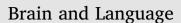
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White matter pathways for prosodic structure building: A case study

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ABSTRACT

The relevance of left dorsal and ventral fiber pathways for syntactic and semantic comprehension is well established, while pathways for prosody are little explored. The present study examined linguistic prosodic structure building in a patient whose right arcuate/superior longitudinal fascicles and posterior corpus callosum were transiently compromised by a vasogenic peritumoral edema. Compared to ten matched healthy controls, the patient's ability to detect irregular prosodic structure significantly improved between pre- and post-surgical assessment. This recovery was accompanied by an increase in average fractional anisotropy (FA) in right dorsal and posterior transcallosal fiber tracts. Neither general cognitive abilities nor (non-prosodic) syntactic comprehension nor FA in right ventral and left dorsal fiber tracts showed a similar pre-post increase. Together, these findings suggest a contribution of right dorsal and inter-hemispheric pathways to prosody perception, including the right-dorsal tracking and structuring of prosodic pitch contours that is transcallosally informed by concurrent syntactic information.

1. Introduction

White-matter fiber bundles connecting left fronto-temporal (and parietal) 'language areas' have become a centerpiece of modern language models (Friederici, 2011) and their divide into functionally specialized dorsal and ventral routes is largely undisputed (Hickok & Poeppel, 2007; Rauschecker & Scott, 2009). However, the established roles of left dorsal and ventral fiber tracts in speech production and semantic comprehension (Fridriksson et al., 2018; Kümmerer et al., 2013; Saur et al., 2008), as well as syntactic parsing (Friederici, 2012; Griffiths, Marslen-Wilson, Stamatakis, & Tyler, 2013; Wilson et al., 2011) ignore one important component of spoken language: Speech prosody, the rhythmic-melodic variations in speech that serve linguistic functions¹ (Cutler, Dahan, & Van Donselaar, 1997). The notable involvement of right-hemispheric fronto-temporal brain areas in linguistic prosodic processing (for reviews, see Baum & Pell, 1999; Belyk & Brown, 2014; Paulmann, 2016; Witteman, van Ijzendoorn, van de Velde, van Heuven, & Schiller, 2011) calls for reflection upon the contribution of right-hemispheric (Sammler, Grosbras, Anwander, Bestelmeyer, & Belin, 2015) as well as inter-hemispheric pathways to natural language comprehension (Friederici & Alter, 2004). Here, we present a case study that lends evidence for the functional *necessity* of right dorsal and transcallosal pathways in linguistic prosodic structure building.

Speakers naturally vary prosodic features such as intonation and rhythm in their utterances to package information into meaningful units and to accentuate thematically relevant words (Cole, 2015; Cutler et al., 1997; Wagner & Watson, 2010). Indeed, we do well in relying on prosodic cues in ambiguous sentences like "Wave at the girl with the hat." to understand at which girl we should wave and in which way (Lehiste, 1973; Snedeker & Trueswell, 2003). This example is one of many to illustrate how the prosodic structure of an utterance, i.e., its organization into smaller phonological or intonational phrases (Selkirk, 1996), can assist language comprehension: The systematic alignment of prosodic phrase boundaries with syntactic and semantic structure (Cooper & Paccia-Cooper, 1980; Selkirk, 1984; Watson & Gibson, 2004) allows listeners to use prosody in their syntactic and semantic interpretation, and *vice versa* (Buxó-Lugo & Watson, 2016; Cole, Mo, & Baek,

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¹ Prosody also conveys paralinguistic information about speakers' emotions, attitudes, and intentions (Hellbernd & Sammler, 2016; Scherer, 1986) which will not be addressed in the present study.

2010). Changes in pitch contour, pre-boundary lengthening and pauses are amongst the most important acoustic cues that signal prosodic boundaries (Ladd, 2008; Pierrehumbert & Hirshberg, 1990) and constrain parsing possibilities.

