

Published in final edited form as:

Brain Lang. 2013 November ; 127(2): 181–191.

Wernicke's Area Revisited: Parallel Streams and Word Processing

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Abstract

Auditory word-form recognition was originally proposed by Wernicke to occur within left superior temporal gyrus (STG), later further specified to be in posterior STG. To account for clinical observations (specifically paraphasia), Wernicke proposed his sensory speech center was also essential for correcting output from frontal speech-motor regions. Recent work, in contrast, has established a role for anterior STG, part of the auditory ventral stream, in the recognition of species-specific vocalizations in nonhuman primates and word-form recognition in humans. Recent work also suggests monitoring self-produced speech and motor control are associated with posterior STG, part of the auditory dorsal stream. Working without quantitative methods or evidence of sensory cortex' hierarchical organization, Wernicke co-localized functions that today appear dissociable. "Wernicke's area" thus may be better construed as two cortical modules, an auditory word-form area (AWFA) in the auditory ventral stream and an "inner speech area" in the auditory dorsal stream.

Keywords

Dual-stream model; word recognition; language comprehension; pure word deafness; Wernicke's aphasia

1. Introduction

The Dual Stream model of auditory cortex, first proposed on the basis of neurophysiological studies in the macaque monkey (Rauschecker, 1997; Rauschecker, 1998b; Romanski *et al.*, 1999; Tian *et al.*, 2001), has had a profound influence on current understanding of language organization in human cortex (Binder *et al.*, 2000; Hickok & Poeppel, 2000; Scott *et al.*, 2000). The similarity between single-cell mechanisms of communication-call processing in

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monkeys and phoneme identification in humans is immediately apparent and has led to a hierarchical model of speech processing in the auditory ventral stream that is now almost universally accepted (Hickok & Poeppel, 2007; DeWitt & Rauschecker, 2012). Adoption of the model, however, was not without controversy. Classical neurology identified posterior superior temporal cortex (ST) as the site of word recognition (Penfield & Roberts, 1959; Geschwind, 1970), but results from monkeys showed anterior, not posterior, ST to be most selective for communication calls (Tian *et al.*, 2001). Posterior ST, on the other hand, was found to be selective for sound location in monkeys (Rauschecker & Tian, 2000; Recanzone, 2000; Tian *et al.*, 2001). This paradox was noted in an early paper on dual-stream concepts in audition and language:

Speech perception in humans is traditionally associated with the posterior portion of the [superior temporal] region, often referred to as “Wernicke’s area.” In rhesus monkeys...neurons in this region...are highly selective for the spatial location of sounds...Neurons in the anterior belt regions, on the other hand, are most selective for [monkey calls] (Rauschecker & Tian, 2000, pp. 11804–11805).

Initially, one could have taken this apparent dissociation between human and monkey cortex as grounds for dismissing the applicability of the monkey model to human speech processing (*i.e.*, divergent evolution). However, the selectivity observed in macaque posterior ST for the location of sound sources was subsequently also observed in humans by numerous studies using functional magnetic resonance imaging (fMRI), as well as electro- and magneto-encephalography (Arnott *et al.*, 2004; Krumbholz *et al.*, 2005; Tata & Ward, 2005; Zimmer & Macaluso, 2005; Ahveninen *et al.*, 2006; Deouell *et al.*, 2007). This generally substantiated comparisons between human and monkey auditory cortex, affirming the role implied by the monkey data for human anterior ST in word recognition. Still, apparent conflict between classical neurological models and the monkey work led to a spectrum of conclusions about the relative involvement of anterior and posterior ST in word recognition (Binder *et al.*, 2000; Hickok & Poeppel, 2000; Scott *et al.*, 2000; Wise *et al.*, 2001; Price *et al.*, 2003; Thierry, Giraud & Price, 2003). This enigma has been partially resolved by the meta-analysis of DeWitt & Rauschecker (2012), which, based on a large amount of data, clearly associates word-form recognition with anterior ST. What, if anything, the dorsal stream contributes to language comprehension is now emerging as a key question. Increasingly, the computational role of posterior ST in language is understood to pertain to its role in sensorimotor integration and control (Hickok & Poeppel, 2007; Rauschecker & Scott, 2009). Recent proposals further emphasize a role for the dorsal stream in sequence processing and syntax, particularly with respect to the computation of sentence-internal relations for syntactically complex sentences (Rauschecker, 2011; Friederici, 2012; Bornkessel-Schlesewsky & Schlewsky, 2013).

Here, we present an analysis of speech processing within the dual-stream architecture of auditory cortex with the aim of clarifying the neural substrates of auditory word-form recognition. The present work builds on a previous study from our lab (DeWitt & Rauschecker, 2012). We extend that work by formal dissection of the roles proposed for Wernicke’s area and by extensive critical review of results from clinical neuroscience. First, we consider word-form recognition within the auditory ventral stream (see 2. Word-form

recognition and the auditory ventral stream). Emphasis is given to outstanding questions, particularly with respect to the relationship between findings from functional imaging (DeWitt & Rauschecker, 2012) and contemporary quantitative findings from aphasiology and neurosurgery (see 3. Causal involvement of anterior STG in word recognition). Next, we perform a historical review of Wernicke's (1874) characterization of his sensory speech center, which helps to clarify what functions should be accounted for in the localization of Wernicke's area and evaluation of the Wernicke's area construct (see 4. A brief history of Wernicke's area). The review also highlights some early misconceptions and oversimplifications about auditory processing that, while reasonable for the time, continue to color contemporary conceptions of Wernicke's area and speech processing. Lastly, we discuss how the disparate functions Wernicke assigned to his sensory speech center, namely word-form recognition, supervision of speech production and inner speech, segregate and embed within the dual-stream model (see 5. Paraphasia, inner speech and the auditory dorsal stream). Consistent with nonhuman primate electrophysiology and neuroanatomy, we conclude that word-form recognition, the principal attribute of Wernicke's area, should be assigned to the auditory ventral stream, whereas the regulation of speech production and inner speech are associated with the auditory dorsal stream.

2. Word-form recognition and the auditory ventral stream

Concurrent with early functional imaging, work in nonhuman primate electrophysiology made breakthroughs into the functional organization of nonprimary auditory cortex, identifying two main processing pathways: a dorsal stream optimized for sensorimotor integration, including spatial processing, and a ventral stream, optimized for object (or pattern) recognition (see Fig. 1) (Rauschecker, Tian & Hauser, 1995; Rauschecker, 1997; Rauschecker, 1998a, 1998b; Kaas & Hackett, 1999; Romanski *et al.*, 1999; Kaas & Hackett, 2000; Rauschecker & Tian, 2000; Tian *et al.*, 2001; Rauschecker & Scott, 2009). This dual-stream organization resembles the functional organization of visual cortex (Ungerleider & Mishkin, 1982; Goodale & Milner, 1992; Van Essen & Gallant, 1994) and suggests greater homologies between the sensory systems than could previously be assumed.

