



# White matter lateralization and interhemispheric coherence to auditory modulations in normal reading and dyslexic adults

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## ABSTRACT

Neural activation of slow acoustic variations that are important for syllable identification is more lateralized to the right hemisphere than activation of fast acoustic changes that are important for phoneme identification. It has been suggested that this complementary function at different hemispheres is rooted in a different degree of white matter myelination in the left versus right hemisphere.

The present study will investigate this structure–function relationship with Diffusion Tensor Imaging (DTI) and Auditory Steady-State Responses (ASSR), respectively. With DTI we examined white matter lateralization in the cortical auditory and language regions (i.e. posterior region of the superior temporal gyrus and the arcuate fasciculus) and white matter integrity in the splenium of the corpus callosum. With ASSR we examined interhemispheric coherence to slow, syllabic-rate (i.e. 4 Hz) and fast, phonemic-rate (i.e. 20 Hz) modulations. These structural and functional techniques were applied in a group of normal reading adults and a group of dyslexic adults for whom previously reduced functional interhemispheric connectivity at 20 Hz has been reported (Poelmans et al. (2012). *Ear and Hearing*, 33, 134–143). This sample was chosen since it is hypothesized that in dyslexic readers insufficient hemispheric asymmetry in myelination might relate to their auditory and phonological problems.

Results demonstrate reduced white matter lateralization in the posterior superior temporal gyrus and the arcuate fasciculus in the dyslexic readers. Additionally, white matter lateralization in the posterior superior temporal gyrus and white matter integrity in the splenium of the corpus callosum related to interhemispheric coherence to phonemic-rate modulations (i.e. 20 Hz). Interestingly, this correlation pattern was opposite in normal versus dyslexic readers. These results might imply that less pronounced left white matter dominance in dyslexic adults might relate to their problems to process phonemic-rate acoustic information and to integrate them into the phonological system.

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## 1. Introduction

### 1.1. Reading and dyslexia

Spoken language comprehension depends on the recognition and interpretation of meaningful units, such as words, phrases or

sentences. These high-level perceptual constructs are assembled from pre-lexical, acoustic-phonetic cues that are integrated and categorized along multiple timescales. In time windows of  $\pm 20$ –80 ms (12–50 Hz) segmental information about for example phoneme identity is clustered, whereas in longer time windows of  $\pm 150$ –300 ms (3–7 Hz), important suprasegmental information about for example syllables is processed (Obrig, Rossi, Telkemeyer, & Wartenburger, 2010; Pöppel, Idsardi, & van Wassenhove, 2008). It is assumed that precise processing of acoustic cues signalling these syllabic- and/or phonemic-rate time windows in speech is crucial for the development of well-specified phonological representations (Nitttrouer, 2006). During development, the explicit awareness of these phonological representations changes in grain size. Preschool children manipulate speech mainly at the syllable level, and it is only during reading acquisition, when children learn that every speech sound (phoneme) corresponds to a written symbol (grapheme), that explicit phoneme level representations

**Abbreviations:** AM, amplitude modulation; ASSR, auditory steady-state responses; DTI, diffusion tensor imaging; FA, fractional anisotropy; CCsplenium, splenium of the corpus callosum; STGp, posterior region of the superior temporal gyrus.

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develop (Anthony, Lonigan, Driscoll, Phillips, & Burgess, 2003; Ziegler & Goswami, 2005).

Difficulties in processing and representing phonological information is considered the core deficit in developmental dyslexia (e.g. Snowling, 2000; but see Ramus & Szenkovits, 2008), a hereditary neurological disorder characterized by severe and persistent reading and/or spelling impairments despite normal intelligence and adequate educational opportunities (Vellutino, Fletcher, Snowling, & Scanlon, 2004). Yet, it remains unspecified whether these phonological problems in dyslexia only implicate the phoneme- or also the syllable level. According to the traditional view of the phonological deficit theory the locus of the deficit is at the phoneme level (de Gelder & Vroomen, 1991; Goswami & East, 2000; Snowling, 2000; Swan & Goswami, 1997), but some recent theories favour a deficit at the syllable level (Goswami, 2002; Lambrecht Smith, Roberts, Locke, & Tozer, 2010; Maionchi-Pino, Magnan, & Ecalle, 2010). In addition, given that several studies have shown that auditory processing skills support a predictive influence on phonological and eventually on reading development (Boets et al., 2011; Corvéeau, Goswami, & Thomson, 2010; Leppänen et al., 2010), it has been suggested that a fundamental deficit in auditory processing indirectly underlies the reading and spelling problems in individuals with developmental dyslexia (e.g. Tallal, 1980; for a review, Farmer & Klein, 1995). Similarly to the discussion on the locus of the phonological deficit, auditory processing problems were originally thought to involve difficulties in processing brief, rapidly successive and fast dynamic acoustic cues characteristic for phonemes, but some recent theories place the locus of an auditory deficit in the slow changing dynamic cues characteristic for syllables (Goswami, 2011). To date, the psychophysical studies are inconsistent as to whether individuals with dyslexia only demonstrate a decreased sensitivity to temporal cues within the syllable range or whether this deficit manifests over a wider range of temporal information (adults: McAnally & Stein, 1997; Menell, McAnally, & Stein, 1999; Witton et al., 1998; Witton, Stein, Stoodley, Rosner, & Talcott, 2002; Stuart, McAnally, McKay, Johnston, & Castles, 2006; children: Lorenzi, Dumont, & Fullgrabe, 2000; Rocheron, Lorenzi, Fullgrabe, & Dumont, 2002). Defining the neurobiological component of how phonemic-rate and syllabic rate acoustic cues are typically integrated into more abstract phonological units and how this deviates in dyslexic readers can assist in finding the locus of the deficit in dyslexia.

