Title: The Role of Right Hemisphere in Language Is Executive Rather than Linguistic

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Abstract

Despite a long history of research favors left lateralization of language, increasing evidence provides support to the claim that the right hemisphere also plays a role in language. Although studies have indicated that the right hemisphere contributes to language representation, the underlying neural mechanisms are partly investigated and remain elusive. In this review, we hypothesize that the right hemisphere is involved in language but its contributions are more likely to be domain-general rather than linguistic. The present work provides a thorough review of the growing body of research that has demonstrated how the right hemisphere is related to language with a focus on specific neural mechanisms underlying various aspects of language, and discusses why some brain regions of the right hemisphere such as supramarginal gyrus are essential for domain-general processes (e.g., verbal working memory) involved in language, rather than directly contributing to language itself.

Introduction

As a fundamental ability of humans, language plays a crucial role in our life. The exact language representation in the human brain remains of interest in the psycholinguistic domain. Perhaps Marc Dax (1836) is the person who introduced the cerebral dominance doctrine, which suggests that language is dominated by the left hemisphere (LH) and contralateral to the preferred hand (Lindell, 2006). Paul Broca presented the brain of patient “Tan,” who had profound loss of language articulation and right hemiparesis. Accordingly, the relationship between the left hemisphere and language production was made clear. Since then, Broca became one of the most influential scientists in shaping our idea that language is left-hemisphere lateralized.

However, the fact that language is mainly supported by the left hemisphere does not exclude the possibility that the right hemisphere could play a role in language. Broca was acutely conscious to make this articulated clear: “this does not mean to say that the LH is the exclusive center of the general capacity of language” (Broca, 1865). The nature of this discovery made people in the medical field ignore this minor difference. Thus, the doctrine of language lateralization (i.e. all aspects of language are subserved by the left hemisphere) spreads in the field until today. Indeed, numerous studies had found that the right hemisphere (RH) plays a role in language (e.g., Riecher et al., 2002; Cancelliere and Kertesz, 1990; Lancker and Seditis, 1992; Aziz-Zadesh et al., 2010; Pichon and Kell, 2013; Olson et al., 2007; Drane et al., 2013; Wong and Gallate, 2012; Gainotti 2012,

2013; Pobric et al., 2017), but fewer studies had provided specific evidence to answer how the RH supports language.

More recently, through the use of advanced neuroimaging and brain stimulation techniques, studies have provided accumulating and precise evidence regarding the contribution of RH to language representation in right-handed subjects and explained the involvement of RH as some non-linguistic functions are required for language (Sollam et al., 2014). For example, Sollam (2014) found that the right opercular inferior frontal gyrus (opIFG), posterior supramarginal gyrus (pSMG), anterior superior temporal gyrus (aSMG), and the right middle superior temporal gyrus (mSTG) contributes to speech production. They also concluded that the involvement of the above-mentioned brain regions within the RH was a result of their roles in motivation and attention or executive control. Deschamps et al. (2014) found that the right SMG is involved in verbal working memory (VBM) but not in phonological processing by manipulating the phonological complexity and WM demands. Gajardo-Vidal et al. (2018) found the right inferior frontal cortex (IFC) links both linguistic and non-linguistic working memory capacity, thus contributes to language comprehension by studying both stroke patients and healthy participants using a combination of behavioral paradigm and neuroimaging techniques. Sammler et al. (2015) found that right hemisphere activations during prosody processing is driven by domain-general processing of acoustic cues in an fMRI-TMS study. Wright et al. (2019) found that the RH supports the motor and emotional aspects of prosody by studying

neurologically impaired patients with acute ischemic RH stroke. Bozic et al. (2010) reported that there were increased activities in both RH and LH regions when general processing complexity increased during mapping from sound to lexical meaning whereas linguistic complexity increases LH activities only. Hartwigsen et al. (2010a) found that the reaction time and error rates increased after applying TMS to right SMG as well as left SMG on healthy participants. Hartwigsen et al. (2010a) suggested that it was possible that the trend towards increased RTs in the auditory perceptual task after effective SMG TMS reflects the demands on phonological short-term memory (Sharp et al., 2010) or acoustic-phonetic processing (Jacquemot and Scott, 2006). However, Hartwigsen et al. (2010a) did not include a condition where they can explain whether or not the left SMG is involved in executive functioning because the effect of TMS was not related to task difficulty according to the measurement of accuracy and response time in the sham TMS group. A recent study answered this question by suggesting repetitive stimulation did not affect on performance where working memory demands are minimized although performance varied as a function of phonological complexity. However, participants were less accurate and slower when performing the tasks after stimulation but the effect of phonology was not influenced during a verbal working memory task where phonological complexity was manipulated. Thus, the contribution of right SMG in phonological decision making is executive rather than linguistic. By using a similar approach from Hartwigsen et al. (2010a), Hartwigsen et al., (2010b) investigated the contribution of the

right posterior inferior gyrus (pIFG) in phonological decision making. They concluded that the right pIFG is necessary for efficient and accurate phonological decision making in a healthy brain, possibly they contribute to inhibition and attentional control required in phonological decision making (Hampshire et al., 2009; 2010). A meta-analysis re-analyzed neuroimaging data from 59 articles that have reported the participation of the RH during phonologica, lexico-semantic, and sentence processing (Vigneau et al., 2011). Vigneau et al. (2011) found that right-hemispheric frontal areas were activated in all tasks, possibly supporting executive functions that are not specific to a given language task. Similarly, a more recent meta-analysis done by Rice et. (2015) suggested that the right anterior temporal lobe (ATL) represents conceptual knowledge in language.

In this review, we come up with the hypothesis that the right hemisphere contributes to executive processes that are required for language representation rather than representing language itself. We will discuss why this hypothesis is true and shed light on the specific right hemisphere neural representation for different aspects of language (Table 1). Specifically, we will discuss speech production, speech comprehension, prosody, mapping from sound to lexical meaning, phonological decisions, lexical-semantic processing in each of the following sections in order. Finally, we will draw conclusions and discuss future directions.

Speech production

Over a century ago, Hughlings-Jackson investigated the claim that the RH is involved in the control of automatic speech (Whitaker, 1998). Jackson (1874) found that the RH could produce non-propositional speech, which was confirmed by an assessment of regional blood flow within the RH. For example, Larsen et al. (1978) found a 10% increase in the blood flow of the RH whereas blood flow in the LH did not change during automatic speech tasks. Ryding et al. (1987) found greater activation in the RH during a reaction task, which confirms the claims of the right hemisphere significantly involved during the non-propositional speech. Numerous studies of patients suffering aphasia after LH damage has confirmed the RH's ability to produce non-propositional speech, which includes a parrot-learned sequence (e.g. nursery rhyme, see Wray, 1992) and generating automatic phrases (e.g. swearwords). Consistent with Jackson's proposal (1874), Levy and Trevarthen (1997) suggested that the role of RH in speech production is different from that of LH, with the RH forming words as motor Gestalt instead of constructing them analytically from a series of phonemes (Lindell, 2006). However, none of these studies provide a comprehensive understanding of the exact mapping and executive contributions of speech production.

Repetitive transcranial magnetic stimulation (rTMS) could create a virtual lesion mode when studying language representation within the right hemisphere. One main advantage of rTMS is its non-invasive character. The functions of cortical areas can be tested with confirmed causality, much as direct current stimulation (DCS) does while the

surgical operation is not required in rTMS (Devlin and Watkins, 2007; Krieg et al., 2014; Picht et al., 2013). DCS, although considered as the gold standard for the mapping of language-eloquent brain areas, cannot examine language representation in healthy participants due to its invasive nature. Thus, rTMS is increasingly used in language mapping research. Previous research has confirmed the effectiveness of using rTMS in language-related cortical area mapping by inducing various kinds of language errors (Epstein, 1998; Epstein et al., 1996; Lioumis et al., 2012; Pascual-Leone et al., 1991; Picht et al., 2013; Sollmann et al., 2013a and 2013b; Sparing et al., 2001; Wassermann et al., 1999). Moreover, rTMS language mapping for left-sided perisylvian tumor patients has shown a good correlation with DCS (Picht et al., 2013) and magnetoencephalography (MEG; Tarapore et al., 2013) in German and English respectively when applying 5 to 7 Hz pulse trains.

A recent study employed rTMS combining with the object naming task (Sollmann et al., 2014) to investigate how RH contributes to speech production. More specifically, they classified the errors induced by rTMS into three main categories: no-response, performance, and hesitation error. They found an overall error rate of 15.5%. These errors were induced by stimulating the right opercular inferior frontal gyrus (opIFG), posterior supramarginal gyrus (pSMG), anterior superior temporal gyrus (aSMG), and the right middle superior temporal gyrus (mSTG) in both male and female participants' brains. In female brains, the right posterior superior temporal gyrus (pSTG) selectively

contributed to speech production. Moreover, language task performance was supported by speech-motor control regions within the RH, which included the right middle precentral gyrus (mPrG), ventral precentral gyrus (vPrG), middle postcentral gyrus (mPoG), and the right ventral postcentral gyrus (vPoG).

Regarding the contention about the causal contribution of subregions in right IFG (Kaplan et al., 2010; Thiel et al., 2005; Naeser et al., 2005), Sollmann et al. (2014) suggested that the right opIFG contributes to attentional control (Bonelli et al., 2012), which is required in the object-naming task. However, further studies are necessary in order to confirm this observation as Sollmann et al. (2014) only used one task. Sollmann et al. (2014) also observed the right triangular part of the inferior frontal gyrus (trIFG) contribution in terms of non-response errors in male participants. Future studies should use diffusion tensor image (DTI) to investigate the inhibitory effect of rTMS on the right trIFG in the male brain; fiber connections might underlie this differential inhibitory effect (Sollmann et al., 2014). As for the right middle frontal gyrus (MFG), its causal contribution to object-naming performance is consistent with a previous study that has found that the right MFG is functionally associated with the left anterior temporal lobe (ATL; Bonelli et al., 2012). MFG has been found to be bilaterally associated with motivation and executive control for goal-directed behavior in fMRI studies (Spielberg et al., 2011), thus Sollmann et al., (2014) suspected that the involvement of the right mMFG and pMFC in speech production is likely to be nonlinguistic and executive.

The activation of supramarginal gyrus (SMG), right aSMG and pSMG was found in Sollmann et al. (2014). Despite SMG was not included in the spatiotemporal model of single-word production (Indefrey, 2011), non-novated dual-site TMS showed that the left and right SMG contributed to phonological decision making in a non-compensatory manner (Hartwigsen et al., 2010; Inderfrey, 2011). Therefore, Sollmann et al. (2014) interpreted the activation of the right SMG as it contributes causally to object-naming tasks, which means that it is not a mere coactivation area. Interestingly, there is also accumulating evidence from neuroimaging studies that suggest that the SMG is also recruited in verbal working memory (VWM) tasks (e.g., Awh et al., 1996; Jonides et al., 1998; Barch and Csernansky, 2007; Kirschen et al., 2006, Koelsch et al.; 2009). It is possible that the activation observed during phonological tasks might be due to VWM given that participants were presented with letters, it is unclear what the common process is. Although functional neuroimaging evidence is consistent with that SMG was involved in phonological processing and in VWM, it is difficult to establish causal links without more direct manipulation of the SMG while engaging in phonological processing.

A recent study investigated whether the contribution of the left and right SMG to phonological processing is domain-specific (e.g. specific to phonology) or domain-general (specific to VWM) using rTMS (Deschamps et al., 2014). Deschamps et al. (2014) used rTMS stimuli that differed in terms of phonological complexity. More specifically, the tasks were designed to modulate phonological complexity while

minimizing WM and modulate both phonological complexity and WM (n-block task). They manipulated phonological complexity by varying the sonority differences between the two first consonants of the initial syllable. Their first experiment in their study demonstrated that repetitive stimulation did not affect performance where WM demands are minimized although performance varied as a function of phonological complexity. Their second experiment showed that subjects were less accurate and slower when performing the tasks after stimulation but the effect of phonology was not influenced during a verbal working memory task where phonological complexity was manipulated. Taken together, these results demonstrated that both the left and right SMG are involved in verbal working memory but not in phonological processing per se (see a detailed description and discussion in section 4). Therefore, we argue that the contribution of SMG in Sollmann et al. (2014) is cognitive rather than linguistic, which is in line with our hypothesis. Regarding the temporal lobe structures, the right mSTG causal contribution was found in object-naming tasks (Sollmann et al., 2014).

Electrocorticography (ECoG) has shown a greater left mSTG gamma activity in the 0-350 ms time window during a visual cued overt-speech task than that the auditory-cued over-speech production task (Leuthardt et al., 2012). The inhibitory effect on the right mSTG found in Sollmann et al. (2014) might reflect a similar function of the right mSTG and left mSTG associated with visually cued overt-speech production given the

coactivation of the right and left temporal structure for semantic integration (Brennan and Pylkkanen, 2012).