Current perspectives on speech processing have incorporated the dual-stream architecture of auditory cortex derived from nonhuman primate work (Binder *et al.*, 2000; Wise *et al.*, 2001; Scott & Wise, 2004; Hickok & Poeppel, 2007), making it the consensus view (but see Nelken *et al.*, 2003; Whalen *et al.*, 2006). The precise course of the auditory ventral stream, however, remained a question of debate: some authors included in it posterior STS (Wise *et al.*, 2001; Hickok & Poeppel, 2007), a site consistent with findings from classical neurology (Penfield & Roberts, 1959; Geschwind, 1970); others rejected posterior STS, concluding word-form recognition occurs in anterior STG (Mesulam, 1998; Binder *et al.*, 2000; Scott & Wise, 2004). While posterior STS happens to be ventral to the Sylvian fissure, the ventral and dorsal streams are defined by cortico-cortical connections originating in the lateral belt areas of auditory cortex and by histoarchitectonic criteria (Kaas & Hackett, 2000; Rauschecker & Tian, 2000). These criteria characterize the posterior ST region in humans as part of the dorsal stream and anterior STG as part of the ventral stream (see Fig. 2A,B).

In a recent paper, we leveraged the observation of large-scale similarity in the auditory and visual systems' functional architectures to address the problem of localizing auditory word-form recognition within the ventral stream (DeWitt & Rauschecker, 2012). We reviewed and synthesized literature bearing on the hypothesis that auditory and visual word recognition are equivalent problems with similar cortical solutions. This led us to hypothesize, as have others (Mesulam, 1998; Cohen *et al.*, 2004), that a cortical region supporting sensory aspects of auditory word recognition (*i.e.*, an AWFA) should exist with properties comparable to those identified for the VWFA (Dehaene *et al.*, 2005) and, more generally, for pattern recognition in the visual ventral stream (Wallis & Rolls, 1997; Riesenhuber & Poggio, 2002; DiCarlo, Zoccolan & Rust, 2012). Specifically, this AWFA should demonstrate selectivity for auditory words (*i.e.*, it should respond more to auditory words than to other sounds). Further, it should demonstrate invariance to certain acoustical changes (*i.e.*, its response should be more sensitive to acoustical differences that affect the phonetic content of utterances than to acoustical differences which do not).

In our analyses, we assessed selectivity with respect to either acoustically matched artificial stimuli or non-speech natural stimuli. Invariance was assessed with respect to adaptation phenomena (Miller, Li & Desimone, 1991), which can be used to probe tolerance for non-category-transformative physical stimulus deformations and sensitivity to category-transformative deformations (Grill-Spector & Malach, 2001). Further, the hierarchical organization of auditory cortex implies increasing representational complexity along the auditory ventral stream (Rauschecker *et al.*, 1995; Binder *et al.*, 2000; Kaas & Hackett, 2000; Rauschecker & Tian, 2000; Rauschecker & Scott, 2009; Chevillet, Riesenhuber & Rauschecker, 2011) similar to that found along the visual cortical hierarchy (Hubel & Wiesel, 1962; Riesenhuber & Poggio, 2002). Therefore, where possible, we assessed processing for phoneme, word, and phrase stimuli separately. As phoneme recognition is a prerequisite of word recognition, we hypothesized peak phoneme processing to localize to an area proximate to primary auditory cortex, relative to the site of peak processing for words. Phrase processing, in contrast, includes phoneme and word recognition, but it also strongly engages semantic and syntactic processing. Accordingly, we hypothesized phrase processing to engage the sites associated with phoneme and word recognition as well as higher-order regions of ST. Separate consideration of phoneme, word and phrase processing, therefore, made the assessment of effects pertaining to word recognition both more precise and more tractable.

To quantitatively assess our predictions, we focused on results from functional brain imaging. To systematically evaluate prior results, we used an anatomically unbiased coordinate-based meta-analytic approach (Turkeltaub *et al.*, 2002). The method found functional imaging results of auditory word recognition to be consistent with principles of hierarchical processing (see Fig. 3) (DeWitt & Rauschecker, 2012). Results supported a left-biased, three-stage model, with analysis of phonemes occurring in mid-STG, lateral to Heschl's gyrus, word recognition occurring in anterior STG, and phrase processing beginning in anterior STS (*c.f.*, Miglioretti & Boatman, 2003). This diverged from the classical model of language organization (Penfield & Roberts, 1959; Geschwind, 1970) and

some contemporary perspectives (Wise *et al.*, 2001; Hickok & Poeppel, 2007), which locate word recognition in posterior ST.

Prior to the advent of contemporary imaging methods, inference that posterior ST was the site of auditory word recognition was warranted by available evidence and methodology. Lesions resulting in auditory comprehension deficits (as well as poor verbal repetition and paraphasia—inaccurate word selection during speech; *i.e.*, Wernicke's aphasia) show greatest overlap in posterior STG (Robson, Sage & Lambon-Ralph, 2012). Simple lesion-overlap (density) mapping, however, is spatially biased, owing to arterial anatomy. For instance, the middle cerebral artery bifurcates and narrows as it progresses along the Sylvian fissure, likely increasing the probability of posterior infarcts. Thus, while the center of mass of most lesions that produce auditory comprehension deficits may be in posterior STG, this could be an epiphenomenon and comprehension deficits might be better explained by the anterior extent of these lesions (*c.f.*, Dronkers *et al.*, 2004). Contemporary methods mitigate spatial bias through the inclusion of control samples (Bates *et al.*, 2003; Rorden & Karnath, 2004). These methods utilize variance in symptom severity to factor out lesion sites that are shared across afflicted individuals but which do not contribute to task-specific impairments (for additional discussion, see 3. Causal involvement of anterior STG in word recognition).

In the first decade and a half of functional imaging, as the field and its methodology matured, reservation in interpretation and deference to well-established theories was prudent. Increasingly, however, functional imaging indicated that revisions to the classical model were required (Mazziotta *et al.*, 1982; Petersen *et al.*, 1988; Wise *et al.*, 1991; Démonet *et al.*, 1992; Binder *et al.*, 1994; Binder *et al.*, 1996; Binder *et al.*, 1997; Mummery *et al.*, 1999; Belin *et al.*, 2000; Binder *et al.*, 2000; Scott *et al.*, 2000; Wise *et al.*, 2001; Belin, Zatorre & Ahad, 2002). As discussed, results from nonhuman primates were prompting revisions in understanding of the functional and anatomical organization of auditory cortex (Kaas & Hackett, 2000; Rauschecker & Tian, 2000; Tian *et al.*, 2001). These results provided a framework for amendment of models of speech processing (Mesulam, 1998; Binder *et al.*, 2000; Hickok & Poeppel, 2000; Wise *et al.*, 2001; Boatman, 2004; Hickok & Poeppel, 2004; Scott & Wise, 2004; Scott, 2005; Hickok & Poeppel, 2007). While the revised models of speech processing generally adopted a dual-stream framework, discrepancy persisted about the site of word-form recognition within the auditory ventral stream. Some authors maintained a site close to canonical Wernicke's area (Hickok & Poeppel, 2000; Wise *et al.*, 2001; Hickok & Poeppel, 2007). Others adopted an anterior STG localization (Binder *et al.*, 2000; Scott & Johnsrude, 2003; Wise, 2003; Scott & Wise, 2004). Although evidence accumulated on the side of anterior localization, skepticism remained (Hickok, 2010). Our meta-analysis systematically and quantitatively weighed two-decades of published findings with bearing on the site of auditory word-form recognition and concluded the preponderance of evidence supports anterior STG localization.