The tracking of these cues has often been associated with the right hemisphere, in line with cue-dependent models of auditory speech perception (Friederici & Alter, 2004; McGettigan & Scott, 2012; Poeppel, 2003; Zatorre, Belin, & Penhune, 2002). These models argue for a relative processing benefit of right auditory cortices for pitch and spectral information (Jamison, Watkins, Bishop, & Matthews, 2006; Johnsrude, Penhune, & Zatorre, 2000; Obleser, Eisner, & Kotz, 2008; Schönwiesner, Rübsamen, & von Cramon, 2005; Zatorre et al., 2002) that unfolds over extended timescales (Giraud et al., 2007; Poeppel, 2003). As a consequence, the right hemisphere may optimally track suprasegmental prosodic features and complement left-hemispheric syntactic and semantic processes, as proposed in the Dynamic Dual Pathway Model of Friederici and Alter (2004). In keeping with this hemispheric division of labor, fMRI and dichotic listening studies reported predominant right fronto-temporal activations (Kyong et al., 2014; Meyer, Alter, Friederici, Lohmann, & von Cramon, 2002; Meyer, Steinhauer, Alter, Friederici, & von Cramon, 2004; Plante, Creusere, & Sabin, 2002) and a left ear advantage (i.e., right hemisphere involvement; Blumstein & Cooper, 1974; Shipley-Brown, Dingwall, Berlin, Yeni-Komshian, & Gordon-Salant, 1988) when listening to filtered or degraded speech with high demands on prosodic processing. Likewise, explicit attention to prosodic pitch contours in statements and questions (compared to processing of phonemes and lexical meaning) induced right-lateralized activity in fronto-temporal regions (Kreitewolf, Friederici, & von Kriegstein, 2014; Sammler et al., 2015). The rightlateralization of prosody is less clear-cut in studies with natural language material (e.g., Perkins, Baran, & Gandour, 1996; Tang, Hamilton, & Chang, 2017), prosody production (Kellmeyer et al., 2013; Peschke, Ziegler, Eisenberger, & Baumgaertner, 2012), and tasks that go beyond the processing of low-level acoustic-prosodic cues such as pitch contour (for reviews showing bilateral involvement, see Baum & Pell, 1999; Belyk & Brown, 2014; Paulmann, 2016; Witteman et al., 2011). This indicates the inevitable interaction of prosodic information with concurrent syntactic (den Ouden, Dickey, Anderson, & Christianson, 2016) or lexical-semantic processes (Domahs, Klein, Huber, & Domahs, 2013; Gandour et al., 2004; van Lancker, 1980) that are hard to separate during natural language comprehension.

The present study focuses on sentence-level prosodic structure building, i.e., the gradual emergence of a (hierarchical) representation of prosodic constituency that aligns with syntactic structure. As outlined above and implied by previous psycholinguistic research, the prosodic parser most likely draws both on acoustic markers for prosodic boundaries (Ladd, 2008; Pierrehumbert & Hirshberg, 1990; Snedeker & Trueswell, 2003) as well as concurrent syntactic structure (Buxó-Lugo & Watson, 2016; Cole et al., 2010) to build prosodic representations. At the neural level, this implies involvement of both right-hemispheric fronto-temporal networks that track relevant prosodic features over time as well as inter-hemispheric exchange to map syntactic and prosodic structure onto each other (Friederici & Alter, 2004).

This assumption naturally raises the question how information is transferred between relevant brain areas. Syntactic structure building in the left hemisphere is known to involve ventral fronto-temporal connections via the inferior fronto-occipital (IFOF) and uncinate fascicles (UF) for simple syntactic parsing, while dorsal connections via the arcuate and superior longitudinal fascicles (AF/SLF) support parsing of complex syntactic structures (Friederici, 2012; Griffiths et al., 2013) (for reviews, see Friederici, 2011; Gierhan, 2013b). Correspondingly, damage to left dorsal fiber tracts (Meyer, Cunitz, Obleser, & Friederici, 2014; Wilson et al., 2011) or their developmental immaturity (Skeide, Brauer, & Friederici, 2016) coincide with reduced comprehension of syntactically complex sentences.