The right pSTG was also confirmed for its causal contribution when performance and no-response error were combined in female brains (Sollmann et al., 2014). The activation of the right pSTG can be explained by that the right pSTG acts as a site of convergence and interface between dorsal and ventral visual streams that contributes to the processing of object-related information (Karnath, 2001). Regarding the question of why the right pSTG was selectively activated in female rather than male brains, a previous study (Kansaku et al., 2000) has shown lateralization differences in the posterior language areas between female and male brains. To be more specific, global language comprehension activated posterior temporal lobes more bilaterally in female brains than brains and activated male brains more to the left posterior temporal lobe. Thus, the female result of the right pSTG disruption in Sollmann et al. (2014) is consistent with the literature. This might relate to the hormone state between the female population tested (see Lindell et al., 2006 for a detailed discussion); future studies will need to address this issue.

Finally, as for the activation of the right postcentral gyrus (PoG) and precentral gyrus (PrG), the vPrG, mPrG, and PoG showed significant causal contribution to object-naming function according to no-response, performance and hesitation errors induced by rTMS. Previous research has demonstrated the vPrG ipsilateral to lesions if a

primary speech arrest site in DCS studies in both LH dominant (Sanai et al., 2008) and RH dominant patients (Chang et al., 2011). Sollman et al. (2014) suggested that the speech motor control region is bilaterally distributed. Again, this notion is consistent with our hypothesis as right PoG and PrG contribute to mouth movement rather than the language itself directly.

Sollman et al. (2014) provided novel and significant insights regarding the left hemispheric contribution to object-naming function. There are several limitations in this kind of non-invasive brain stimulation method in language studies. For example, a recent study comparing rTMS language mapping and DCS revealed that there was a lower positive predictive value (PPV) in rTMS than DCS (Picht et al., 2013). However, Picht et al. (2013) had only investigated the left hemisphere, the right-hemispheric rTMS-based language mapping PPV value should also be lower than DCS. As a result, cortical areas that were related to language error during rTMS in the current study are not likely to be essential for language function but should be considered as language-related. Due to this, the findings from Sollman et al. (2014) might overestimate the contribution of some cortical areas to essential language function.

Comparing the rTMS results in Sollman et al. (2014) with previous DCS-based data, the rTMS-based approach had a higher error rate in general. For example, in a DCS-based study, Chang et al. (2011) stimulated more than 331 cortical sites of the RH in 15 patients, which led to the identification of 27-language positive spots in a patient

group with the size as small as 7. Furthermore, Duffau et al. (2008) performed intraoperative cortico-subcortical stimulation with a group of 9 low-grade glioma patients, which induced speech arrest in only 1 out of 9 low-grade glioma patients and induced speech arrest in only 1 out of the 5 patients respectively. Sollman et al. (2014) proposed that the high sensitivity and low specificity might be one reason to explain why it would lead to higher error distributions. Therefore, it is very likely that rTMS in Sollman et al. (2014) not only identified essential cortical language sites but also language-involved regions in general (Picht et al., 2013).

Speech comprehension

Language comprehension requires the listener to develop a model of what is being communicated, which relies on the ability to integrate the many components of a sentence, contextualize the representation, and decide how to act upon it (Lindell, 2006). Zaidel (1978) and Baynes et al. (1992) demonstrated that the disconnected RH processes a richly endowed lexicon and a significant receptive language ability by testing split-brain patients, whose callosum has been sectioned to relieve intractable epilepsy. A similar result was provided by Gazzaniga et al. (1997): although the split-brain patient in their study was not able to verbally name stimuli presented to his left visual field which corresponds to RH, he could correctly point to earth unnamed left visual field stimulus, which confirmed the comprehension of the written words. Miller et al. (1968) provided

more evidence to the contribution of the RH's comprehension skill using the dichotic listening paradigm introduced by Kimura (1961). Specifically, participants were asked to locate an object from a group located in front of them, but screened from view, with different instructions played to each ear (e.g., "Now pick up the paper clip" was presented in one ear whereas "Now find us the eraser" was heard in the other ear). Milner et al. (1968) found that participants demonstrated a strong preference for objects named through the left ear with a partial to complete neglect of objects named through the right ear. Thus, their result indicated that RH plays a role in language comprehension. The RH has increased sensitivity for variations in pitch according to Zatorre et al. (1992). In their study, Zatorre et al. (1992) used PET to examine differences in hemispheric activation in response to acoustically-presented speech syllables. They found that judgments of pitch prompted RH activation with foci observed in the right prefrontal cortex (PFC) whereas there was increased activation in the LH, particularly Broca's area. The results suggested that LH was largely responsible for phonetic processing whereas RH mediated pitch discrimination. It is also consistent with past research that indicated a dissociation between phonetic and pitch processing in LH evoked potentials (e.g. Wood et al., 1971). The RH also plays a critical role in the pragmatic aspects of speech and is also necessary to interpret an utterance in its context properly. It is well acknowledged that the message conveyed by a sentence is more than just the sum of its parts (i.e. words, Beeman and Ciarello, 1998). Thus, the ability to interpret and produce narrative discourse relies on the

ability to make cohesive and coherent ties between phrases and to establish connections between and within a sentence to draw out the overall meaning conveyed by a text (Marini et al., 2015). Functional neuroimaging data has also confirmed that RH plays an essential role in drawing together disparate elements to form a comprehensive sentence (e.g. Gernsbacher and Kaschak, 2003). As a result of RH damage, patients displayed impairments in the ability to coherently integrate (e.g. Marini et al., 2005; Beeman et al., 2000), interpret (e.g. Kaplan et al., 1990) and infer (Beeman, 1993) narrative discourse.

Gajardo-Vidal et al. (2018) studied both stroke patients and healthy participants using a combination of behavioral paradigm and neuroimaging techniques, and found that the inferior frontal cortex (IFC) links to both linguistic and non-linguistic working memory capacity, which plays an important role in executive control. The principal advantage of lesion study is that they could demonstrate the unsubstitutable function of particular brain areas for a particular cognitive function, whereas activations are correlational. Specifically, in the first experiment, they demonstrated that right hemisphere stroke survivors are more likely to have impairments in auditory to the sentence matching task, while left hemispheric stroke survivors are more likely to have difficulties with the spoken picture description task. For patients with a right hemispheric stroke, the majority (n=9) had a normal performance on linguistic (semantic, phonological, or syntactic) or perceptual (visual or auditory) processing. The second experiment indicated that these nine patients had significantly more damage to the right

inferior frontal sulcus and dorsal parts of the superior longitudinal fasciculus than those patients who also had a right hemispheric stroke but did not find impairments in the auditory sentence-to-picture mapping task. In experiments 3 and 4, then used functional magnetic resonance imaging (fMRI) to study neurologically normal patients using the same set of language tasks with a focus on the activation of previously identified regions in patients. There are two main advantages of functional neuroimaging: (1) they provide data about the unimpaired cognitive system, whereas lesions can induce plasticity and compensatory processes that may result in functional reorganization inpatient studies (Duffau, 2005; Keidel et al., 2010). (2) Functional neuroimage covers the whole brain, whereas lesion studies only provide insights into the brain area that has been damaged in particular patient cohorts. They found that the right inferior frontal cortex was activated in auditory sentence-to-picture mapping matching and matching when the demand for linguistic and non-linguistic working memory was high.

The importance of good executive function for speech comprehension has been demonstrated by manipulating ambiguity in the sentence content (Key-DeLyria and Altmann, 2016). For example, individuals with higher IQ scores and faster processing speech had a high chance to answer ambiguous sentence comprehension questions correctly (Engelhardt et al., 2017) and older adults with better inhibition skills had better sentence comprehension scores than individuals who had poor inhibition skills (Yoon et al., 2015). Interestingly, another study found that syntactic interference effects during

sentence comprehension can be predicted by general WM capacity but not by phonological WM capacity as measured by digital span (Tan et al., 2017), which highlights the role of executive WM in sentence comprehension that is overt and beyond the contribution of VWM and might explain why participants from Gajardo-Vidal et al. (2018) were not found to have abnormal low digit spans.

Previous studies have also shown the recruitment of right inferior frontal lobe (IFL) in sentence comprehension, particularly for older compared to younger neurologically normal participants (Wingfield and Grossman, 2006), when sentences are reversible or in dominant (de Almeida et al., 2016), when words are ambiguous (Mason and Just, 2007), and when participants who have aphasia after LH stroke are recovering their sentence comprehension abilities (van Oers et al., 2010; Kielar et al., 2016; Mohr et al., 2014).

Together, these experiments demonstrated the contribution of the right inferior frontal cortex in working memory capacity (executive function) which is needed for normal speech comprehension (Gajardo-Vidal et al., 2018). Again, this finding is by following per our hypothesis that the role of RH in the language is domain-general rather than linguistic.

Prosody

Affective prosody refers to the variation in pitch, rate, loudness, and rhythm (i.e., stress, pause, or duration of components) of speech to convey emotions (Wright et al., 2018). A sentence like “it’s so nice to see you” could be taken as several meanings depending on if it is spoken with cheerful surprise, boredom, or sarcasm. If the patient is unable to understand humor, emotions, and sarcasm, and the patient’s friends and family members are unknown of this, it might weaken the patient’s relationship with his or her friends and family members (Sheppard and Hillis, 2018).

Studies have shown that production and recognition of affective prosody may be impaired by focal or diffuse brain damage (Pell, 2002; Pell, 2006) due to RH stroke (Ross and Mesulam, 1979; Ross and Monnot, 2008; Tippet and Ross, 2015), Parkinson’s disease (Péron et al., 2015), frontotemporal dementia (Dara et al., 2013, Rankin et al., 2009, Rankin et al., 2005), schizophrenia (Dondaine et al., 2014), and other neurological diseases (Bais et al., 2010, Kipps et al., 2007). Several studies have shown dissociations between production and recognition of affective prosody impairment, and some studies have demonstrated repetition or mimicking of affective prosody can be impaired or spared disproportionately. However, only few have investigated distinct cognitive, perceptual, and motor mechanisms that underlie affective prosody production and recognition (but see Bower et al., 1993).

Several studies have proposed the neural systems underlying the production or comprehension of affective prosody. For example, Brück et al. (2011) proposed a

neurobiological model of emotional information based on a review of functional neuroimaging studies and lesion studies of effective prosody. In this model, affective prosody is first processed by the thalamus, which is connected to both an explicit pathway and an implicit pathway. The explicit pathway consists of extraction of acoustic cues in the middle part of superior temporal gyrus (mSTG), integration of the acoustic cues into a single percept in the posterior superior temporal gyrus (pSTG), and finally the percept in the orbitofrontal cortex and the dorsolateral prefrontal cortex (DLPFC). The implicit pathway directly projects to the amygdala, nucleus accumbens, and medial frontal cortex to induce an emotional response. There is evidence—primarily from fMRI studies and Parkinson’s disease—that the basal ganglia also involves in the recognition of affective prosody. Importantly, the role may be a more general one of the processing of working memory or acoustic information. Another neurobiological model that shares some features is a three-stage model (Schirmer and Kotz, 2006), which includes: (1) acoustic analysis in bilateral auditory processing areas; (2) integration of emotionally significant acoustic information into an emotional “gestalt” along with the central stream from the STG to the anterior superior temporal sulcus (STS), which seems to be lateralized to RH; and higher-order cognitive processes that yield evaluative explicit evaluative judgments of the derived emotional gestalt processed by the orbitofrontal cortex and the right inferior gyrus (Kotz et al., 2006; Wildgruber et al., 2016).

It is clear that the LH also plays a role in processing affective prosody although the RH might have a dominant role in affective prosody as demonstrated by fMRI studies (Kotz et al., 2003; Wildgruber et al., 2006) and lesion studies in which LH stroke resulted in impaired affective prosody production and/or recognition (Baum and Pell, 1997, 1999; Cancelliere and Kertesz, 1990; Schlanger et al., 1976). Moreover, the integration of information from the two hemispheres via the corpus callosum is critical for the accurate processing of affective prosody (Paul et al., 2003). Previous results have also provided support that elements of prosody perception are different lateralized, with pitch is processed mostly in the RH whereas duration and intensity are mainly processed in the LH (Zatorre et al., 2002; Lancker and Sidtis, 1992). However, there is no clear evidence that emotional valence or type of emotion influences the areas that are engaged significantly in all of the studies that support these neurobiological models.

A recent study with a novel paradigm using audio morphing combined with fMRI and TMS showed that prosody perception takes dual routes along dorsal and ventral pathways in the RH (Sammler et al., 2015). Specifically, in their first experiment, they found that categorization of stimuli that gradually varied in their prosodic pitch contour (between statement and questions) involving (1) an auditory ventral pathway along the superior temporal lobe (STL) and (2) auditory-motor dorsal pathways connecting posterior and inferior frontal/premotor areas. In their second experiment, inhibitory stimulation of the right premotor cortex as a key node of the dorsal stream that decreased

participant's performance in prosody categorization, which argued for a role for motor involvement in prosody perception.