In the same time period, work on the visual system's analogous problem, visual word-form recognition, progressed more effectively. There, an area within the visual ventral stream, the eponymously named visual word-form area (VWFA), has come to be widely regarded and intensively studied as the crucial site for visual word-form recognition (Cohen *et al.*, 2000; McCandliss, Cohen & Dehaene, 2003; Dehaene *et al.*, 2005). Although interpretational

questions remain (Baker *et al.*, 2007; Dehaene & Cohen, 2011; Price & Devlin, 2011), localization of the VWFA within ventral occipitotemporal cortex (VOT) is now largely uncontroversial. Identification of this VOT site, analogous to macaque infero-temporal cortex, permitted detailed, mechanistic investigations to proceed, producing a prolific literature (Cohen *et al.*, 2004; Binder *et al.*, 2006; Gaillard *et al.*, 2006; Baker *et al.*, 2007; Vinckier *et al.*, 2007; Turkeltaub *et al.*, 2008; Glezer, Jiang & Riesenhuber, 2009; Dehaene *et al.*, 2010; Braet, Wagemans & Op de Beeck, 2012; Rauschecker *et al.*, 2012; Wandell, Rauschecker & Yeatman, 2012). Resolving debate about the AWFA's location within ST may similarly position the field to make advances in unlocking the nature of representation within the auditory ventral stream.

3. Causal involvement of anterior STG in word recognition

Although an unprecedented amount of evidence is now amassed indicating the involvement of anterior STG in word recognition, there remains a paucity of direct evidence from neurological and neurosurgical studies to conclude that anterior STG's involvement is causal. Some reports provide compelling evidence in support of causality (Malow *et al.*, 1996; Hamberger *et al.*, 2001; Hamberger *et al.*, 2003; Miglioretti & Boatman, 2003; Dronkers *et al.*, 2004; Hamberger *et al.*, 2005; Boatman, 2006; Hamberger *et al.*, 2007; Matsumoto *et al.*, 2011; Rogalski *et al.*, 2011; Kümmerer *et al.*, 2013). A direct relationship, however, has yet to be demonstrated between the anatomical location of auditory word-form recognition (indicated by single-subject brain imaging) and behavioral impairment resulting from surgical procedures, such as reversible electrical interference or clinical resection, as has been shown for the VWFA (Gaillard *et al.*, 2006) and the fusiform face area (Parvizi *et al.*, 2012).

The relative scarcity of causal evidence for anterior STG involvement in word recognition is partly attributable to the typical reliance of intraoperative language mapping on outcome measures that assess non-auditory processing, namely single word reading, visual object naming and speech arrest (Hamberger *et al.*, 2007; Sanai, Mirzadeh & Berger, 2008). Those studies that assessed auditory processing typically investigated acoustic-phonetic feature detection (Boatman, Lesser & Gordon, 1995; Boatman *et al.*, 1997; Miglioretti & Boatman, 2003; Boatman, 2006) or sentence comprehension (Malow *et al.*, 1996; Hamberger *et al.*, 2001; Hamberger *et al.*, 2003; Miglioretti & Boatman, 2003; Hamberger *et al.*, 2005; Hamberger *et al.*, 2007; Matsumoto *et al.*, 2011). Though important levels of inquiry, neither level specifically assesses word-form recognition. The former assesses the stage prior to word-form recognition (*i.e.*, phoneme recognition) while the latter assesses phrase comprehension, which includes semantic and syntactic processing. More refined methods (Miglioretti & Boatman, 2003; Hickok *et al.*, 2008; Goll *et al.*, 2010; Rogalski *et al.*, 2011; Bormann & Weiller, 2012; Thothathiri, Kimberg & Schwartz, 2012) will be required in future investigations for the specific evaluation of auditory word-form recognition. It should be noted, however, that resection of sites implicated in auditory sentence comprehension by electrical interference does increase the incidence of post-operative impairment in auditory comprehension (Hamberger *et al.*, 2005). Although the sites resected in that study were not reported in detail, similar studies report a greater likelihood of impairment on auditory

sentence comprehension from stimulation of anterior ST (Hamberger *et al.*, 2001; Hamberger *et al.*, 2003; Miglioretti & Boatman, 2003; Hamberger *et al.*, 2007).

Anterior temporal lobectomies are relatively common. Rarely, however, do studies report postoperative language decline. This might be attributable to three factors. First and foremost, the candidate AWFA extends from 45 mm distal of the temporal pole to 70 mm distal (DeWitt & Rauschecker, 2012). Standard resections typically remove 35–55 mm of the anterior temporal lobe, with the majority of resections removing 45 mm or less, sparing much of the area in question (Hermann, Wyler & Somes, 1991; Schwartz *et al.*, 1998; Seidenberg *et al.*, 1998; Patariaia *et al.*, 2005; Alpherts *et al.*, 2008; Helmstaedter *et al.*, 2008; Kho *et al.*, 2008; Bidet-Caulet *et al.*, 2009; Binder *et al.*, 2011). Further, resections are sometimes performed differentially, sparing a greater portion of STG relative to the middle and inferior temporal gyri, also decreasing the likelihood of resections including the candidate AWFA (Schwartz *et al.*, 1998; Patariaia *et al.*, 2005; Alpherts *et al.*, 2008; Bidet-Caulet *et al.*, 2009; Binder *et al.*, 2011). Second, intraoperative language mapping may indicate language function and, thereby, spare the candidate AWFA from resection. Third, there is a dearth of reported outcomes at short-term follow-up ($t < 6$ weeks). Researchers tend instead to report outcomes for longer recovery durations ($t > 6$ months) (Hermann *et al.*, 1991; Schwartz *et al.*, 1998; Davies, Risse & Gates, 2005; Patariaia *et al.*, 2005; Bidet-Caulet *et al.*, 2009). Given the relative competency of the non-dominant hemisphere during the incapacitation of the dominant hemisphere (Hickok *et al.*, 2008), compensatory plasticity in the contralateral hemisphere could account for a low incidence of postoperative impairment at long-term follow-up, even when resections include the candidate AWFA. Interestingly, classical models have a similar evidentiary problem. There is a dearth of evidence associating posterior ST resection with auditory comprehension deficits. Indeed, when studies report posterior ST resection, they often argue they observe an absence of language decline (Petrovich *et al.*, 2004; Sarubbo *et al.*, 2012).

