal activations during the perception of distorted speech do not occur in passive listening studies (Davis and Johnsrude, 2007). Dufor and colleagues demonstrated in their study on sine-wave speech that the network, processing these stimuli, can be completely altered, depending on the expectancy and the prior knowledge of the participants (Dufor et al., 2007). Only when participants expected to perceive these sounds as speech sounds, did the typical, mainly left lateralised inferior frontal and temporal network emerge. Moreover, premotor areas also became involved during this processing. Interestingly, dyslexic subjects were not able to activate this network to the same degree. Osnes recently replicated this expectancy effect by using sounds that only partially included phonetic information of vowels (Osnes et al., 2012). The functional relevance of the additional involvement of premotor and inferior frontal areas during attentive listening is still under debate. However, there is emerging evidence that this reflects a functional connectivity between the dorsal and ventral stream rather than parallel processing of the acoustic input. Davis and Johnsrude suggest this interaction between speech perception and speech production networks ensure that speech is perceived categorically (Davis and Johnsrude, 2007). Generally, categorical perception is an important aspect in speech perception, as it ensures that speech related acoustic signals are not perceived as an acoustic continuum but rather as clearly separable phonetic information (Davis and Johnsrude, 2007; Liebenthal, 2005). In this respect, the observed premotor involvement in the study by Osnes et al. (2011b) may indicate such a categorical perception, facilitating the perception of a distorted sound as speech sound.

By contrast, Hickok (2012) suggests that the dorsal stream does not provide such a forward prediction that could facilitate recognition of speech, rather that the dorsal stream provides a forward connection as motor control function. Evidence for this view comes in particular from lesion studies, demonstrating that damage to the motor system does not disturbed speech perception, while TMS studies, on the other hand, demonstrate at least a weak influence (Hickok, 2012). Interestingly, a recent, yet unpublished study in persons who stutter, demonstrated an increased activation of the dorsal stream in a pure perception task, namely the afore mentioned sound morphing task, where white noise gradually morphed into a CV-syllable (Martinsen et al., unpublished). This result may indeed reflect a disturbed forward prediction of motor control function rather than a disturbed speech recognition process in persons who stutter.

A different explanation of motor responses in speech perception tasks has been provided by Venezia and co-workers. They relate the motor response during a syllable discrimination to a response-bias (Venezia et al., 2012). In their study, they manipulated the bias by changing the ratio of targets in a discrimination task, where participants were asked to make a same-difference discrimination on consonant-vowel syllables that were masked with Gaussian noise. They found a modulation of motor activity without modulating speech discrimination abilities.

In summary, the ongoing controversial discussion on motor involvement in speech perception remains unsolved. Several studies, using both neuroimaging as well as TMS, indicate either a motor involvement during speech perception or do not indicate a direct involvement of motor related areas. Clearly, motor studies are needed to bring these two opposing views together into an overall framework, and first attempts are already made, as outlined above. Further, longitudinal studies in subjects with developmental speech disorders may help in this respect as specific disturbances within the dorsal stream during the development of speech and language competences may help understanding the specific functions of motor related areas also in perceptual processes.

4. Discussion

This review reports the mechanisms of speech comprehension from a neuroanatomical perspective. Although there is emerging evidence for the dual-stream model for speech perception and comprehension, there are still several uncertainties that have to be investigated further. The model should probably be expanded in the future. There are a couple of brain areas that are not included in the dual-stream model. These are areas that are repeatedly detected in neuroimaging studies of speech comprehension, although they are not specifically language related areas. In particular, these are the angular gyrus, supramarginal gyrus, but also subcortical areas, like the basal ganglia, anterior insula, and cerebellum. They clearly contribute to the perception of speech and to the processing of speech content. However, these areas are also involved in several other non-linguistic functions. Thus, an inclusion into a language model is questionable but plausible. In this respect, the supramarginal gyrus may be at the intersection of dorsal and ventral stream, since it demonstrates a categorical perception of phonological information and is related to phonological working memory (Obleser and Eisner, 2009; Turkeltaub and Coslett, 2010). These are functions relevant for both the ventral and dorsal stream. The angular gyrus, however, has been repeatedly reported in various semantic operations (Binder and Desai, 2011; Seghier, 2013) and may be part of the proposed ventral stream (see Fig. 2).

The current dual-stream model proposes a bilateral ventral stream and a left-lateralised dorsal stream. Neuroimaging studies clearly support this view. In fact, it appears that there is a kind of lateralisation gradient within the ventral stream with an increasing leftward asymmetry as the linguistic functions become more abstract and, perhaps, also more modality independent (Peelle, 2012; Specht, 2013). Thus, the left lateralisation increases from the posterior superior temporal area towards the ventral anterior temporal lobe. The current dual-stream model, however, does not clearly differentiate between the ventral stream of the left and right hemispheres. The neuroimaging studies reviewed in this article indicate that the left ventral stream is particularly involved in phonetic discrimination, phonological processing, as well as lexical, semantic, and combinatorial processes. The right ventral stream, however, is more involved in voice identification and processing of prosody. Therefore, one probably has to divide the ventral stream into a left and right ventral stream, thus extending the dual-stream model into something like a “triple-stream” model. Obviously, future research has to explore this in more detail.

One important question in this respect is the inter-hemispheric communication, which is a pre-requisite for a bi-hemispheric processing, especially when addressing where the processed information converges into a common percept. As discussed in relation with the dichotic listening task, the corpus callosum is an important factor and inter-individual variations in corpus-callosum size correlate with the strength of the REA. Thus, future studies on speech perception and functional asymmetry have to take into account the individual structural variability, not only within the corpus callosum, but also individual variability in other language related structures like the depth of the STS and the configuration of the different segments of the arcuate fasciculus. In particular the arcuate fasciculus has already been identified to correlate with behavioural measures while behavioural consequences of inter-individual variability of STS depth has not been explored in detail yet.

Another inter-individual source of variability are concentrations of neurotransmitter. It has been shown that both, the concentration of glutamate (Falkenberg et al., 2012) as well as gamma-Aminobutyric acid (GABA) (Muthukumaraswamy et al., 2012) may influence the fMRI signal. Thus, pure neuroimaging approaches, focussing only on fMRI results and neglecting structural as well as metabolic inter-individual variability may overlook important sources of information that could help disentangling the network for speech comprehension. Although this review broadly excluded the electrophysiological literature, it has to be mentioned that they are an important contributor to our current understanding of speech perception processes.

In conclusion, functional neuroimaging studies broadly and convincingly support the dual-stream model by reliably mapping the ventral stream for speech perception and speech comprehension, and the dorsal-stream – although not covered by this review – for speech production. However, as any model is the dual-stream model an abstraction of the true language network and future work may focus more on the functional and structural left-right asymmetry within the temporal lobe by taking into account the inter-individual functional and structural variability.

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