Results from Sammler et al. (2015) highlighted a relative dominant pattern of brain activations, consistent with prevailing cue-dependent models of prosody, which propose that hemispheric specialization is driven by non-prosody-specific (domain-general) processing of acoustic cues. These suggest a processing benefit of the RH for spectral information which unfolds over extended timescales. As a result, this implies that white-matter tracts in the right hemisphere qualify as main routes of prosody perception. Note that Smaller et al., (2015) did not exclude the involvement of LH pathways, but rather, they favor the view that their experimental design was particularly sensitive to the right hemispheric component of a perhaps more extended bilateral network. Particularly, it remains to be specific in which way the results generalize to sentence-level prosodic functions such as phrasing or accentuation. One conceivable situation is that time-sensitive prosodic processes of the right dorsal stream interact transcallosal with sentence-level syntactic and semantic processing in the LH. Interestingly, this rightwards asymmetry included the OMS. Though surprising, this finding is in line with the mounting evidence of a right premotor advantage in auditory-feedback control and may indicate a projection of auditory asymmetries up to premotor areas given a bilateral organization of voice control, and may indicate a project of auditory asymmetries to premotor areas. There were two expectations to the RH

domination, which were (1) a left-dominant activation in the intraparietal sulcus (IPS), both of which might be related to the cortical sensorimotor control of (stimulated) vocalization and (2) a bilateral (right-trended) activation in the supplementary motor area (SMA).

Neurobiological models of generation for affective prosody during speech production has been implicated to rely on a right-lateralized network (Riecker et al., 2002), basal ganglia (Cancelliere and Kertesz, 1990; Lancker and Sidtis, 1992), or bilateral perisylvian network (Aziz-Zadeh et al., 2010). Pichon and Kell (2013) found support for the participation of all these networks/regions in different aspects of prosody generation. In this fMRI study, there was increased ipsilateral connectivity between the right ventral and dorsal striatum and between the striatum and the anterior STG, the right anterior insula, and the temporal lobe. Moreover, there was increased connectivity between the right dorsal striatum and the right inferior frontal gyrus (Brodmann area 44), and the left orbitofrontal cortex and the inferior temporal gyrus. In the execution phase, connectivity increases between the right ventral striatum and the right dorsal striatum, and between dorsal striatum and bilateral inferior frontal gyrus and right STG, also between the right dorsal striatum and right anterior hippocampus and bilateral amygdala.

While these neurobiological models help to understand the areas of the brain engaged in affective prosody production and/or recognition, they are unspecified regarding the cognitive processes that underlie the ubiquitous and socially imperative tasks of recognizing the conveying emotion through prosody (Wright et al., 2018). To

develop a cognitive architecture of the representations and processes that underlie expression and recognition of affective prosody, Wright et al. (2018) started by considering the computational demands of recognizing and expressing emotions through changes in the acoustic features of speech. It is first important to parse and analyze the paralinguistic features of the utterance. This kind of analysis requires recognition of differences in pitch (frequency), rhythm (stress, pauses, and duration of various segments), rate, and loudness (intensity). Then, it is necessary to match a set of acoustic features with an emotion. To do this, access to an abstract representation of what “angry,” “happy,” “sad” and so on sound like is needed. Speakers of a language or a culture share these abstract representations of acoustic characteristics that convey emotion (ARACCE). The ARACCE (whether stored or computed online) would specify the acoustic features of each emotion and allow access to the semantic representation (meaning) of that emotion. Thus, the ARACCE can compare to the lexical orthographic representation of reading and spelling, in that it mediates between the semantic representation and input or output processes. The semantic representation would then specify an automatic response (e.g. sympathetic or parasympathetic response), as well as the meaning and valence, and could overlap with semantic representations of other emotions. For instance, heartbroken and disappointed share the same meaning, but vary in valence. To express emotion through prosody, one would have to access the abstract representation of the acoustic features of that emotion (the ARACCE) from the semantic representation of that emotion.

After that, one would need to convert the ARACCE to a motor program to produce these acoustic features. Finally, one has to implement the motor program when speaking (Fig. 2). Note that the discussion here was as though these mechanisms were activated in sequence, it is also likely that some operate in parallel during production or comprehension of speech. Also, there might be feedforward or feedback interaction between levels that are not described here.

Wright et al. (2018) recruited four neurologically impaired patients with acute ischemic RH stroke or frontotemporal dementia (FTD) by using the Affective Prosody Battery designed to assess processing at each proposed level. The cases reported in Wright et al. (2008) are consistent with the notion that processes involved in recognition of affective prosody are dependent on a ventral stream of processing, which is a sound to a meaning network from the superior temporal cortex to the inferior and anterior temporal cortex. This processing stream is comparable to the ventral stream of the processing of language in the LH. Specifically, Case 1 and 2 had the right superior or anterior lesions (also right anterior insula and anterior basal ganglia in Case 1). Wright et al. (2018) suggested that the deficit is reminiscent of “pure word deafness” except that it was involved in the processing of affective prosody. Pure word deafness is often accompanied by focal lesions involving the left auditory cortex (mid STG area) that also disrupts callosal fibers from the right auditory cortex while most posterior STG is intact. Although Case 1 did not appear to have acute ischemia involving the right auditory

cortex, the patient was tested during the acute phase of the stroke. Perfusing imaging did not provide evidence for an ischemic penumbra that affected the right auditory cortex. However, it is possible that diaschisis acutely disrupted the right auditory cortex. Case 2, who had impaired access to acoustic features of emotion from speech had acute infarct involving right middle STG. The potential “affective” acoustic analyzer in the right middle STG might be analogous to the proposed role of left middle STG in propositional language.

Case 3 proposed in Wright et al. (2018) had deficient access to an “abstract-representation of acoustic characteristics that convey emotion (ARACCE),” which is reminiscent of Wernicke’s proposed LH mechanism in the analogous area that is required for word comprehension. It is also analogous to access to the phonological input lexicon. However, Wright et al. (2018) could not draw any conclusions about the localization of this function as Case 3 had greater diffuse right temporal atrophy than left.

Overall, Wright et al. (2018) provided a conceptual framework for identifying disposable impairments in production and recognition of affective prosody. However, it did not provide evidence for selective deficits in all of the components. They have identified individuals with an impairment in other components like a semantic representation of emotions but were not able to demonstrate that the deficit is selective. Specifically, the impairment is reflected in the impaired matching of emotions to synonyms (with spared matching frequency-matched emotions to a synonym), impaired

matching of emotion to synonyms, and failing to match names of emotions to faces or phrases that describe an emotional event. However, it is not possible to determine the status of access to the ARACCE directly because an impaired understanding of the meaning of the emotional words also disrupts the performance on matching acoustic features and spoken sentences to emotion (Wright et al., 2018). All errors in Wright et al. (2018) could be regarded as “semantic errors” because forced-choice responses were limited to semantically related, in contrast to evaluating lexical-semantics in LH stroke patients, which resulted in similar semantic error across tasks (Hillis et al., 1990). It was also difficult to identify whether production deficits were semantic errors or other types of errors.

Participants with impairments in different components of the architecture proposed by Wright et al. (2018) had different areas of brain damage (focal atrophy or stroke). As the authors pointed out, it was not possible to make inferences about the areas/networks essential for any component until a sufficient number of participants are identified and without disruption of that level of processing to show a statistical association between the prosody deficit and the region of damage. Also notice that the few individuals Wright et al. (2018) identified with semantic deficits had bilateral anterior atrophy. Importantly, right atrophy is greater than left. Wright et al. (2018) did not observe the impairment after unilateral stroke. The deficit might be analogous to the more general amodal semantic

deficit found in people with semantic variant primary progressive aphasia (see Zahn et al., 2009), with left greater than right temporal atrophy.

Finally, the participant with a subcortical parietal infarct and hypoperfusion of the inferior parietal cortex had selective impairment of accessing the ARACCE for output, which is in line with the proposal that prosody expression is dependent on a dorsal stream of processing from temporal cortex to inferior parietal cortex, and the cortex. These brain regions form a “meaning to motor production” network, which is comparable to a dorsal stream of processing of language in the left hemisphere (Saur and Hartwigsen, 2012; Kummerer et al., 2013; Poeppel and Hickok, 2004). Furthermore, previous data have indicated that this area is most likely to be associated with the direct motor programming of affective prosody is right inferior-posterior frontal regions, which is homologous to Broca’s area (Ross and Monnot, 2008; Wright et al., 2016), also in the dorsal stream.

Functional imaging and lesion studies also provide evidence that the limbic system which includes anterior cingulate, anterior insula, and amygdala are also important for processing emotions (Tippett and Ross, 2015). All of the patients in Wright et al. (2018) had lesions to the right insula. Thus, the possibility of insular damage is contributed to one or more impairments in affective prosody. However, future studies of patients with and without insular damage and deficits in prosody processing should be conducted to clarify the role of the insula in affective prosody (Wright et al., 2018).

Sarcasm (a kind of affective prosody) is a way to express criticism in a humorous or a non-aggressive way (Davis et al., 2015). Understanding that another person is being sarcastic, instead of sincere, from the spoken language requires several distinct cognitive and phonological processes. A recent study studied RH ischemic stroke patients and used multivariable linear regression with education, age, and percent damage to each of the 8 white matter tracts as the independent variable and percent accuracy on sarcasm recognition as a dependent variable (Davis et al., 2015). Davis and colleagues (2016) found that percent damage to the sagittal stratum was the only independent predictor of error rate on sarcasm and damage to the sagittal stratum had the greatest weight. Results indicate that the right sagittal stratum has an important role in sarcasm comprehension.

The sagittal stratum consists of a large bundle of white matter fibers that serve to connect frontal, temporal, parietal, occipital, and cingulate regions to the thalamus and other deep structures. Moreover, it carries both afferent and efferent fibers between the thalamus and cortex. Davis et al. (2016) suggested it makes sense that damage to this white matter tract would disrupt recognition of sarcasm in the absence of contextual cues given that thalamus is essential for processing both auditory and visual information. Moreover, affective prosody after lesions of the right thalamus was damaged (Mitchell and Ross, 2013). Studies in patients also identified impaired affective empathy in patients with right thalamic strokes. It was plausible that lesions in specific nuclei of the thalamus

and their connections at least acutely disrupt the processing of auditory cues that normally would allow one to detect insincerity in a tone of voice (Davis et al., 2016).

Mapping from sound to lexical meaning

One hundred fifty years of neuropsychology research has shown that the critical role of the left hemisphere perisylvian networks which links left inferior frontal and posterior temporal brain areas in supporting key combinatorial language function in the domain of inflectional morphology and syntax (Bozic et al., 2010). In the meantime, evidence of lesion study and neuroimaging study shows the ability to construct a semantic and pragmatic interpretation of incoming speech and dynamic access to lexical meaning can impact despite the damage in the left perisylvian language areas, which implies a distributed bihemispheric substrate. In an event-related fMRI study of lexical processing.

Bozic et al. (2010) tested the hypothesis that speech comprehension is supported by two independent but separable systems with distinct functional roles: a specialized LH perisylvian system, which supports the core morpho-syntactic function that is unique to human language, and a bihemispheric fronto-temporal system, which supports sound-to-meaning mapping and general perceptual processing demands and processes of pragmatic inference by asking participants to play a gap detection task while being scanned in the fMRI scanner. They manipulated whether a word ends in an inflectional

rhyme pattern, which would modulate specifically linguistic complexity and whether it has whether a word ends in the IRP, invoking specifically linguistic complexity, and whether it has an embedded stem, invoking general processing complexity.

The results from Bozic et al. (2010) confirmed these hypotheses. First, they provide evidence for the bilateral foundations of speech comprehension. Compared with a well-matched acoustic baseline, spoken words produced bilateral activation in middle temporal lobes, anterior cingulate, and angular gyrus. Consistent with the LH dominance for language function, Bozic et al. (2010) found stronger LH lexical activation in angular and inferior frontal gyri (BA39, BA 44/45).