Analogous to the temporal lobectomy literature, studies of aphasia lesion mapping have not traditionally emphasized the role of anterior ST in auditory word comprehension. Simple density mapping of Wernicke's aphasia lesions finds the center of mass of lesions to be in posterior ST, but the lesions commonly extend into anterior STG (Ogar *et al.*, 2011; Robson *et al.*, 2012). Similarly, lesion mapping that utilizes both control samples and continuous symptom severity data implicates both anterior and posterior ST in auditory sentence comprehension (Saygin *et al.*, 2003; Dronkers *et al.*, 2004). Further, with respect to comprehension deficits, this work expressly dissociates posterior STG from surrounding regions: lesions of posterior STG were not found to affect comprehension. Importantly, work specifically investigating auditory word recognition (as opposed to sentential comprehension) exclusively implicates anterior ST (Rogalski *et al.*, 2011). In patients for whom auditory word recognition is spared, deficits in auditory sentence comprehension, which can therefore be attributed to deficits in syntactic processing, are associated with lesions of posterior ST and inferior parietal lobule (IPL) (Thothathiri *et al.*, 2012). This result is consistent with the view that anterior ST must be spared for auditory word recognition to be intact. When either single-word auditory comprehension is factored out (Fridriksson *et al.*, 2010) or general auditory comprehension is spared (Buchsbaum,

Padmanabhan & Berman, 2011b), word repetition deficits are associated with lesions of posterior ST and IPL. Again, this is consistent with the view that sensory aphasias that spare auditory word recognition should spare anterior ST. These results also dissociate posterior ST lesions with auditory word recognition deficits. Finally, when considering subcortical lesions, the integrity of tracts associated with the auditory ventral stream is closely associated with auditory comprehension, whereas the integrity of tracts associated with the dorsal stream is associated with vocal repetition (Kümmerer *et al.*, 2013).

While there is a sizable literature associated with pure word deafness (see 7. Appendix A), it is nonetheless a rare condition (Buchman *et al.*, 1986; Poeppel, 2001). Consequently, there are no group-level lesion-mapping studies of the disorder (*i.e.*, only case studies). Well-documented cases of patients with circumscribed cortical lesions are similarly rare. Recent literature, utilizing modern brain imaging, provides two general impressions (Praagstra *et al.*, 1991; Engelien *et al.*, 1995; Clarke *et al.*, 2000; Fung, Sue & Somerville, 2000; Wang *et al.*, 2000; Kaga *et al.*, 2004; Stefanatos, Gershkoff & Madigan, 2005; Iizuka *et al.*, 2007; Miceli *et al.*, 2008; Kim *et al.*, 2011; Slevc *et al.*, 2011; Palma *et al.*, 2012; Suh *et al.*, 2012). First, while bilateral ST lesions are common (Geschwind, 1965; Buchman *et al.*, 1986; Poeppel, 2001), left hemisphere lesions can be sufficient (Stefanatos *et al.*, 2005; Slevc *et al.*, 2011; Palma *et al.*, 2012). Second, while some cases involve lesions of mid- to posterior ST (Kim *et al.*, 2011; Slevc *et al.*, 2011) and others involve mid- to anterior ST (Engelien *et al.*, 1995; Stefanatos *et al.*, 2005; Iizuka *et al.*, 2007; Palma *et al.*, 2012), the commonly affected region appears to be mid STG, lateral to Heschl's gyrus—the putative site of phoneme recognition (Boatman *et al.*, 1995; Boatman *et al.*, 1997; Miglioretti & Boatman, 2003; Liebenthal *et al.*, 2005; Boatman, 2006; Liebenthal *et al.*, 2010; DeWitt & Rauschecker, 2012). In sum, clinical results are highly suggestive of a causal role for mid- to anterior STG in word recognition. What remains to be demonstrated, however, is direct correspondence between results from fMRI and behavioral impairment following lesion or functional inactivation.

4. A brief history of Wernicke's area

In the 1860s, Paul Broca established the presence of a motor speech center in the left inferior frontal gyrus (IFG) (for review, see Dronkers *et al.*, 2007). Reflecting on Broca's observations, Carl Wernicke (1874) postulated a complementary sensory speech center, for the storage and collection of auditory images (representations) of speech sounds—referred to today as Wernicke's area. Initially, Wernicke recognized STG *in toto* as the site of auditory imagery and did not attempt to specifically localize auditory word representations within STG. Rather, he noted only that a circumscribed region ought to exist somewhere within STG (see Fig. 2C), analogous to the circumscribed speech-motor region within IFG:

The first temporal gyrus [STG], which is sensory in nature, may be regarded as the center of acoustic images...[It] may be regarded as the central terminal of the acoustic nerve, and the first frontal gyrus [IFG], including Broca's area, as the central terminal of the nerves controlling the speech musculature (Wernicke, 1874/1977, p. 103).

This view is clarified and reiterated in subsequent passages.

As details of the ascending auditory tracts and the hierarchical organization of auditory cortex were not yet known in 1874, Wernicke assumed direct innervation of the greater extent of STG by ascending fibers. His model, therefore, lacked an equivalent to primary auditory cortex and a theory of representational transformation along auditory cortex, resulting in large inaccuracies. Wernicke, for reasons supported by behavioral observations but anatomically flawed, nonetheless posited that only a portion of STG functions as a sensory speech center:

The area containing acoustic imagery...is not identical to the broad radiation of the acoustic nerve itself, since complete loss of acoustic imagery with intact bilateral hearing has been observed in aphasia...In spite of destruction of the central acoustic radiation, which carries the sounds of words, perception of noise and musical tone would still be intact (Wernicke, 1874/1977, p. 105).

Wernicke implies the functional consequence of incomplete deafferentation of STG is auditory agnosia. Within the context of sensory aphasia, according to Wernicke, the prominent feature is verbal auditory agnosia (word deafness). Wernicke describes similar consequences for cortical lesions:

When...the cortex of the first temporal convolution [STG] is destroyed, memory for the acoustic images designating...objects is erased, though memory for concepts may continue existing in full clarity. This is because the acoustic image of the name for the concept of an object is generally incidental to the concept, whereas palpable, tangible imagery is intrinsic (Wernicke, 1874, p. 22).¹

Wernicke is clearly dissociating word-form representation from semantic representation. He, therefore, principally characterizes his sensory speech center as an AWFA.

Wernicke subsequently ascribes a secondary function to the sensory speech center: a corrective role in the activation of motor representations during speech production:

Apart from lack of understanding, the patient [with sensory aphasia] has aphasic phenomena in speaking, owing to an absence of unconscious correction exerted by the speech sound image (Wernicke, 1874, p. 23).²

The “aphasic phenomena in speaking” to which Wernicke refers are paraphasias—Kussmaul (1877) had yet to coin the term—which commonly co-occur with auditory comprehension deficits. At the time, as is clear from later writings (Wernicke, 1886/1977), all the cases of sensory aphasia that Wernicke had seen to date included paraphasia. Thus, Wernicke’s ascription of a corrective role to his sensory speech center reflects both a clinically motivated desideratum and the assumption that only a single functional module is lesioned in Wernicke’s aphasia.