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the right hemisphere for the perception of prosodic pitch contours in statements and questions (Sammler et al., 2015). This finding was remarkable because the relevance of right-hemispheric and particularly right dorsal tracts in speech and language has been questioned until very recently (Hickok, 2012). Indeed, direct right dorsal fronto-temporal connections were often found to be anatomically weaker than their left-hemispheric counterparts (Fernández-Miranda et al., 2015; Glasser & Rilling, 2008; Parker et al., 2005; Powell et al., 2006; Thiebaut de Schotten, Ffytche, et al., 2011) and have been studied nearly exclusively in the context of atypical language lateralization (Duffau, Leroy, & Gatignol, 2008; Vassal, Le Bars, Moritz-Gasser, Menjot, & Duffau, 2010), e.g., during aphasia rehabilitation (Forkel et al., 2014: Schlaug, Marchina, & Norton, 2009). What has remained unexplored so far is the potential contribution of right dorsal tracts to the processing of suprasegmental prosodic information in speech. Our data on statement and question discrimination lend initial evidence for that, albeit only for single words (Sammler et al., 2015; for converging evidence in emotional prosody perception, see Frühholz, Gschwind, & Grandjean, 2015; Glasser & Rilling, 2008). It seems plausible, though, that the capacity of (right) AF/SLF and temporal-premotor loops to constantly monitor sound and pitch (Guenther & Vladusich, 2012; Houde & Chang, 2015; Zarate, 2013) may benefit the acoustic detection of prosodic boundaries in sentences. A yet bolder proposal that awaits testing is the potential involvement of right dorsal fronto-temporal tracts in more advanced prosodic structuring, beyond basic pitch tracking (Bornkessel-Schlesewsky & Schlesewsky, 2013).

The interaction between the lateralized syntax and prosody streams requires a dynamic exchange between the two hemispheres (Friederici & Alter, 2004; Steinmann & Mulert, 2012). Several studies suggest that syntax-prosody alignment hinges particularly on the cross-talk between the temporal lobes via commissural fibers that cross through the posterior third of the corpus callosum (CC; Friederici, von Cramon, & Kotz, 2007; Sammler, Kotz, Eckstein, Ott, & Friederici, 2010; for the anatomy of CC, see Hofer & Frahm, 2006; Huang et al., 2005). Accordingly, patients with permanent lesions in the posterior CC no longer processed prosodic (or syntactic) irregularities that were only detectable if the syntactic (or prosodic) context was taken into account (Friederici et al., 2007; Sammler et al., 2010). The present study extends these findings to a new case with temporary dysfunctions of relevant white matter tracts.

We report the case of a patient in whom right dorsal and transcallosal connectivity were transiently compromised due to a vasogenic peritumoral edema, allowing assessment of potential prosodic deficits and their recovery in the same individual. Vasogenic edemas are extracellular edemas; other than cytotoxic edemas they infiltrate white matter, not cell bodies (Stokum, Gerzanich, & Simard, 2016), i.e., leave the neurons largely intact if the edema is medically treated to induce its reabsorption. Nevertheless, vasogenic edemas can compromise function in that they compress tissue and disturb information flow along the infiltrated white matter tracts. While the underlying neurophysiological mechanisms are still not fully understood, resulting physical or cognitive deficits are typically alleviated over the course of edema reabsorption (e.g., Bizzi et al., 2012). We capitalized on this phenomenon to probe the involvement of right dorsal and inter-hemispheric tracts in prosody perception in a patient with vasogenic edema infiltrating right AF/SLF and the posterior corpus callosum.

One important consideration for our investigation is that vasogenic edemas are seen around brain tumors. Our patient was diagnosed with a benign convexity meningioma (grade I) in the right parietal region. This type of meningioma is a slow-growing tumor on the surface of the brain, i.e., not invading grey matter. In line with a slow growth rate, symptoms typically have an insidious onset such as slowly evolving headache, suggestive of increased intracranial pressure, or a protracted history of partial seizures (Rockhill, Mrugala, & Chamberlain, 2007). Complete excision of the meningioma is often curative. Slow growth allows for functional compensation; among intracranial tumors, meningiomas are the ones with the highest incidental discovery rate, and

Recently, we demonstrated a similar multi-pathway architecture in

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