## 1.2. Auditory and phonological processing in normal readers

According to the hierarchical model of speech processing (Hickok & Pöppel, 2007), early cortical structures such as Heschl's gyrus and the supratemporal plane are sensitive to unstructured and simple time-structured acoustic signals, respectively, whereas higher level structures such as the superior temporal gyrus are best responsive to complex sublexical spectrotemporal signals and are thought to be involved in the construction of sound-based representations of speech (Hickok & Pöppel, 2004). Next, at the level of the anterior and posterior superior temporal sulcus an abstract representation of speech units, insensitive to acoustic variances, is obtained (Okada et al., 2010; Peelle, Eason, Schmitter, Schwarzbauer, & Davis, 2010). From the superior temporal cortex, speech signals are processed in two parallel streams. In a *ventral stream*, sound-based representations of speech are mapped onto conceptual representations (Rauschecker & Scott, 2009; Pöppel et al., 2008). This stream engages areas in the left anterior superior temporal sulcus and middle temporal gyrus. It is evidenced that the ventral anatomical counterpart of this sound-to-meaning stream is the extreme capsule fiber system or inferior fronto-occipital fasciculus (Frey, Campbell, Pike, & Petrides, 2008; Wong,

Chandrasekaran, Garibaldi, & Wong, 2011). In addition, starting from the posterior temporal cortex, a *dorsal stream* projects towards inferior parietal and frontal (Broca's and premotor) regions and is functionally responsible for mapping phonemic representations onto motor representations (Pöppel et al., 2008) and for sustaining the phonological aspects of speech perception (Chevillet, Jiang, Rauschecker, & Riesenhuber, 2013; Saur et al., 2010). Saur et al. (2010) demonstrated that the functional connection between the frontal and temporoparietal components is mediated via the arcuate fasciculus (often used interchangeably with the superior longitudinal fasciculus (Brauer, Anwender, & Friederici, 2011) or as one of its subdivision (Makris et al., 2005)). Thus, phonological processing during speech perception depends both on acoustically-based processes in the posterior temporal areas but also on a dorsal interaction with frontal regions.

Of special interest with regard to how phonemic- and syllabic-rate acoustic cues are processed is the large body of evidence that the activation of these areas is mainly lateralized to the left hemisphere during the phonetic analysis of speech (for a review see Tervaniemi & Hugdahl, 2003). According to the domain-driven hypothesis, linguistic aspects of speech drive this lateralization (Dehaene-Lambertz et al., 2005, 2010; Rosen, Wise, Chadha, Conway, & Scott, 2011) whereas the signal-driven hypothesis assumes that spectrotemporal aspects determine the left–right bias. According to the latter hypothesis, spectral acoustic cues and slow temporal modulations are preferentially processed in the right auditory cortex, whereas temporal acoustic analyses, such as the analysis of duration as well as faster modulations, are rather left lateralized (for a review see Pöppel et al., 2008; Zatorre & Gandour, 2008). According to Pöppel et al. (2008), this functional specialization is situated in the non-primary auditory cortex and rooted in the length of integration windows, being between 20 and 50 ms (i.e. 12–50 Hz) in the left and between 150 and 300 ms (i.e. 3–7 Hz) in the right hemisphere. Hence, the signal-driven hypothesis explains a left lateralization for phoneme identification (e.g. Jäncke, Wüstenberg, Schulze, & Heinze, 2002; Dehaene-Lambertz & Gliga, 2004; Zatorre, Meyer, Gjedde, & Evans, 1996) and a right lateralization for prosody and syllable identification (Meyer, Alter, Friederici, Lohmann, & von Cramon, 2002; Zatorre, Evans, Meyer, & Gjedde, 1992; Zatorre, 1988) based on the length of the integration windows of important acoustic cues instead of their linguistic content (like domain-driven models). Growing experimental evidence supports the claim that not linguistic but rather acoustic-temporal characteristics drive hemispheric asymmetry (Boemio, Fromm, Braun, & Pöppel, 2005; Husain et al., 2006; Joanisse & Gati, 2003; Zaehle, Wüstenberg, Meyer, & Jancke, 2004). Nevertheless, there remain points of discrepancies across studies such as the observation that phonemes and fast modulations sometimes engage a bilateral activation pattern instead of a clear left dominance (fast modulated non-speech: Belin et al., 1998; Boemio et al., 2005; Pöppel et al., 2008; Telkemeyer et al., 2009; consonant-vowel-combination: Benson, Richardson, Whalen, & Lai, 2006; Binder et al., 2000; Joanisse & Gati, 2003). It seems that experience and familiarity with phonetic categories interact with these hemispheric patterns of specialization.

In addition to their functional specialization, the left and right primary auditory and superior temporal cortices also differ in volume (e.g. review Shapleske, Rossell, Woodruff, & David, 1999), an asymmetry which is mainly present in white rather than in grey matter (Penhune, Zatorre, MacDonald, & Evans, 1996; Warrier et al., 2009). This finding fits with the hypothesis of Zatorre & Belin, 2001; Zatorre, Belin, & Penhune, 2002) that the observed functional hemispheric asymmetry for spectrotemporal information is specifically related to hemispheric asymmetry of *white matter myelination*, rather than to *volume* asymmetry per se. A more myelinated left auditory cortex would lead to faster neural

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