Later works include five main addenda (Wernicke, 1886/1977, 1906/1977). First, responding to Kussmaul (1877) and Lichtheim (1885), Wernicke discussed pure word deafness (see 7. Appendix A), which he referred to as subcortical sensory aphasia. He attributed pure word deafness to deafferentation of the sensory speech center. Second, he

¹Authors’ translation.

developed his notion of the corrective influence (during word selection) exerted by speech sound imagery on speech motor imagery. Over development, he argued, the repeated association of auditory and motor word representations conjoins them into “word-concept” representations (*c.f.* Lichtheim, 1885), which form the basis of inner speech (reviewed by Geva *et al.*, 2011). Wernicke believed the inner-speech faculty is spared in acquired pure word deafness, explaining the absence of paraphasia. Third, he expressly localized his sensory speech center to left STG, something only implied previously. He also, however, allowed that transient aphasia (recovery) might be explained by plasticity in right STG. Fourth, he circumscribed the portion of STG posited to contain his sensory speech center. Citing “numerous pathological findings at hand,” but without identifying them, he describes the center as being confined to the “posterior third of half of [sic]” STG (*p.* 235) and “an adjoining strip” of medial temporal gyrus (Wernicke, 1906/1977, *p.* 225). As Wernicke reproduced and endorsed the anatomical diagrams of Von Monakow and Déjérine in his section on neuroanatomy (*p.* 272), “numerous pathological findings” may have been an allusion to their work. Lastly, his views of the relevance of his sensory speech center to written comprehension, which were ambivalent in 1874, evolved (see 8. Appendix B). Wernicke’s ultimate position was that the sensory speech center was essential for orthography-to-phonology mapping (*i.e.*, phonological reading) and that this was attributable to the center’s role in inner speech.

In the century following Wernicke’s observations, Wernicke’s area was increasingly understood to be limited to the posterior third of STG with various formulations about which adjacent cortical regions should be included as well (for reviews, see Bogen & Bogen, 1976; Rauschecker & Scott, 2009). In the 1960s, Geschwind revived the Wernicke-Lichtheim model of aphasia (reviewed by Catani & Mesulam, 2008; Eling, 2011), presenting the most focal interpretation, including only the most posterior aspect of STG (see Fig. 2D).

5. Paraphasia, inner speech and the auditory dorsal stream

Where is Wernicke’s area? Answering this question today—with the benefit of far greater understanding of neuroanatomy and cortical processing than either Wernicke or Geschwind had access to—we might conclude that the functions Wernicke subsumes within a single area are actually performed by multiple cortical areas (*c.f.*, Goldstein, 1927, 1948; Mesulam, 1998; Wise *et al.*, 2001). The hypothesis most strongly supported by available empirical data for the location of Wernicke’s AWFA is anterior STG (DeWitt & Rauschecker, 2012). This region, however, is neither a strong candidate site for encoding representations that resemble Wernicke’s word-concepts (*i.e.*, inner speech) nor for performing the corrective function Wernicke ascribes to them.

Cortical monitoring of self-produced speech and the correction of speech motor programs is most parsimoniously viewed as a dorsal-stream function (Wise *et al.*, 2001; Hickok & Poeppel, 2007; Rauschecker & Scott, 2009). To coordinate speech production, motor control theory (Guenther, 1994; Rauschecker & Scott, 2009; Golfinopoulos, Tourville & Guenther, 2010; Rauschecker, 2011; Hickok, 2012) posits the mapping of auditory representations of self-produced speech sounds into the frame of reference of the speech articulators (Cohen & Andersen, 2002; Dhanjal *et al.*, 2008). Multimodal articulator-encoded speech

representations are then reconciled with expectations, derived from efference copy, of the intended consequences of the activated motor representation. Finally, the difference between expectation and feedback (error) is transmitted to frontal cortex and used in updating motor output. The temporo-parietal sites most strongly associated with auditory feedback and speech production are posterior PT, posterior STG, and SMG (Hamberger *et al.*, 2003; Towle *et al.*, 2008; Golfinopoulos *et al.*, 2010; Takaso *et al.*, 2010; Zheng, Munhall & Johnsrude, 2010; Golfinopoulos *et al.*, 2011), regions associated with the auditory dorsal stream.

Accordingly, paraphasia could result from dorsal-stream lesions that disrupt circuitry involved in rectifying unintended output, hypothetically, even prior to overt speech production (*c.f.*, Lichtheim, 1885). Consistent with this, lesion mapping associates paraphasia with posterior ST and IPL (Buchsbaum *et al.*, 2011a). Wernicke's theory of paraphasia is that word selection requires integrated auditory-motor representations (word-concepts), which develop through repeated association during speech production (*c.f.*, Pulvermüller, 1999; Garagnani, Wennekers & Pulvermüller, 2007). This is reminiscent of the articulator-encoded speech representations posited for the dorsal stream. Wernicke viewed word-concept representation as the basis for inner speech. Localizing inner speech on the basis of articulatory rehearsal in the phonological loop (Baddeley, 2003) indicates a posterior ST locus (Buchsbaum *et al.*, 2005). Similarly, localization based on covert rhyme and homophone judgment indicates an IPL locus (Geva *et al.*, 2011). Thus, the qualities Wernicke associated with paraphasia (*i.e.*, word-concepts and inner speech) suggest dorsal-stream localization. Further, phonological reading, which Wernicke also associates with his speech center *via* inner speech, also localizes to posterior ST and IPL (see 8. Appendix B).

In a dispute with Kussmaul over terminology for what is now called Wernicke's aphasia, Wernicke said:

“Word-deafness” describes only one part of that which we see as an indivisible, unitary picture: for in addition to their word-deafness, such patients are also always aphasic [paraphasic] (Wernicke & Friedlander, 1883/1977, p. 171).

Importantly, Wernicke is speaking of sensory aphasia resulting from a cortical lesion. When Wernicke later acknowledged pure word deafness (Wernicke, 1886/1977), he referred to it as subcortical sensory aphasia. Thus, Wernicke never entertained the possibility that there could be multiple speech centers within ST, each optimized for different functions—and furthermore that sensory aphasia (*i.e.*, Wernicke's aphasia) might result from extensive lesions, disrupting multiple cortical modules (see 8. Appendix B).

Freud (1891), citing a case in which a meningioma adjacent to STG caused pure word deafness, concluded the disorder was not due to subcortical lesion. This, he argued, could be reconciled with cases in which cortical lesions produced Wernicke's aphasia through the assumption that pure word deafness was attributable to “incomplete lesions” of Wernicke's area. Goldstein (1927, 1948) recognized a cortical locus for pure word deafness—though he acknowledged subcortical loci as well—and dissociated cortical regions specialized for auditory word-form representation and inner speech. From consideration of historical cases (Henschen, 1918; Poetzl, 1919), Goldstein (1948) attributed pure word deafness to lesions of

“the middle part of the left first temporal convolution [STG]...a region close to Heschl’s area” (p. 222). Localization of inner speech, he felt, could not yet be decided. Nonetheless, he speculated posterior STG and adjacent areas (*i.e.*, planum temporale, insula and IPL) were involved. While acknowledging Goldstein’s observations, Geschwind (1970) rejected Goldstein’s dissociation of auditory word-form recognition and inner speech. Instead, while Geschwind (1965) correctly maintained mid- (or anterior) STG was a “major outflow” of primary auditory cortex, he surmised that its lesion would merely disconnect posterior STG from primary auditory cortex, a view which lacks support from modern neuroanatomy and is impoverished with respect to representational transformation in cortical processing.