Second, Bozic et al. (2010) demonstrated a functional dissociation between the specific components of this complex fronto-temporal network. Simple words (e.g. dream) showed an essentially bilateral pattern of middle temporal activation. The activation pattern shifted anteriorly to inferior frontal regions when there was an increase in general processing complexity due to the presence of embedded stems (e.g. activation in the claim condition versus simple words condition). Importantly, this frontal activation was fully bilateral, recruiting both the left and right inferior frontal gyrus (BA45/BA47). By using a parametric analysis that showed significant modulation of the activity in bilateral frontal regions by the competition due to the presence of embedded stems, Bozic et al. (2010) further confirmed the bilateral foundation of this subsystem. However, when a different type of processing demand (especially linguistic complexity) was introduced,

the activation shifted to a strongly left-lateralized pattern of IFC activity (BA45). These peaks of activity in the prefrontal sites extended into more posterior temporal regions at a lower threshold, which was consistent with the view that activity in right IFC, and the right IFC reflect the membership of broader fronto-temporal networks according to previous research (e.g., Miller and Cohen, 2001; Tyler et al., 2002; Tyler and Marslen-Wilson, 2008; Stamatakis et al., 2005). Multivariate analyses indicated a component that dissociated words that do and do not have embedded stem showed a robust bilateral fronto-temporal distribution whereas the orthogonal components that dissociated words with and without a potential past tense ending demonstrated a primarily left-lateralized activation pattern. These findings support our hypothesis that the role of RH in the language is domain-general rather than linguistic by demonstrating that there were increased activities in both RH and LH regions when general processing complexity increased during mapping from sound to lexical meaning whereas linguistic complexity increases LH activities only.

Phonological decisions

Functional neuroimaging studies have found that both the left and right posterior inferior frontal gyri (pIFG; Chee et al., 1999; Devlin et al., 2003; Poldrack et al., 1999; Shibahara, 2004; Tremblay et al., 2004) and supramarginal gyrus (SMG; Devlin et al.,

2003; McDermott KB et al., 2003; Price et al., 1997; Buchsbaum BR et al., 2009) were activated when making phonological decisions. To confirm these findings, Hartwigsen et al. (2010a) used transcranial magnetic stimulation (TMS) on healthy participants to test whether the right SMG in the right hemisphere contributes to modality independent (i.e. auditory and visual) phonological decisions (Hartwigsen et al., 2010a) and the functional relevance of the right pIFG for auditory and visual phonological decision making (Hartwigsen et al., 2010b).

Specifically, in Hartwigsen et al. (2010a), behaviorally, they found that the reaction time and error rates increased after applying TMS to right SMG as well as left SMG. This finding indicated that right SMG activation is essential for efficient and accurate phonological decisions in the brain. Moreover, they concluded that the left and right SMG can compensate for one another because the participants did not perform worse when bilateral SMG was stimulated than unilateral SMG was stimulated by TMS (Hartwigsen et al., 2010a). In other words, if phonological decisions can be made with either the left and right SMG, then the dual-site TMS over both the left and right SMG should have a larger effect than applying TMS over either left or right SMG alone. The precise role of the SMG is still unclear. A good question to ask is that is the SMG directly involved in phonological processing (e.g. subvocal articulation)? An alternative explanation would be that the SMG is involved in executive processing that is essential for phonological decision making. As an example, Romero et al. (2006) found that 5 Hz

TMS applied to the left SMG significantly disrupted the judgments on visually presented words in a variety of tasks, which provided evidence that the left SMG is involved in short-term retention of verbal material as well as phonological judgments. Nevertheless, Hartwigsen et al. (2010a) excluded explanations regarding general executive processing in their study as the effect of TMS was not related to task difficulty according to the measurements of accuracy and response time in the sham TMS group. By contrast, task difficulty was greatest during the auditory perceptual task. However, there were no significant differences between the linguistic tasks. Moreover, the effects of effective TMS were greatest in the phonological task, but with only a non-significant trend during the auditory perceptual task. It is also possible that the trend towards increased RTs in the auditory perceptual task after effective SMG TMS reflects the demands on phonological short-term memory (Sharp et al., 2010) or acoustic-phonetic processing (Jacquemot and Scott, 2006).

However, Hartwigsen et al., (2010a) did not include a condition where they can explain whether or not the left SMG is involved in executive functioning because the effect of TMS was not related to task difficulty according to the measurement of accuracy and response time in the sham TMS group. A recent study investigated whether the contribution of the left and right SMG to phonological processing is domain-specific (e.g. specific to phonology) or more domain-general (specific to verbal working memory) by using rTMS (Deschamps et al., 2014). Their first experiment in their study demonstrated

that repetitive stimulation did not affect on performance where working memory demands are minimized although performance varied as a function of phonological complexity. Their second experiment showed that subjects were less accurate and slower when performing the tasks after stimulation but the effect of phonology was not influenced during a verbal working memory task where phonological complexity was manipulated. Together, these results demonstrated that both the left and right SMG are involved in verbal working memory but not in phonological processing per se. This bilateral pIFG activation was surprising given theoretical models of language models focused on the importance of LH rather than the RH and most lesion studies emphasized that phonological processing is more impaired after left than right inferior frontal damage (e.g. Winhuisen et al, 2007; Wilde, 2009; Dewarrat et al., 2009).

Hartwigsen et al., (2010b) used a similar approach from Hartwigsen et al. (2010a) to investigate the contribution of the right posterior inferior gyrus (pIFG) in phonological decision making. They found an increase in reaction times and error rates following TMS to both the left pIFG and the right pIFG indicated that they both are necessary for accurate and efficient phonological decisions in the healthy brain. Moreover, the left and right pIFG cannot compensate for one another because the phonological decision performance was not worse for bilateral pIFG than unilateral pIFG. In other words, the dual-site TMS over the left and right pIFG would produce a greater lesion effect if phonological decisions are possible for either left or the right pIFG if phonological

decisions can be made with either the left or right pIFG. By contrast, Hartwigsen et al. (2010b) demonstrated that the behavioral effect of TMS on phonological judgments was the same for unilateral and bilateral TMS, suggesting that the left and right pIFG are equally important for accurate phonological decision making in a healthy brain.

The disruptive effect of TMS was independent of the presentation modality (i.e. visual or auditory) and was present during unilateral as well as bilateral TMS. Thus, it cannot be explained by the claim that the contralateral hemisphere plays a compensatory role (e.g. Price and Frinston, 2002). By contrast, both the main experiment and the subsequent follow-up experiment manipulating TMS intensity indicated that the lesion effect of unilateral TMS to the right pIFG was comparable to the lesion effect triggered by unilateral TMS to the left pIFG or bilateral TMS to the right and left pIFG.

Furthermore, it cannot be explained by a speed-accuracy trade-off because the detrimental effects of right pIFG TMS on reaction times were paralleled by an increase in error rates. Although the TMS-induced change in behavioral measures was more salient for reaction times than error rates, TMS over pIFG but not aIFG increased error rates, especially when given over the RH. Thus, Hartwigsen et al. (2010b) concluded that the right pIFG is necessary for efficient and accurate phonological decision making in the healthy brain. The alternative account that favors our hypothesis would be that the right pIFG is involved in domain general processing that is required in language rather than contributing to language directly. For example, studies have found that the right IFG was

recruited during inhibition and attentional control (Hampshire et al., 2009; 2010). Future studies should test whether the role of the right pIFG in phonological decision making is domain-general or linguistic.

Lexico-semantic processing

A recent meta-analysis re-analyzed neuroimaging data from 59 articles that have reported the participation of the RH during phonological, lexico-semantic, and sentence processing (Vigneau et al., 2011). The key benefit of the meta-analysis approach is that meta-analysis identifies consistent results across a large number of studies. Thus, it is resistant to the weakness that a single study might have (e.g. reproducibility). The results suggested that right-hemispheric frontal areas were activated in all tasks, and they support executive functions that are not specific to a given language task. Specifically, the activation of two RH clusters were detected in more than one language component: the right F3opd (at the junction between the pars opercularis of the inferior frontal gyrus and the middle frontal sulcus) was activated by the three language components, while the right anterior insula was recruited both during sentence processing and lexico-semantic task.

The right F3opd was also involved when manipulation of verbal material was required as during tasks involving semantic associations between object and subordinate-level words (Adams and Janata, 2002) and during semantic selection tasks

(Wagner et al., 2001). The right F3opd was recruited by more complex tasks such as comparison of complex sentences (embedded sentences or subject-object) with simple sentences during the sentence/text processing (Ben Shachar et al., 2004; Constable et al., 2004).

The right anterior insula also coactivated with the right F3opd frequently during the semantic, phonological, and sentence/text task (Vigneau et al., 2011), which suggested that these two areas should be involved in similar processes that are not specific for a given language component. Moreover, the right anterior insular was found to activate unilaterally during tasks involving auditory attention. These tasks include target detection in selective attention tasks with binaural presentation (Lanke and Shah, 2002), the categorical perception of syllables (Poeppel et al., 2004), and the identification of a syllable in low SN ratio (Sekeyama et al., 2003).

The involvement of above mentioned frontal areas was not specific for a given language component, rather, they were activated whenever the WM of verbal material was needed (Vigneau et al., 2011). The role of the right anterior insula might not be specific for the verbal material as previous studies have found that its activity during executive tasks where the participants had to encode verbal, spatial, and numerical information in working memory (Zago et al., 2008). Specifically, in their study, Zago et al. (2008) proposed that the anterior insula is part of the central executive frontal network. As a result, the involvement of the right anterior insula was found during tasks

may depend on the demand for the executive process rather than the language process per se. This notion is also consistent with recent data on metaphor processing under different processing difficulties, showing that difficulty influenced RH contribution while the activity of LH was related to linguistic parameters (Yang et al., 2009). Another meta-analysis also has demonstrated that the anterior insula was left lateralized during linguistic tasks while right hemisphere is right lateralized during spatial memory tasks (Wager and Smith, 2003).

In Vigneau et al. (2011), unilateral activation clusters were identified in the right frontal lobe, which were likely related to the attentional process as they did not show activations in simple tasks such as repetition, listening or reading. The right F2ant (located in the anterior part of the middle frontal gyrus) was recruited during selective attention to the left ear while participants attended a target syllable compared to the detection of syllables which occur binaurally (Jancke and Shah, 2002). The right F2ant was also involved during tasks previously mentioned as involved in an attentional component (Poldrack et al., 1999; Sekiyama et al., 2003). The activation of this region would correspond to an additional recruitment of the right F3opd in the processing of sounds from the subdominant ear according to Jancke and Shah (2002). In a dichotic listening task, Vigneau et al. (2011) have shown the recruitment of this region along with a rightward asymmetry. The right F2ant was recruited when participants were required to detect deviants compared to standard tones (Petit et al., 2007), which suggests that it is

involved in auditory selective attention but not specifically for language (Vigneau et al., 2011).

Results from Vigneau et al. (2011) demonstrated a limited RH involvement during tasks that require access to semantic representation such as reading, semantic priming and semantic retrieval. The only clusters that gathered RH lexico-semantic activations were the right F3opd and the right anterior part of the insula (INSant). As discussed earlier, these two clusters lack specificity for semantic processing. Additionally, no cluster was identified in the temporal lobe (Vigneau et al., 2011). One possible interpretation is that this result relates to the fact that these contracts included only high-level reference tasks.

The low RH involvement in lexico-semantic tasks is consistent with the absence of consequence of rTMS applied on the frontal cortex within the RH during verb generation performances of healthy participants (Thiel et al., 2005). It is also in line with the split-brain patient studies that showed poor reading performance of the RH. It is also consistent with Wada studies which showed deficits in object naming and word reading after LH anesthesia (Fedio et al., 1997). In one review, Gazzaniga (2000) concluded that a lexicon is rarely present in the isolated RH, and when present, it is limited. However, split-brain patients could recognize written or auditory words using their RH when they gave non-verbal answers (Searleman, 1997), and the observation of partial recovery in lexical processing after LH lesion seems to be at odds with the apparent absence of RH contribution found in Vigneau et al. (2011). The huge LH asymmetry during

lexico-semantic tasks evidenced in Vigneau et al. (2011) might be the result of the transcallosal inhibition originated from the LH towards the RH in healthy participants. This hypothesis was proposed by different researchers as the best explanation for the RH frontal activation during language tasks in phase in the acute stage after LH injuries (Thulborn et al., 1999; Price and Crinion, 2005). It is supported by the observation that a suppressive action of rTMS on the right inferior frontal gyrus led to improvement of picture naming in aphasic patients (Naeser et al., 2005). This phenomenon has also been found in the motor system. The rTMS suppressive stimulation of the LH primary motor area in stroke patients improved their right paretic hand functions (Grefkes et al., 2009). This hypothesis contradicts with our hypothesis that the role of RH in language is domain-general, future studies need to confirm it.