6. Conclusions

Wernicke originally proposed a site within left STG to subserve auditory word-form recognition. On the basis of post-mortem case studies, classical neurology came to understand the location of “Wernicke’s area” to be within posterior STG (and adjacent areas of cortex). Wernicke posited a secondary function for his sensory speech center, namely the maintenance of correct motor output. In contrast, work on speech processing in humans with functional neuroimaging (consistent with electrophysiological work on the processing of species-specific vocalizations in nonhuman primates), has increasingly come to implicate left anterior STG as the site of auditory word-form recognition. Although causal involvement in word-form recognition is yet to be specifically demonstrated for this site, quantitative neurological and neurosurgical investigations support such a role. Similarly, contemporary understanding of auditory cortex associates speech-motor control with posterior ST. Wernicke’s area, functionally defined, therefore appears to consist of two areas: an AWFA in anterior STG and an “inner-speech area” in posterior STG/IPL. This critical reappraisal of speech processing in auditory cortex and, specifically, of the Wernicke’s area construct suggests a new framework for the assessment and diagnosis of sensory aphasia, as well as new procedures for the intra-operative mapping of language function.

Acknowledgments

We thank Anna Seydell-Greenwald for assistance with historical research. This work was supported by an award from the William Orr Dingwall Foundation (to I.D.), National Science Foundation Grants BCS-0519127 and OISE-0730255 (to J.P.R.), National Institute on Deafness and Other Communication Disorders Grant 1RC1DC010720 (to J.P.R.) and National Institute on Neurological Disorders and Stroke Grant 2R56NS052494 (to J.P.R.).

Appendix A

Further historical notes on pure word deafness

If we are to believe Wernicke (Wernicke & Friedlander, 1883/1977), Kussmaul (1877) coined the term “word deafness” (“Worttaubheit”). He used it to describe selective deficits in auditory word comprehension, as distinct from (generalized) deafness. Contrary to common citation (*e.g.*, Auerbach *et al.*, 1982; Coslett, Brashear & Heilman, 1984), Kussmaul neither used the term “pure word deafness” (“reine Worttaubheit”) nor, as noted by Wernicke (Wernicke & Friedlander, 1883/1977), described a case that was

uncomplicated by other maladies (e.g., paraphasia). Kussmaul's usage, however, implied what came classically to be regarded as pure word deafness. For instance, he described "word deafness with paraphasia," which implies a dissociability of components. Wernicke (1886/1977) attributed the first case description of pure word deafness (though not referring to it as such) to Lichtheim (1885), whose writing appeared subsequent to Kussmaul's (1877) (for discussion, see Eling, 2011). Lichtheim variously described the condition as "isolated word deafness" and "outer commissural word deafness." "Pure word deafness" was in use by 1889 when Starr (1889) used it to describe auditory comprehension deficits unaccompanied by impairments in reading, writing and speaking, consistent with what was implied by Kussmaul's usage. Liepmann (1898)—who provided the first anatomical description of pure word deafness—is also sometimes cited as coining the term. The chronology and his exact terminology ("reine Sprachtaubheit"), however, are incorrect.

Initially, Wernicke (Wernicke & Friedlander, 1883/1977) disputed the existence of pure word deafness, arguing that word deafness (assuming a lesion of his sensory speech center) was always accompanied by paraphasia. Consequently, he conjectured lesions prior to his sensory speech center would cause "primary deafness with no trace of aphasia" (p. 104)—though other remarks suggest auditory agnosia would result from cortical deafferentation (see 4. *A brief history of Wernicke's area*) (Wernicke, 1874/1977). Subsequent to Lichtheim's case, Wernicke (1886/1977) claimed to have "never doubted the theoretical possibility" of pure word deafness (p. 185). Wernicke's later works (1886/1977, 1906/1977) also revised the theoretical consequence of lesions prior to his speech center. He now theorized such lesions could result in pure word deafness from selective destruction of ascending fibers, hypothetically affecting only those projections into left temporal cortex that carry the limited portion of the auditory spectrum over which speech sounds are conveyed. Owing to Wernicke's initial hesitation, Kussmaul (1877) and Lichtheim (1885) may be credited with conception of the disorder, if not the term itself.

Notably, "pure" has taken a different emphasis in contemporary usage (Buchman *et al.*, 1986; Polster & Rose, 1998; Poeppel, 2001; Pinard *et al.*, 2002). Today, pure is often regarded as expressly connoting the sparing of non-verbal sound comprehension, as opposed to connotation of a lack of additional aphasic complications. This is chiefly a matter of emphasis but it carries a subtle distinction. By either usage, patients with pure word deafness have auditory word comprehension deficits; they do not present with other language deficits (e.g., paraphasia or alexia); and, they have residual hearing. Modern usage further distinguishes between residual hearing that simply involves the ability to detect and discriminate sounds (auditory agnosia) and residual hearing in which non-verbal sound comprehension is spared (pure word deafness). Wernicke, Kussmaul and Lichtheim's consideration of residual sound processing did not overtly distinguish between low-level perception and the comprehension of spectro-temporally complex non-verbal sounds (e.g., environmental sounds or music). Indeed, Wernicke's theory of pure word deafness includes cortical deafness for the speech-related portion of the human frequency range. Therefore, while current usage is not starkly inconsistent with classical usage, its emphasis and entailments are a modern innovation. Under contemporary usage, cases of pure word

deafness are very rare (Buchman *et al.*, 1986; Polster & Rose, 1998). In the present analysis, we are concerned merely with the classical dissociation.

Appendix B

Written comprehension

Wernicke initially describes his sensory speech center to be non-essential for written comprehension in readers who have attained fluent whole-word reading:

The individual who has been exposed to minimal training in reading may comprehend the written word only after it has been heard. But the educated person...may be able to grasp general meaning after a glance at the page without awareness of the individual words...The first case presents symptoms of alexia apart from his aphasia. The second...reveals intact comprehension of all written material in striking contrast to his lack of comprehension of the spoken word (Wernicke, 1874/1977, pp. 108–109).

Although lacking precision and nuance, Wernicke is clearly differentiating phonological reading (*i.e.*, “sounding words out”) from whole-word reading. In the case of the former but not the latter, he posits the need for acoustic images to intermediate access to meaning.