Representation of conceptual knowledge

Convergent evidence has suggested the bilateral anterior temporal lobes (ATLs) as important for the semantic representation of words, people, objects, and social concepts (Olson et al., 2007; Sergent et al., 1992; Marinkovic et al., 2003; Visser et al., 2010; Patterson et al., 2007; Pobric et al., 2007; Lambon Ralph et al., 2010; Lambon Ralph, 2014). More recently, research attention has been shifted to investigating the specific functions of the right and left ATLs (Olson et al., 2007; Drane et al., 2013; Wong and Gallate, 2012; Gainotti, 2012, 2013; Olson et al., 2013; Pobric et al., 2017; Visser et al.,

2010; Lambon Ralph et al., 2010; Lambon Ralph, 2014). Using activation likelihood estimation (ALE), a recent study did a meta-analysis on 97 functional neuroimaging studies on the role of ATLs in conceptual knowledge (Rice et al., 2015). They found that the overall pattern of bilateral recruitment of the ATLs across different stimulus types is in line with the notion of a distributed system, which was developed by the observations of the consequences of bilateral ATL damage versus unilateral ATL damage (Lambon Ralph et al., 2010; Schariro et al., 2013). The left ATL recruitment bias for word retrieval tasks is consistent with discoveries from various patient groups, which includes the unilateral resection in patients with temporal lobe epilepsy (Seidenberg et al., 2002; Drane et al., 2013; Lambon Ralph et al., 2012) and the consequences of left-dominant ATL atrophy in SD (Lambon Ralph et al., 2001). However, there was still some disagreement between the results of this meta-analysis and many other clinical studies on the consequence of ATL damages. For example, many clinical studies have found that abnormalities in social behaviors are more prevalent in patients with greater right ATL damage (Edwards-Lee et al., 1997; Miller et al., 1997; Chan et al., 2009; Zahn et al.).

Regarding the left-right ATL differences, there was not one disparity between the meta-analysis on functional neuroimaging results and neuropsychology literature (Rice et al., 2015). Given that both L>R and R>L semantic dementia patients had altered social behavior and neuropsychiatric features when being tested (Chan et al., 2009), the bilateral activations for social concepts were consistent with the neuropsychological literature.

However, the lack of a right-biased activation for face-based stimuli was surprising for face-based stimuli is surprising given findings that have demonstrated face recognition deficits in patients with progressive or chronic damage to the right ATL (Ellis et al., 1989; Tranel et al., 1997; Evans et al., 1995; Damasio et al., 2004). Recently, Drane et al. (2013) directly compared left and right ATL-resected temporal lobe epilepsy patients on various aspects of face processing. They found that the left ATL-resected patients were more anomia than the right ATL counterparts. Moreover, the reverse was also true for face familiarity and identification; the left ATL cases were mildly impaired when compared with controls, the right ATL group was significantly worse. Future research should explore this issue in more detail. Bilateral activation should be expected if different components of a task (e.g. face recognition vs. name retrieval) were supported separately by each hemisphere. Again, this result is consistent with our hypothesis that the areas in the RH represent conceptual aspects of where areas in the LH represent semantic knowledge; they work together to represent conceptual knowledge. However, an alternative hypothesis raised by Drane et al. (2013). More specifically, following the convergent inputs and outputs of the contralateral ATL region, the representations, as a result, are not transmodal in nature. Rather, the patients in the study have demonstrated a prosopagnosic impairment in which identification of familiar people was impaired when presented as faces but was much better when the same information was probed from a different modality (e.g. spoken names). This might suggest some sort of disruption

between visual input and the semantic system rather than the deficit within the semantic system itself. It might be possible that the right ATL patients who demonstrated visual face recognition because the right visual input (from the ventral occipito-temporal regions) is lateralized to the RH even though one's knowledge itself is bilaterally distributed across the ATL. If this hypothesis is correct, then the prosopagnosia of the right ATL patients would follow from the same neurocomputational principle of different connectivity which many used to explain the left ATL basis for speech production (Schapiro et al., 2013; Lambon et al., 2001).

By contrast, using a high-level contrast, Vigneasu et al. (2011) identified unilateral activation clusters in the temporal lobe when processing contextual information.

Considering that the tasks selected for the processing of context belonged to high-level contrast, Vigneau et al. (2010) suggested that the RH participation during sentence/text processing maybe important according to the number of RH-unilateral peaks, which is for sure related to the fact that pragmatic processes come into play at both the sentence-text levels. Notably, sentence/text processing is the sole component in which RH-unilateral clusters were found in the temporal lobe. Thus, the right temporal lobe plays a role in sentence/text comprehension.

These findings were in line with the observation that patients with temporal lobe damage who did not show any aphasic but had problems with tasks related integration that relied on the processing of context. Moreover, these patients typically missed the

general idea of story conversations (Jung-Beeman, 2005), who were impaired in the interpreting a narrative discourse (Kaplan et al., 1990), who had impairments in the coherent integration of meaning (Beeman et al., 2000), and lack inference-related capacities (Beeman, 1993). Moreover, they also display discrepancies between everyday discourse and its context (Faure, 1993). According to Londell, the RH allows one to move beyond the literal meaning of a word, which is a task necessary to appropriately interpret an utterance in context (Lindell, 1996).

The right T1 (posterior part of the right superior temporal aggregated) unilateral peaks were found during comprehension of auditory sentences from previous studies: understanding stories (Ferstl and von Cramon, 2002), listening to permuted narrative (Kansakuy et al., 2000), syntactic movement study (Ben Shachar et al., 2004), and in tasks targeting the use of context (Kircher et al., 2001; Vogeley et al., 2001; Luke et al., 2002). The right T2p (the middle part of the STS) aggregated peaks of activation from tasks that involve the processing of context such as reading a dialog (Homae et al., 2003), evaluating the semantic plausibility on sentences (Zysset et al., 2002), generating the final word of a sentence (Kircher et al., 2001). Thus, this area is involved in context processing, which is consistent with another meta-analysis conducted by Ferstl et al. (2000), revealing bilateral temporal activation when context processing was compared to the language baseline. Moreover, the authors went one step more to demonstrate that this RH-temporal participant is unilateral and thus RH specific when high-level contrasts are

chosen (Ferstl et al., 2000). Thus, this might explain why Rice et al. (2015) found a bilateral representation of conceptual knowledge but the meta-analysis in Vigneau et al. (2011) only showed right-lateralized activation peaks in the temporal lobe.

Concluding remarks

To summarize, we reviewed the contributions of the right hemisphere (RH) to speech production, speech comprehension, prosody, mapping from sound to lexical meaning, phonological decisions, and lexical-semantic processing. Understanding of neural mechanisms and the distinct contributions of individual brain regions to language is of great importance, not only for neuroscience research that aims to understand the brain organizations and their functional roles, but also for clinical research focusing on the mechanisms and interventions of speech-related conditions, such as aphasia. For example, neurologists and physiologists have debated for a century whether the RH recruitment facilitates or impedes recovery from stroke. Some earlier case studies argued that RH plays a role in aphasia rehabilitation (see Basso (1989) for a review). With the development of research technology, the exact role of RH becomes less clear (Terkeltaub et al., 2012). Some functional imaging studies have found compensatory RH involvement during aphasia recovery whereas others have concluded that RH activity is totally “ineffective” (e.g. Postman-Caucheteux et al., 2010; Richter et al., 2008). Thus,

understanding the exact contribution of RH in language could help clinicians better diagnose and make better therapy plans for aphasia patients.

Evidence from multiple studies aligns with our hypothesis that the role of the right hemisphere in language is domain-general rather than linguistic. However, there are at least three limitations observed in the reviewed studies that could potentially weaken this hypothesis: (1) most studies failed to disassociate domain-general functions from language-specific functions since language is a highly complicated cognitive process that requires multiple domain-general processes to work in coordination. (2) Most of these studies tested language within the context of a task, which made the explanation that the recruitment of the RH in language likely due to extraneous task-induced language demand rather than language itself. (3) Previous functional imaging research has primarily relied on univariate analysis, which can only show that different brain regions are activated at the same time, but gives no insights into how these regions covary together or can be separated into functionally differentiable systems (Campell et al. 2018). Further, many lesion studies have reported the coactivations of RH homologous areas. However, these coactivations could not be explained using the claim that they are recruited by domain-general operations rather than domain-general processes. Unlike the transient disruption created by TMS, lesions caused by brain injury can provide information regarding the brain plasticity after brain damage. Specifically, damage to the areas in the language network can result in brain reorganization, which increased

activities in the areas homologous to the damaged tissue (Blasi et al., 2002; Thomas et al., 1997; Buckner et al., 1996; Cao et al., 1999; Winhuisen et al., 2005). Again, this has to do with brain plasticity, which is beyond the scope of our discussion.

Taken together, we suggest that the role of the right hemisphere in language is domain-general rather than linguistic. We propose three specific directions for future research: First, future work should have designs that allow for conditions in which language demand is controlled but executive demand is varied. Secondly, most existing works focused on aphasia induced by stroke, and few studies have recruited patients with other neurological conditions that may affect language functions, such as traumatic brain injury and brain tumor. Studies focusing on these patients will enable a more comprehensive understanding of language functions and processes. Lastly, from a technical perspective, approaches to separate domain-general RH systems from language specific LH systems is to use data-driven methods like independent components analysis (ICA), which decomposes the ongoing fMRI signal into a set of independent brain regions that covary together over time. Campbell et al. (2016) and Davis et al. (2014) recently used this approach to differentiate domain-general networks and the domain-specific syntax system successfully .

References

- Alexander, G. M., Altemus, M., Peterson, B. S., & Wexler, B. E. (2002). Replication of a premenstrual decrease in right-ear advantage on language-related dichotic listening tests of cerebral laterality. *Neuropsychologia*, 40(8), 1293-1299.
- Aziz-Zadeh, L., Sheng, T., & Gheytanchi, A. (2010). Common premotor regions for the perception and production of prosody and correlations with empathy and prosodic ability. *PloS one*, 5(1).
- Awh, E., Jonides, J., Smith, E. E., Schumacher, E. H., Koeppe, R. A., & Katz, S. (1996). Dissociation of storage and rehearsal in verbal working memory: Evidence from positron emission tomography. *Psychological Science*, 7(1), 25-31
- Barch, D. M., & Csernansky, J. G. (2007). Abnormal parietal cortex activation during working memory in schizophrenia: verbal phonological coding disturbances versus domain-general executive dysfunction. *American Journal of Psychiatry*, 164(7), 1090-1098.
- Baum, S. R., & Pell, M. D. (1997). Production of affective and linguistic prosody by brain-damaged patients. *Aphasiology*, 11(2), 177-198.
- Baum, S. R., & Pell, M. D. (1999). The neural bases of prosody: Insights from lesion studies and neuroimaging. *Aphasiology*, 13(8), 581-608.
- Broca, P. (1865). Sur la faculté du langage articulé. *Bulletin de la Soci-été d'Anthropologie de Paris*, 6, 377-393.
- Bozic, M., Tyler, L. K., Ives, D. T., Randall, B., & Marslen-Wilson, W. D. (2010). Bihemispheric foundations for human speech comprehension. *Proceedings of the National Academy of Sciences*, 107(40), 17439-17444.
- Bais, L., Hoekert, M., Links, T. P., Knegtering, R., & Aleman, A. (2010). Brain asymmetry for emotional prosody in Klinefelter's syndrome: Causal relations investigated with tms. *Schizophrenia research*, 2(117), 233-234.
- Brennan, J., & Pykkänen, L. (2012). The time-course and spatial distribution of brain activity associated with sentence processing. *Neuroimage*, 60(2), 1139-1148.
- Buchsbaum BR, D'Esposito M (2009) Repetition suppression and reactivation in auditory-verbal short-term recognition memory. *Cereb Cortex* 19:1474-1485.
- Bonelli, S. B., Thompson, P. J., Yogarajah, M., Vollmar, C., Powell, R. H., Symms, M. R., ... & Duncan, J. S. (2012). Imaging language networks before and after anterior temporal lobe resection: results of a longitudinal fMRI study. *Epilepsia*, 53(4), 639-650.
- Baynes, K., Tramo, M. J., & Gazzaniga, M. S. (1992). Reading with a limited lexicon in the right hemisphere of a callosotomy patient. *Neuropsychologia*, 30(2), 187-200.

Beeman, M. (1993). Semantic processing in the right hemisphere may contribute to drawing inferences from discourse. *Brain and language*, 44, 80-80.

Beeman, M. J., & Chiarello, C. (1998). Complementary right-and left-hemisphere language comprehension. *Current directions in psychological science*, 7(1), 2-8.

Beeman, M. J., Bowden, E. M., & Gernsbacher, M. A. (2000). Right and left hemisphere cooperation for drawing predictive and coherence inferences during normal story comprehension. *Brain and language*, 71(2), 310-336.

Bowers, D., Bauer, R. M., & Heilman, K. M. (1993). The nonverbal affect lexicon: theoretical perspectives from neuropsychological studies of affect perception. *Neuropsychology*, 7(4), 433.

Brück, C., Kreifelts, B., & Wildgruber, D. (2011). Emotional voices in context: a neurobiological model of multimodal affective information processing. *Physics of Life Reviews*, 8(4), 383-403.

Buckner, R. L., Corbetta, M., Schatz, J., Raichle, M. E., & Petersen, S. E. (1996). Preserved speech abilities and compensation following prefrontal damage. *Proceedings of the national Academy of Sciences*, 93(3), 1249-1253.

Blasi, V., Young, A. C., Tansy, A. P., Petersen, S. E., Snyder, A. Z., & Corbetta, M. (2002). Word retrieval learning modulates right frontal cortex in patients with left frontal damage. *Neuron*, 36(1), 159-170.

Cancelliere, A. E., & Kertesz, A. (1990). Lesion localization in acquired deficits of emotional expression and comprehension. *Brain and cognition*, 13(2), 133-147.

Campbell, K. L., Samu, D., Davis, S. W., Geerligs, L., Mustafa, A., & Tyler, L. K. (2016). Robust resilience of the frontotemporal syntax system to aging. *Journal of Neuroscience*, 36(19), 5214-5227.

Campbell, K. L., & Tyler, L. K. (2018). Language-related domain-specific and domain-general systems in the human brain. *Current opinion in behavioral sciences*, 21, 132-137.

Cao, Y., Vikingstad, E. M., George, K. P., Johnson, A. F., & Welch, K. M. A. (1999). Cortical language activation in stroke patients recovering from aphasia with functional MRI. *Stroke*, 30(11), 2331-2340.

Chee, M. W., O'Craven, K. M., Bergida, R., Rosen, B. R., & Savoy, R. L. (1999). Auditory and visual word processing studied with fMRI. *Human brain mapping*, 7(1), 15-28.

Catani, M., Jones, D. K., & Ffytche, D. H. (2005). Perisylvian language networks of the human brain. *Annals of Neurology: Official Journal of the American Neurological Association and the Child Neurology Society*, 57(1), 8-16.

Chang, E. F., Wang, D. D., Perry, D. W., Barbaro, N. M., & Berger, M. S. (2011). Homotopic organization of essential language sites in right and bilateral cerebral hemispheric dominance. *Journal of neurosurgery*, 114(4), 893-902.

Chan, D., Anderson, V., Pijnenburg, Y., Whitwell, J., Barnes, J., Scallan, R., ... & Fox, N. C. (2009). The clinical profile of right temporal lobe atrophy. *Brain*, 132(5), 1287-1298.

C. Wilde, M. (2010). Lesion location and repeatable battery for the assessment of neuropsychological status performance in acute ischemic stroke. *The Clinical Neuropsychologist*, 24(1), 57-69.

Devlin, J. T., Matthews, P. M., & Rushworth, M. F. (2003). Semantic processing in the left inferior prefrontal cortex: a combined functional magnetic resonance imaging and transcranial magnetic stimulation study. *Journal of cognitive neuroscience*, 15(1), 71-84.

Dewarrat, G. M., Annoni, J. M., Fornari, E., Carota, A., Bogousslavsky, J., & Maeder, P. (2009). Acute aphasia after right hemisphere stroke. *Journal of neurology*, 256(9), 1461-1467.

Devlin, J. T., & Watkins, K. E. (2007). Stimulating language: insights from TMS. *Brain*, 130(3), 610-622.

Deschamps, I., Baum, S. R., & Gracco, V. L. (2014). On the role of the supramarginal gyrus in phonological processing and verbal working memory: evidence from rTMS studies. *Neuropsychologia*, 53, 39-46.

Damasio, H., Tranel, D., Grabowski, T., Adolphs, R., & Damasio, A. (2004). Neural systems behind word and concept retrieval. *Cognition*, 92(1-2), 179-229.

Drane, D. L., Ojemann, J. G., Phatak, V., Loring, D. W., Gross, R. E., Hebb, A. O., ... & Barsalou, L. (2013). Famous face identification in temporal lobe epilepsy: support for a multimodal integration model of semantic memory. *Cortex*, 49(6), 1648-1667.

Dara, C., Kirsch-Darrow, L., Ochfeld, E., Slenz, J., Agranovich, A., Vasconcellos-Faria, A., ... & Korte, K. B. (2013). Impaired emotion processing from vocal and facial cues in frontotemporal dementia compared to right hemisphere stroke. *Neurocase*, 19(6), 521-529.

Davis, C. L., Oishi, K., Faria, A. V., Hsu, J., Gomez, Y., Mori, S., & Hillis, A. E. (2016). White matter tracts critical for recognition of sarcasm. *Neurocase*, 22(1), 22-29.

Davis, S. W., Zhuang, J., Wright, P., & Tyler, L. K. (2014). Age-related sensitivity to task-related modulation of language-processing networks. *Neuropsychologia*, 63, 107-115.

Duffau, H. (2005). Lessons from brain mapping in surgery for low-grade glioma: insights into associations between tumour and brain plasticity. *The Lancet Neurology*, 4(8), 476-486.

Dondaine, T., Robert, G., Péron, J., Grandjean, D., Vérin, M., Drapier, D., & Millet, B. (2014). Biases in facial and vocal emotion recognition in chronic schizophrenia. *Frontiers in psychology*, 5, 900.

de Almeida, R. G., Riven, L., Manouilidou, C., Lungu, O., Dwivedi, V. D., Jarema, G., & Gillon, B. (2016). The neuronal correlates of indeterminate sentence comprehension: an fMRI Study. *Frontiers in human neuroscience*, 10, 614.

ELLIS, A. W., YOUNG, A. W., & CRITCHLEY, E. M. (1989). Loss of memory for people following temporal lobe damage. *Brain*, 112(6), 1469-1483.

Evans, J. J., Heggs, A. J., Antoun, N., & Hodges, J. R. (1995). Progressive prosopagnosia associated with selective right temporal lobe atrophy: A new syndrome?. *Brain*, 118(1), 1-13.

Edwards-Lee, T., Miller, B. L., Benson, D. F., Cummings, J. L., Russell, G. L., Boone, K., & Mena, I. (1997). The temporal variant of frontotemporal dementia. *Brain: a journal of neurology*, 120(6), 1027-1040.

Engelhardt, P. E., Nigg, J. T., & Ferreira, F. (2017). Executive function and intelligence in the resolution of temporary syntactic ambiguity: An individual differences investigation. *The Quarterly Journal of Experimental Psychology*, 70(7), 1263-1281.

Epstein, C. M., Lah, J. J., Meador, K., Weissman, J. D., Gaitan, L. E., & Dihenia, B. (1996). Optimum stimulus parameters for lateralized suppression of speech with magnetic brain stimulation. *Neurology*, 47(6), 1590-1593.

Epstein, C. M. (1998). Transcranial magnetic stimulation: language function. *Journal of Clinical Neurophysiology*, 15(4), 325-332.

Fedio, P., August, A., Patronas, N., Sato, S., & Kufta, C. (1997). Semantic, phonological, and perceptual changes following left and right intracarotid injection (Wada) with a low amytal dosage. *Brain and Cognition*, 33(1), 98-117.

Fernández, G., Weis, S., Stoffel-Wagner, B., Tendolkar, I., Reuber, M., Beyenburg, S., ... & Reul, J. (2003). Menstrual cycle-dependent neural plasticity in the adult human brain is hormone, task, and region specific. *Journal of Neuroscience*, 23(9), 3790-3795.

Gajardo-Vidal, A., Lorca-Puls, D. L., Hope, T. M., Parker Jones, O., Seghier, M. L., Prejawa, S., ... & Price, C. J. (2018). How right hemisphere damage after stroke can impair speech comprehension. *Brain*, 141(12), 3389-3404.

Gazzaniga, M. S., LeDOUX, J. E., & Wilson, D. H. (1977). Language, praxis, and the right hemisphere: Clues to some mechanisms of consciousness. *Neurology*, 27(12), 1144-1144.

Gernsbacher, M. A., & Kaschak, M. P. (2003). Neuroimaging studies of language production and comprehension. *Annual review of psychology*, 54(1), 91-114.

Gur, R. C., Alsop, D., Glahn, D., Petty, R., Swanson, C. L., Maldjian, J. A., ... & Gur, R. E. (2000). An fMRI study of sex differences in regional activation to a verbal and a spatial task. *Brain and language*, 74(2), 157-170.

Gainotti, G. (2012). The format of conceptual representations disrupted in semantic dementia: a position paper. *Cortex*, 48(5), 521-529.

Gainotti, G. (2013). Laterality effects in normal subjects' recognition of familiar faces, voices and names. Perceptual and representational components. *Neuropsychologia*, 51(7), 1151-1160.

Gazzaniga, M. S. (1983). Right hemisphere language following brain bisection: A 20-year perspective. *American Psychologist*, 38(5), 525.

- Grefkes, C., Nowak, D. A., Wang, L. E., Dafotakis, M., Eickhoff, S. B., & Fink, G. R. (2010). Modulating cortical connectivity in stroke patients by rTMS assessed with fMRI and dynamic causal modeling. *Neuroimage*, 50(1), 233-242.
- Hampshire, A., Thompson, R., Duncan, J., & Owen, A. M. (2009). Selective tuning of the right inferior frontal gyrus during target detection. *Cognitive, Affective, & Behavioral Neuroscience*, 9(1), 103-112.
- Hampshire, A., Chamberlain, S. R., Monti, M. M., Duncan, J., & Owen, A. M. (2010). The role of the right inferior frontal gyrus: inhibition and attentional control. *Neuroimage*, 50(3), 1313-1319.
- Hausmann, M., & Güntürkün, O. (2000). Steroid fluctuations modify functional cerebral asymmetries: the hypothesis of progesterone-mediated interhemispheric decoupling. *Neuropsychologia*, 38(10), 1362-1374.
- Hillis, A. E., Rapp, B., Romani, C., & Caramazza, A. (1990). Selective impairment of semantics in lexical processing. *Cognitive neuropsychology*, 7(3), 191-243.
- Hartwigsen, G., Baumgaertner, A., Price, C. J., Koehnke, M., Ulmer, S., & Siebner, H. R. (2010a). Phonological decisions require both the left and right supramarginal gyri. *Proceedings of the National Academy of Sciences*, 107(38), 16494-16499.
- Hartwigsen, G., Price, C. J., Baumgaertner, A., Geiss, G., Koehnke, M., Ulmer, S., & Siebner, H. R. (2010b). The right posterior inferior frontal gyrus contributes to phonological word decisions in the healthy brain: evidence from dual-site TMS. *Neuropsychologia*, 48(10), 3155-3163.
- Indefrey, P. (2011). The spatial and temporal signatures of word production components: a critical update. *Frontiers in psychology*, 2, 255.
- Jonides, J., Schumacher, E. H., Smith, E. E., Koeppe, R. A., Awh, E., Reuter-Lorenz, P. A., ... & Willis, C. R. (1998). The role of parietal cortex in verbal working memory. *Journal of neuroscience*, 18(13), 5026-5034.
- Jacquemot, C., & Scott, S. K. (2006). What is the relationship between phonological short-term memory and speech processing?. *Trends in cognitive sciences*, 10(11), 480-486.
- Keidel, J. L., Welbourne, S. R., & Ralph, M. A. L. (2010). Solving the paradox of the equipotential and modular brain: a neurocomputational model of stroke vs. slow-growing glioma. *Neuropsychologia*, 48(6), 1716-1724.
- Knecht, S., Draeger, B., Deppe, M., Bobe, L., Lohmann, H., Floel, A., et al. (2000). Handedness and hemispheric language dominance in healthy humans. *Brain*, 123, 2512-2518.
- Kielar, A., Deschamps, T., Jokel, R., & Meltzer, J. A. (2016). Functional reorganization of language networks for semantics and syntax in chronic stroke: Evidence from MEG. *Human brain mapping*, 37(8), 2869-2893.

Krieg, S. M., Sollmann, N., Hauck, T., Ille, S., Meyer, B., & Ringel, F. (2014). Repeated mapping of cortical language sites by preoperative navigated transcranial magnetic stimulation compared to repeated intraoperative DCS mapping in awake craniotomy. *BMC neuroscience*, 15(1), 20.

Koelsch, S., Schulze, K., Sammler, D., Fritz, T., Müller, K., & Gruber, O. (2009). Functional architecture of verbal and tonal working memory: an fMRI study. *Human brain mapping*, 30(3), 859-873.

Key-DeLyria, S. E., & Altmann, L. J. (2016). Executive function and ambiguous sentence comprehension. *American journal of speech-language pathology*, 25(2), 252-267.

Kaplan, E., Naeser, M. A., Martin, P. I., Ho, M., Wang, Y., Baker, E., & Pascual-Leone, A. (2010). Horizontal portion of arcuate fasciculus fibers track to pars opercularis, not pars triangularis, in right and left hemispheres: a DTI study. *Neuroimage*, 52(2), 436-444.

Kirschen, M. P., Davis-Ratner, M. S., Jerde, T. E., Schraedley-Desmond, P., & Desmond, J. E. (2006). Enhancement of phonological memory following transcranial magnetic stimulation (TMS). *Behavioural neurology*, 17(3-4), 187-194.

Kotz, S. A., Meyer, M., & Paulmann, S. (2006). Lateralization of emotional prosody in the brain: an overview and synopsis on the impact of study design. *Progress in brain research*, 156, 285-294.

Kipps, C. M., Duggins, A. J., McCusker, E. A., & Calder, A. J. (2007). Disgust and happiness recognition correlate with anteroventral insula and amygdala volume respectively in preclinical Huntington's disease. *Journal of cognitive neuroscience*, 19(7), 1206-1217.