Subsequent to Grashey (1885), Wernicke (1886/1977) substantially revised his views on written speech. He now stated that, without qualification, lesion of the sensory speech center causes both alexia and agraphia. Wernicke’s final work (1906/1977), however, amended his position again. He re-acknowledged whole-word reading, both for fluent readers of alphabetic orthographies as well as for readers of logographic orthographies. However, he regarded whole-word reading as sufficiently minor in contribution (relative to phonological reading) to be negligible and, therefore, dismissed it. Crucially, Wernicke viewed dependency of written comprehension and of writing upon his sensory speech center to be a function of inner speech and its role in phonological decoding (*i.e.*, orthography-to-phonology mapping).

Contemporary dual-stream theory of reading posits a role for posterior ST and IPL, part of the auditory dorsal stream, in phonological reading (Jobard, Crivello & Tzourio-Mazoyer, 2003). Consistent with developmental transition from predominant reliance on phonological reading to whole word reading, the engagement of IPL in reading diminishes with reading fluency (Turkeltaub *et al.*, 2003). Activation in the region also correlates with measures of phonemic awareness (Turkeltaub *et al.*, 2003), key to the acquisition of fluent reading (Shaywitz, 1998). Further, IPL lesions strongly affect phonological reading (Philipose *et al.*, 2007; Brambati *et al.*, 2009; Wilson *et al.*, 2009; Linkersdörfer *et al.*, 2012). Similarly, as literacy increases, posterior STS shows greater engagement during reading (Dehaene *et al.*, 2010). Its lesion is also associated with deficits in phonological reading (Silani *et al.*, 2005; Brambati *et al.*, 2009).

With respect to aphasia, deficits in reading comprehension are often associated with Wernicke’s aphasia (Geschwind, 1970). We, however, are unaware of any empirical work that has specifically investigated the likelihood of reading deficits given auditory

comprehension deficits and paraphasia. As case reports show dissociability (Ellis, Miller & Sin, 1983), reading deficits observed in individuals with Wernicke's aphasia may reflect the typically large lesion volume of middle cerebral artery accidents associated with Wernicke's aphasia, which frequently involve anterior ST, posterior ST and IPL (Robson *et al.*, 2012). That is, patients presenting with both auditory and reading comprehension deficits may have large lesions, disrupting multiple cortical modules. Thus, it remains unclear whether lesions disrupting auditory word-form recognition or inner speech necessarily also disrupt reading comprehension.

In summary, the aspects of reading comprehension Wernicke associated with his sensory speech center relate to phonological reading *via* inner speech. Both phonological reading and inner speech are functions neuroanatomically associated with the auditory dorsal stream. Though deficits in auditory and written comprehension are often observed together, the dissociability of their neural substrates (or aspects of them) and their precise neuroanatomy requires further study.

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Highlights

- Studies in monkeys have established a dual-stream model for auditory cortex.
- Recent work affirms close homologies between human and monkey cortex.
- Classical “Wernicke’s area” has both dorsal- and ventral-stream components.
- Anterior STG, part of the ventral stream, supports auditory word-form recognition.
- Posterior ST/IPL, part of the dorsal stream, support functions of “inner speech.”

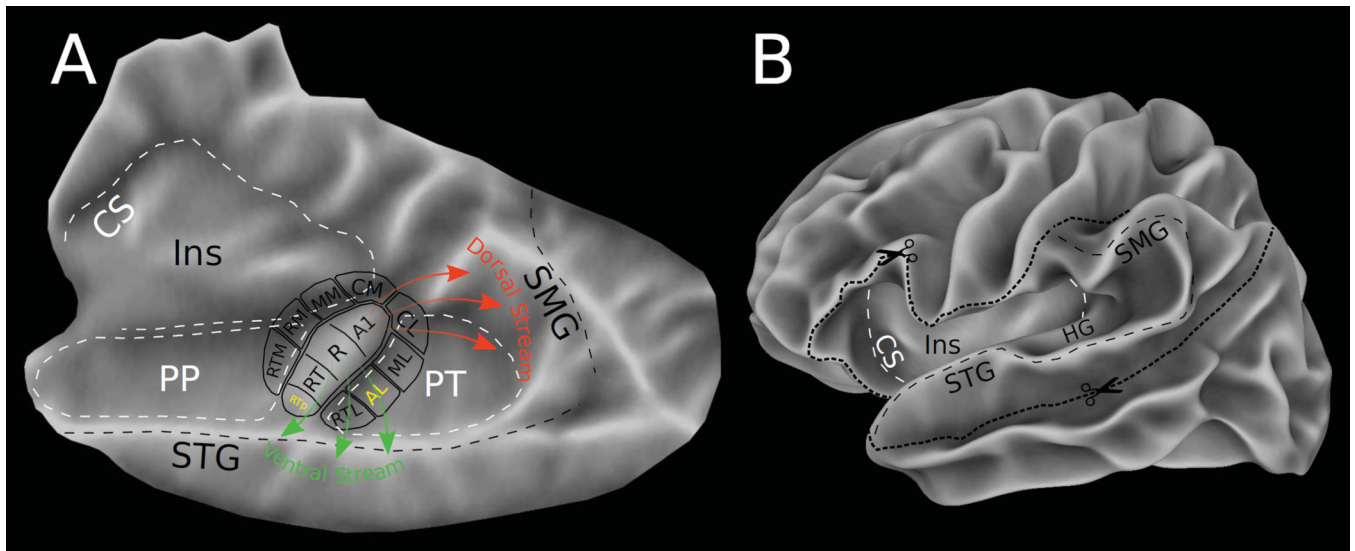


Fig. 1. A composite illustration of human auditory cortex and macaque auditory fields
 Relative to the macaque, human auditory cortex is rotated $\sim 45^\circ$ off the anterior-posterior axis of the superior temporal plane (Galaburda & Sanides, 1980; Rademacher *et al.*, 2001; Fullerton & Pandya, 2007; Hackett, 2011) with primary auditory cortex [core, Brodmann's area (BA) 41] located along Heschl's gyrus (HG) and secondary auditory cortex (lateral and medial belt, BA 42 and 52, respectively) located in planum polare (PP) and planum temporale (PT). To facilitate comparisons with the macaque literature, names of functionally-defined macaque subfields are shown on a flatmap of human anatomy (core: A1, R, RT, RTp; lateral belt: CL, ML, AL, RTL; medial belt: CM, MM, RM, RTM) (A). Subfield delineation is estimated from relative field sizes in the macaque, scaled with respect to the volume of human core (Penhune *et al.*, 1996; Rademacher *et al.*, 2001) and functionally localized according to tuning characteristics (Rauschecker *et al.*, 1995; Chevillet *et al.*, 2011). The composite figure implies a course for the human ventral and dorsal streams along the superior temporal plane. Fields exhibiting heightened selectivity for monkey calls are shown in yellow: lateral belt field AL (Tian *et al.*, 2001; Tsunada, Lee & Cohen, 2011) and area RTp (Kikuchi, Horwitz & Mishkin, 2010). For orientation, the cortical patch shown in flatmap (A) is outlined on the cortical surface (dashed line with scissor markers) (B). Additional points of reference include the circular sulcus (CS), insular cortex (Ins),