Kansaku, K., Yamaura, A., & Kitazawa, S. (2000). Sex differences in lateralization revealed in the posterior language areas. *Cerebral Cortex*, 10(9), 866-872.

Karnath, H. O. (2001). New insights into the functions of the superior temporal cortex. *Nature Reviews Neuroscience*, 2(8), 568-576.

Kimura, D. (1961). Cerebral dominance and the perception of verbal stimuli. *Canadian Journal of Psychology/Revue canadienne de psychologie*, 15(3), 166.

Kummerer, D., Hartwigsen, G., Kellmeyer, P., Glauche, V., Mader, I., Kloppel, S., ... & Saur, D. (2013). Damage to ventral and dorsal language pathways in acute aphasia. *Brain* 136 (Pt 2): 619-629.

Kaplan, J. A., Brownell, H. H., Jacobs, J. R., & Gardner, H. (1990). The effects of right hemisphere damage on the pragmatic interpretation of conversational remarks. *Brain and language*, 38(2), 315-333.

Lambon Ralph MA . 2014. Neurocognitive insights on conceptual knowledge and its breakdown. *Philos Trans R Soc Lond B Biol Sci*. 369:1-12.

Leuthardt, E., Pei, X. M., Breshears, J., Gaona, C., Sharma, M., Freudenburg, Z., ... & Schalk, G. (2012). Temporal evolution of gamma activity in human cortex during an overt and covert word repetition task. *Frontiers in human neuroscience*, 6, 99.

Lioumis, P., Zhdanov, A., Mäkelä, N., Lehtinen, H., Wilenius, J., Neuvonen, T., ... & Mäkelä, J. P. (2012). A novel approach for documenting naming errors induced by navigated transcranial magnetic stimulation. *Journal of neuroscience methods*, 204(2), 349-354.

Lindell, A. K. (2006). In your right mind: Right hemisphere contributions to language processing and production. *Neuropsychology review*, 16(3), 131-148.

Larsen, B., Skinhøj, E., & Lassen, N. A. (1979). Cortical activity of left and right hemisphere provoked by reading and visual naming. A rCBF study. *Acta Neurologica Scandinavica. Supplementum*, 6-7.

Lioumis, P., Zhdanov, A., Mäkelä, N., Lehtinen, H., Wilenius, J., Neuvonen, T., ... & Mäkelä, J. P. (2012). A novel approach for documenting naming errors induced by navigated transcranial magnetic stimulation. *Journal of neuroscience methods*, 204(2), 349-354.

Levy, J., & Trevarthen, C. (1977). Perceptual, semantic and phonetic aspects of elementary language processes in split-brain patients. *Brain*, 100(1), 105-118.

Lancker, D. V., & Sidtis, J. J. (1992). The identification of affective-prosodic stimuli by left-and right-hemisphere-damaged subjects: all errors are not created equal. *Journal of Speech, Language, and Hearing Research*, 35(5), 963-970.

Mitchell, R. L., & Ross, E. D. (2013). Attitudinal prosody: What we know and directions for future study. *Neuroscience & Biobehavioral Reviews*, 37(3), 471-479.

Marinkovic, K., Dhond, R. P., Dale, A. M., Glessner, M., Carr, V., & Halgren, E. (2003). Spatiotemporal dynamics of modality-specific and supramodal word processing. *Neuron*, 38(3), 487-497.

Marini, A., Carlomagno, S., Caltagirone, C., & Nocentini, U. (2005). The role played by the right hemisphere in the organization of complex textual structures. *Brain and language*, 93(1), 46-54.

Mariën, P., Paghera, B., De Deyn, P. P., & Vignolo, L. A. (2004). Adult crossed aphasia in dextrals revisited. *Cortex*, 40(1), 41-74.

McGlone, J. (1980). Sex differences in human brain asymmetry: A critical survey. *Behavioral and brain sciences*, 3(2), 215-227.

Miller, B. L., Darby, A., Benson, D. F., Cummings, J. L., & Miller, M. H. (1997). Aggressive, socially disruptive and antisocial behaviour associated with fronto-temporal dementia. *The British journal of psychiatry*, 170(2), 150-155.

Milner, B., Taylor, L., & Sperry, R. W. (1968). Lateralized suppression of dichotically presented digits after commissural section in man. *Science*, 161(3837), 184-185.

Miller, E. K., & Cohen, J. D. (2001). An integrative theory of prefrontal cortex function. *Annual review of neuroscience*, 24(1), 167-202.

McDermott, K. B., Petersen, S. E., Watson, J. M., & Ojemann, J. G. (2003). A procedure for identifying regions preferentially activated by attention to semantic and phonological relations using functional magnetic resonance imaging. *Neuropsychologia*, 41(3), 293-303.

Mason, R. A., & Just, M. A. (2007). Lexical ambiguity in sentence comprehension. *Brain research*, 1146, 115-127.

Meltzer, J. A., McArdle, J. J., Schafer, R. J., & Braun, A. R. (2010). Neural aspects of sentence comprehension: syntactic complexity, reversibility, and reanalysis. *Cerebral cortex*, 20(8), 1853-1864.

Mohr, B., Difrancesco, S., Harrington, K., Evans, S., & Pulvermüller, F. (2014). Changes of right-hemispheric activation after constraint-induced, intensive language action therapy in chronic aphasia: fMRI evidence from auditory semantic processing1. *Frontiers in Human Neuroscience*, 8, 919.

Naeser, M. A., Martin, P. I., Theoret, H., Kobayashi, M., Fregni, F., Nicholas, M., ... & Pascual-Leone, A. (2011). TMS suppression of right pars triangularis, but not pars opercularis, improves naming in aphasia. *Brain and language*, 119(3), 206-213.

Naeser, M. A., Martin, P. I., Nicholas, M., Baker, E. H., Seekins, H., Kobayashi, M., ... & Doron, K. W. (2005). Improved picture naming in chronic aphasia after TMS to part of right Broca's area: an open-protocol study. *Brain and language*, 93(1), 95-105.

Olson, I. R., Plotzker, A., & Ezzyat, Y. (2007). The enigmatic temporal pole: a review of findings on social and emotional processing. *Brain*, 130(7), 1718-1731.

Price, C. J., & Crinion, J. (2005). The latest on functional imaging studies of aphasic stroke. *Current opinion in neurology*, 18(4), 429-434.

Patterson, K., Nestor, P. J., & Rogers, T. T. (2007). Where do you know what you know? The representation of semantic knowledge in the human brain. *Nature Reviews Neuroscience*, 8(12), 976-987.

Pascual-Leone, A., Gates, J. R., & Dhuna, A. (1991). Induction of speech arrest and counting errors with rapid-rate transcranial magnetic stimulation. *Neurology*, 41(5), 697-702.

Price CJ, Moore CJ, Humphreys GW, Wise RJS (1997) Segregating semantics from phonological processes during reading. *J Cogn Neurosci* 9:727-733.

Picht, T., Krieg, S. M., Sollmann, N., Rösler, J., Niraula, B., Neuvonen, T., ... & Meyer, B. (2013). A comparison of language mapping by preoperative navigated transcranial magnetic stimulation and direct cortical stimulation during awake surgery. *Neurosurgery*, 72(5), 808-819.

Pujol, J., Deus, J., Losilla, J. M., & Capdevila, A. (1999). Cerebral lateralization of language in normal left-handed people studies by functional MRI. *Neurology*, 52, 1038-1043.

Picht, T., Krieg, S. M., Sollmann, N., Rösler, J., Niraula, B., Neuvonen, T., ... & Meyer, B. (2013). A comparison of language mapping by preoperative navigated transcranial magnetic stimulation and direct cortical stimulation during awake surgery. *Neurosurgery*, 72(5), 808-819.

Poeppel, D., & Hickok, G. (2004). Towards a new functional anatomy of language.

Poldrack, R. A., Wagner, A. D., Prull, M. W., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. (1999). Functional specialization for semantic and phonological processing in the left inferior prefrontal cortex. *Neuroimage*, 10(1), 15-35.

Pichon, S., & Kell, C. A. (2013). Affective and sensorimotor components of emotional prosody generation. *Journal of Neuroscience*, 33(4), 1640-1650.

Pell, M. D. (2002). Evaluation of nonverbal emotion in face and voice: Some preliminary findings on a new battery of tests. *Brain and Cognition*, 48(2-3), 499-504.

Pell, M. D. (2006). Cerebral mechanisms for understanding emotional prosody in speech. *Brain and language*, 96(2), 221-234.

Péron, J., Cekic, S., Haegelen, C., Sauleau, P., Patel, S., Drapier, D., ... & Grandjean, D. (2015). Sensory contribution to vocal emotion deficit in Parkinson's disease after subthalamic stimulation. *cortex*, 63, 172-183.

Patel, S., Oishi, K., Wright, A., Sutherland-Foggio, H., Saxena, S., Sheppard, S. M., & Hillis, A. E. (2018). Right hemisphere regions critical for expression of emotion through prosody. *Frontiers in neurology*, 9, 224.

Pobric, G., Jefferies, E., & Ralph, M. A. L. (2007). Anterior temporal lobes mediate semantic representation: mimicking semantic dementia by using rTMS in normal participants. *Proceedings of the National Academy of Sciences*, 104(50), 20137-20141.

Riecker, A., Wildgruber, D., Dogil, G., Grodd, W., & Ackermann, H. (2002). Hemispheric lateralization effects of rhythm implementation during syllable repetitions: An fMRI study. *NeuroImage*, 16(1), 169-176.

Ross, E. D. (2000). Affective prosody and the aprosodias. *Principles of behavioral and cognitive neurology*, 2, 316-326.

Rasmussen, T., & Milner, B. (1975). Clinical and surgical studies of the cerebral speech areas in man. In K. J. Zulch, O. Creutzfeld, & G. C. Galbraith (Eds.), *Cerebral localization* (pp. 238-257). New York: Springer-Verlag.

Ralph, M. A. L., Sage, K., Jones, R. W., & Mayberry, E. J. (2010). Coherent concepts are computed in the anterior temporal lobes. *Proceedings of the National Academy of Sciences*, 107(6), 2717-2722.

Romero, L., Walsh, V., & Papagno, C. (2006). The neural correlates of phonological short-term memory: a repetitive transcranial magnetic stimulation study. *Journal of cognitive neuroscience*, 18(7), 1147-1155.

Ryding, E., Brådvik, B., & Ingvar, D. H. (1987). Changes of regional cerebral blood flow measured simultaneously in the right and left hemisphere during automatic speech and humming. *Brain*, 110(5), 1345-1358.

Ross, E. D., & Mesulam, M. M. (1979). Dominant language functions of the right hemisphere?: Prosody and emotional gesturing. *Archives of neurology*, 36(3), 144-148.

Ross, E. D., & Monnot, M. (2008). Neurology of affective prosody and its functional–anatomic organization in right hemisphere. *Brain and language*, 104(1), 51-74.

Ross, E. D. (2000). Affective prosody and the aprosodias. *Principles of behavioral and cognitive neurology*, 2, 316-326.

Rankin, K. P., Salazar, A., Gorno-Tempini, M. L., Sollberger, M., Wilson, S. M., Pavlic, D., ... & Miller, B. L. (2009). Detecting sarcasm from paralinguistic cues: anatomic and cognitive correlates in neurodegenerative disease. *Neuroimage*, 47(4), 2005-2015.

Riecker, A., Wildgruber, D., Dogil, G., Grodd, W., & Ackermann, H. (2002). Hemispheric lateralization effects of rhythm implementation during syllable repetitions: An fMRI study. *NeuroImage*, 16(1), 169-176.

Sammler, D., Grosbras, M. H., Anwander, A., Bestelmeyer, P. E., & Belin, P. (2015). Dorsal and ventral pathways for prosody. *Current Biology*, 25(23), 3079-3085.

Sollmann, N., Hauck, T., Hapfelmeier, A., Meyer, B., Ringel, F., & Krieg, S. M. (2013a). Intra-and interobserver variability of language mapping by navigated transcranial magnetic brain stimulation. *BMC neuroscience*, 14(1), 150.

Sollmann, N., Picht, T., Mäkelä, J. P., Meyer, B., Ringel, F., & Krieg, S. M. (2013b). Navigated transcranial magnetic stimulation for preoperative language mapping in a patient with a left frontoopercular glioblastoma: Case report. *Journal of neurosurgery*, 118(1), 175-179.

Sollmann, N., Tanigawa, N., Ringel, F., Zimmer, C., Meyer, B., & Krieg, S. M. (2014). Language and its right-hemispheric distribution in healthy brains: an investigation by repetitive transcranial magnetic stimulation. *Neuroimage*, 102, 776-788.

Schirmer, A., & Kotz, S. A. (2006). Beyond the right hemisphere: brain mechanisms mediating vocal emotional processing. *Trends in cognitive sciences*, 10(1), 24-30.

Sparing, R., Mottaghy, F. M., Hungs, M., Brüggmann, M., Foltys, H., Huber, W., & Töpper, R. (2001). Repetitive transcranial magnetic stimulation effects on language function depend on the stimulation parameters. *Journal of Clinical Neurophysiology*, 18(4), 326-330.

Spielberg, J. M., Miller, G. A., Engels, A. S., Herrington, J. D., Sutton, B. P., Banich, M. T., & Heller, W. (2011). Trait approach and avoidance motivation: lateralized neural activity associated with executive function. *Neuroimage*, 54(1), 661-670.

Szaflarski, J. P., Binder, J. R., Possing, E. T., McKiernan, K. A., Ward, B. D., & Hammeke, T. A. (2002). Language lateralization in left- handed and ambidextrous people: fMRI data. *Neurology*, 59, 238– 244.

Saur, D., & Hartwigsen, G. (2012). Neurobiology of language recovery after stroke: lessons from neuroimaging studies. *Archives of physical medicine and rehabilitation*, 93(1), S15-S25.

Sanai, N., Mirzadeh, Z., & Berger, M. S. (2008). Functional outcome after language mapping for glioma resection. *New England Journal of Medicine*, 358(1), 18-27.

Shibahara, N. (2004). Picture-name priming in the cerebral hemispheres: Evidence for phonological access in the right hemisphere. *Perceptual and motor skills*, 99(1), 305-314.

Sheppard, S. M., & Hillis, A. E. (2018). That's right! Language comprehension beyond the left hemisphere. *Brain*, 141(12), 3280-3289.

Sharp, D. J., Awad, M., Warren, J. E., Wise, R. J., Vigliocco, G., & Scott, S. K. (2010). The neural response to changing semantic and perceptual complexity during language processing. *Human brain mapping*, 31(3), 365-377.

Schlanger, B. B., Schlanger, P., & Gerstman, L. J. (1976). The perception of emotionally toned sentences by right hemisphere-damaged and aphasic subjects. *Brain and Language*, 3(3), 396-403.

Stamatakis, E. A., Marslen-Wilson, W. D., Tyler, L. K., & Fletcher, P. C. (2005). Cingulate control of fronto-temporal integration reflects linguistic demands: A three-way interaction in functional connectivity. *Neuroimage*, 28(1), 115-121.

Sergent, J., Ohta, S., & MACDONALD, B. (1992). Functional neuroanatomy of face and object processing: a positron emission tomography study. *Brain*, 115(1), 15-36.

Searleman, A. (1977). A review of right hemisphere linguistic capabilities. *Psychological Bulletin*, 84(3), 503.

Thiel, A., Habedank, B., Winhuisen, L., Herholz, K., Kessler, J., Haupt, W. F., & Heiss, W. D. (2005). Essential language function of the right hemisphere in brain tumor patients. *Annals of Neurology: Official Journal of the American Neurological Association and the Child Neurology Society*, 57(1), 128-131.

Tremblay, T., Monetta, L., & Joanne, Y. (2004). Phonological processing of words in right-and left-handers. *Brain and cognition*, 55(3), 427-432.

Thomas, C., Altenmüller, E., Marckmann, G., Kahrs, J., & Dichgans, J. (1997). Language processing in aphasia: changes in lateralization patterns during recovery reflect cerebral plasticity in adults. *Electroencephalography and clinical Neurophysiology*, 102(2), 86-97.

Tan, Y., Martin, R. C., & Van Dyke, J. A. (2017). Semantic and syntactic interference in sentence comprehension: A comparison of working memory models. *Frontiers in psychology*, 8, 198.

Tarapore, P. E., Findlay, A. M., LaHue, S. C., Lee, H., Honma, S. M., Mizuiri, D., ... & Mukherjee, P. (2013). Resting state magnetoencephalography functional connectivity in traumatic brain injury. *Journal of neurosurgery*, 118(6), 1306-1316.

Tranel, D., Damasio, H., & Damasio, A. R. (1997). A neural basis for the retrieval of conceptual knowledge. *Neuropsychologia*, 35(10), 1319-1327.

Tyler, L. K., Randall, B., & Marslen-Wilson, W. D. (2002). Phonology and neuropsychology of the English past tense. *Neuropsychologia*, 40(8), 1154-1166.

Tyler, L. K., & Marslen-Wilson, W. (2008). Fronto-temporal brain systems supporting spoken language comprehension. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363(1493), 1037-1054.

Thulborn, K. R., Carpenter, P. A., & Just, M. A. (1999). Plasticity of language-related brain function during recovery from stroke. *Stroke*, 30(4), 749-754.

van Oers, C. A., Vink, M., van Zandvoort, M. J., van der Worp, H. B., de Haan, E. H., Kappelle, L. J., ... & Dijkhuizen, R. M. (2010). Contribution of the left and right inferior frontal gyrus in recovery from aphasia. A functional MRI study in stroke patients with preserved hemodynamic responsiveness. *Neuroimage*, 49(1), 885-893.

Vigneau, M., Beaucousin, V., Hervé, P. Y., Jobard, G., Petit, L., Crivello, F., ... & Tzourio-Mazoyer, N. (2011). What is right-hemisphere contribution to phonological, lexico-semantic, and sentence processing?: Insights from a meta-analysis. *Neuroimage*, 54(1), 577-593.

Visser, M., Embleton, K. V., Jefferies, E., Parker, G. J., & Ralph, M. L. (2010). The inferior, anterior temporal lobes and semantic memory clarified: novel evidence from distortion-corrected fMRI. *Neuropsychologia*, 48(6), 1689-1696.

Wong, C., & Gallate, J. (2012). The function of the anterior temporal lobe: a review of the empirical evidence. *Brain research*, 1449, 94-116.

Wickens, S., & Perry, C. (2015). What do you mean by that?! An electrophysiological study of emotional and attitudinal prosody. *PloS one*, 10(7).

Wood, C. C., Goff, W. R., & Day, R. S. (1971). Auditory evoked potentials during speech perception. *Science*, 173(4003), 1248-1251.

Winhuisen, L., Thiel, A., Schumacher, B., Kessler, J., Rudolf, J., Haupt, W. F., & Heiss, W. D. (2005). Role of the contralateral inferior frontal gyrus in recovery of language function in poststroke aphasia: a combined repetitive transcranial magnetic stimulation and positron emission tomography study. *Stroke*, 36(8), 1759-1763.

Wilson, S. M., Saygin, A. P., Sereno, M. I., & Iacoboni, M. (2004). Listening to speech activates motor areas involved in speech production. *Nature neuroscience*, 7(7), 701.

Wray, A. (1992). *The focusing hypothesis: The theory of left hemisphere lateralised language re-examined* (Vol. 3). John Benjamins Publishing.

Wildgruber, D., Ackermann, H., Kreifelts, B., & Ethofer, T. (2006). Cerebral processing of linguistic and emotional prosody: fMRI studies. *Progress in brain research*, 156, 249-268.

Wassermann, E. M., Blaxton, T. A., Hoffman, E. A., Berry, C. D., Oletsky, H., Pascual-Leone, A., & Theodore, W. H. (1999). Repetitive transcranial magnetic stimulation of the dominant hemisphere can disrupt visual naming in temporal lobe epilepsy patients. *Neuropsychologia*, 37(5), 537-544.

Wright, A., Saxena, S., Sheppard, S. M., & Hillis, A. E. (2018). Selective impairments in components of affective prosody in neurologically impaired individuals. *Brain and cognition*, 124, 29-36.

Wingfield, A., & Grossman, M. (2006). Language and the aging brain: patterns of neural compensation revealed by functional brain imaging. *Journal of Neurophysiology*, 96(6), 2830-2839.

Yoon, J., Campanelli, L., Goral, M., Marton, K., Eichorn, N., & Obler, L. K. (2015). The effect of plausibility on sentence comprehension among older adults and its relation to cognitive functions. *Experimental aging research*, 41(3), 272-302.

Zahn, R., Moll, J., Iyengar, V., Huey, E. D., Tierney, M., Krueger, F., & Grafman, J. (2009). Social conceptual impairments in frontotemporal lobar degeneration with right anterior temporal hypometabolism. *Brain*, 132(3), 604-616.

Zaidel, E., Buser, P. A., & Rougeul-Buser, A. (1978). Cerebral correlates of conscious experience.

Zatorre, R. J., Meyer, E., Gjedde, A., & Evans, A. C. (1996). PET studies of phonetic processing of speech: review, replication, and reanalysis. *Cerebral cortex*, 6(1), 21-30.

Study	Participants	Task(s) used	Region(s) of the right hemisphere studied	Domain-general process(es) of the brain regions studied	Aspects of language supported by the brain regions studied
Sollmann et al. (2014)	50 (25f, 25m)	Object naming task using 131 colored pictures	opIFG, pSMG, aSMG, mSTG, mPrG, vPrG, mPoG, vPoG, mMFG, pMFG and pSTG (selectively in female brains)	Attention; motivation and executive control	Speech production
Deschamps et al. (2014)	16 (11f, 5m; experiment 1); 15 (9f, 6m; experiment 2)	Judgment (“same” or “different”) to pairs of auditory stimuli (experiment 1); working memory task (experiment 2)	SMG	Verbal working memory	Phonological processing
Gajardo-Vidal et al. (2018)	109 (41f, 68m) with RH stroke and 369 (105f, 264m) with LH stroke (experiment 1); 9 with RH stroke (experiment 2); 25 neurologically normal (15f, 10m, experiment 3); 25 neurologically normal (12f, 13m, experiment 4)	Sentence production, sentence or auditory repetition, naming (verb, object, color), and auditory sentence/word-to-picture matching using 180 different pairs formed from 120 object concepts	IFC	Working memory, executive processing	Speech comprehension
Bozic et al. (2010)	12 (5f, 7m)	Gap detection task	IFG	Processing of nonlinguistic complexity	Mapping from sound to lexical meaning
Wright et al. (2018)	64 (60 healthy, neurotypical; 4 neurologically impaired)	identification of acoustic features/ features to match emotion words/ emotions from sentences; matching synonyms/emotions to	insula	Processing of emotions	Prosody

		situations/emotion labels to pictures; sentence reading/repetition.			
Hartwigsen et al., 2010a	28 (16f, 12m)	Phonological task (categorization of words as having 2 or 3 syllables); semantic task (categorization of words as representing a natural or manmade item); perceptual task (auditory and visual)	SMG	Phonological short-term memory	Phonological decisions
Hartwigsen et al., 2010b	35 (18f, 17m)	Phonological task (categorization of words as having 2 or 3 syllables); semantic task (categorization of words as representing a natural or manmade item)	pIFG	Speech production	Phonological decisions
Davis et al., 2016	24 with RH stroke	identification of tone of voice (sarcastic or sincere)	Sagittal stratum	Not mentioned	Prosody
Sammler et al., 2015	23 in study 1 and 32 in study 2	prosody categorization task	pSTS, TP, aSTS, PMC, IFG, ACC, and SMA	Speech perception, memory, motor function, decision making, planning of movements	Prosody

Table. 1. List of studies that investigated the contribution of the right hemisphere to language , summarized by participants, task(s) used, brain region(s) of the right hemisphere studied, and the associated domain-general process(es) and language-related aspects. Subjects from all studies have no history of neurological disorders if not otherwise specified. All studies except Davis et al., 2016, where the categories of handedness of participants were not specified, used right-handed subjects. opIFG: opercular inferior frontal gyrus; pSMG: posterior supramarginal gyrus; aSMG: anterior superior temporal gyrus; mSTG: middle superior temporal gyrus; mPrG: middle precentral gyrus; vPrG: ventral precentral gyrus; mPoG: middle postcentral gyrus; vPoG: ventral postcentral gyrus; mMFG: middle middle frontal gyrus; pMFG: posterior middle

frontal gyrus; pSTG: posterior superior temporal gyrus; SMG: supramarginal gyrus; IFC: inferior frontal cortex; IFG: inferior frontal gyrus; pIFG: posterior inferior frontal gyrus; pSTS: posterior superior temporal sulcus; TP: temporal pole; aSTS: anterior superior temporal sulcus; PMC: premotor cortex; IFG: inferior frontal gyrus; ACC: anterior cingulate cortex; SMA: supplementary motor area.

Fig. 1. Brain regions within the RH that were recruited during speech production, speech comprehension, prosody, mapping from sound to lexical meaning, phonological decisions, lexical-semantic processing. Specifically, these regions include the middle frontal gyrus, inferior frontal gyrus, middle precentral gyrus, middle postcentral gyrus, supramarginal gyrus, angular gyrus, superior temporal gyrus, middle superior temporal gyrus, intraparietal sulcus, superior temporal sulcus, cingulate gyrus and the insula. We hypothesize that the contribution of these RH brain regions to language is executive rather than linguistic.