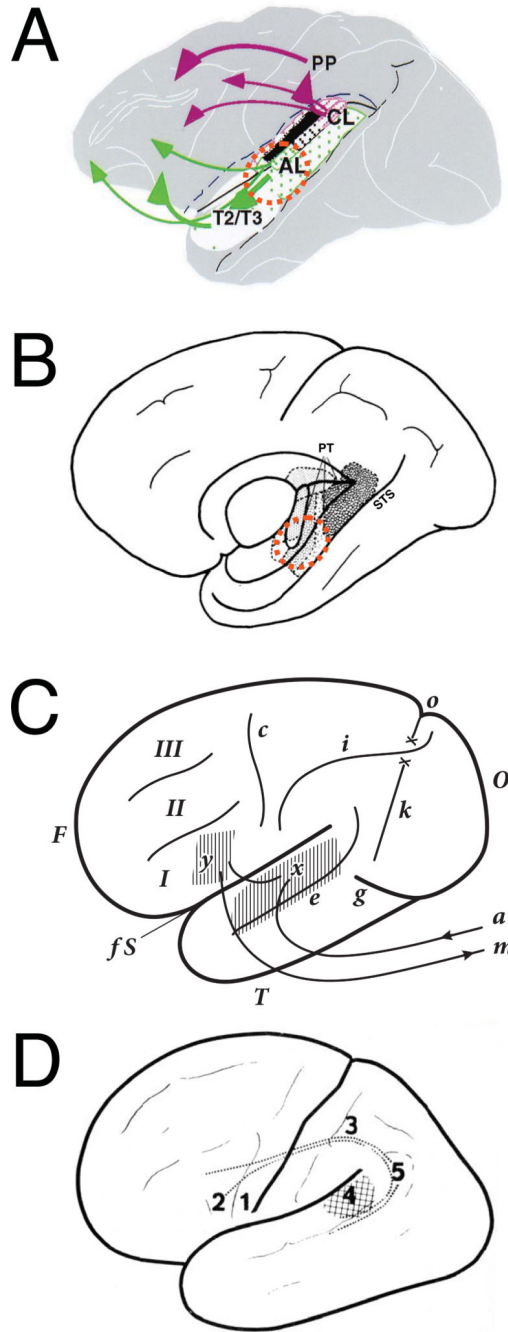


Fig 2. Anatomical predictions for the site of auditory word-form recognition
 (A) In the macaque, communication call processing is strongly associated with anterior-lateral portions of the superior temporal plane, specifically areas AL (circled) (adapted from Rauschecker & Tian, 2000). (B) The putatively homologous human site resides at the anterior-lateral aspect of Heschl's gyrus (circled) (adapted from Galaburda & Sanides, 1980). (C) This site is within the territory originally proposed by Wernicke (shaded region marked *x*) (adapted from Wernicke, 1881) but (D) is inconsistent with the location given for Wernicke's area by Geschwind (shaded region marked 4) (adapted from Geschwind, 1969).

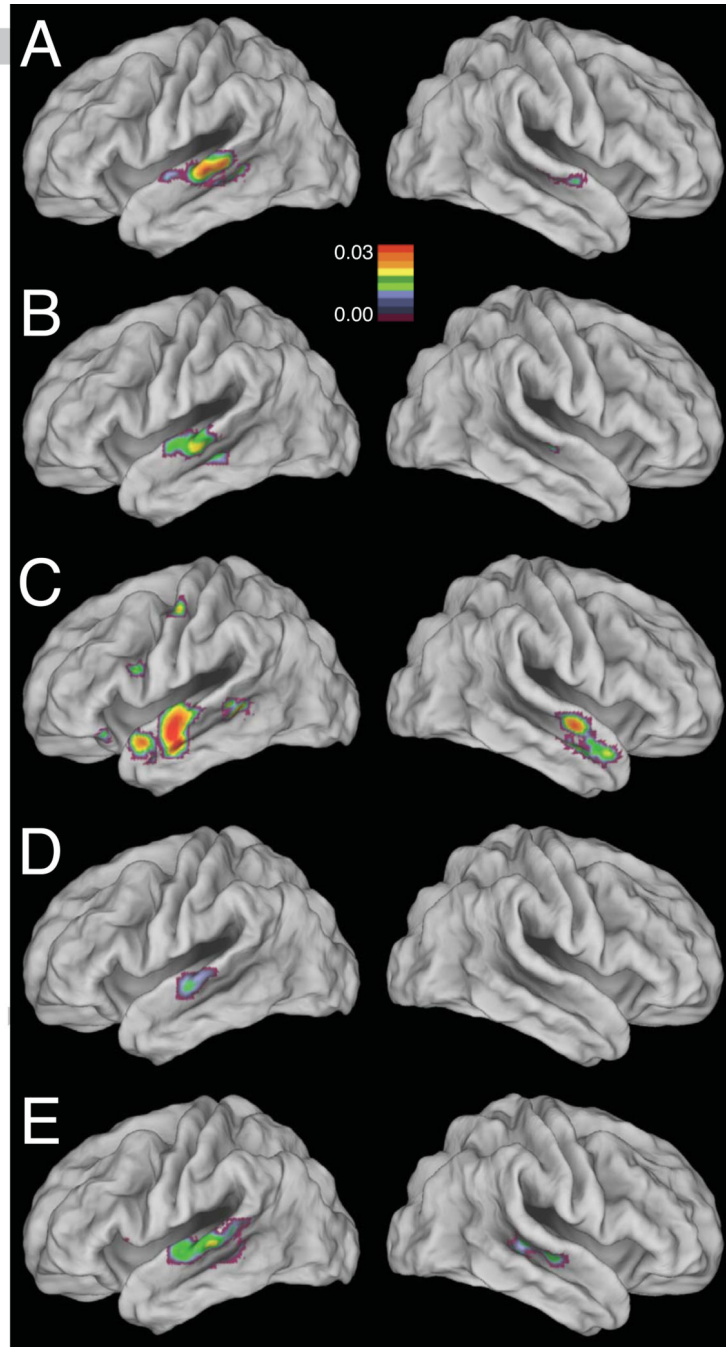


Fig. 3. Meta-analyses of auditory-word processing

Analyses of studies comparing brain response to speech stimuli versus matched control sounds (A–C), indicative of selectivity for speech sounds, found a leftward bias and an anterior progression in peak effects with phoneme-length studies' peak focus density in left mid-STG (A), word-length studies' peak density in left anterior STG (B), and phrase-length studies' peak density in left anterior STS (C). Peak density for studies investigating phonetically specific adaptation (D), indicative of invariant representation, was found in left mid- to anterior STG. Peak density for areal specialization studies (E), which compared

brain response to speech stimuli versus other natural non-speech sounds, also indicative of selectivity for speech sounds, was greatest in left STG. Intensity represents ALE value. Adapted from DeWitt & Rauschecker (2012).