



Dorsal and ventral pathways in language development



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ABSTRACT

The dorsal and ventral information streams between inferior frontal and temporal language regions in the human brain are implemented by two fiber connections that consist of separable tracts. We compared the maturation of the two connections including their subcomponents in three different age groups: newborn infants, 7-year-old children, and adults. Our results reveal a maturational primacy of the ventral connection in the language network associating the temporal areas to the inferior frontal gyrus during early development, which is already in place at birth. Likewise, a dorsal pathway from the temporal cortex to the premotor cortex is observable at this early age. This is in contrast to the dorsal pathway to the inferior frontal gyrus which matures at later stages in development and might play a role in more complex language functions.

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1. Introduction

One hundred and fifty years ago the seminal work of the French physician and anthropologist Paul Broca provided an important insight into the brain basis of the human faculty of language (Broca, 1865). One of his patients suffering from a severe aphasia was only able to pronounce the sole syllable *tan* although his understanding of language was apparently intact. Even when he tried to speak full sentences with his voice following a sentential melody, his utterance was nothing but a stream of *tans*. After this patient passed away, Broca investigated his brain *ex vivo* and observed a lesion in the left inferior frontal gyrus (IFG), an area that became known as Broca's area.

Only a few years later, the German neurologist Carl Wernicke described the role of lesions to the superior temporal gyrus (STG) in aphasia as derived from the symptom patterns of his patients (Wernicke, 1874). In his work, Wernicke suggested separating motor (expressive) aphasia, occurring as a result of a lesion to the IFG, from sensory (receptive) aphasia, as a result of a lesion to the posterior part of the STG, later on labeled as Wernicke's area. He also assumed a third type of aphasia, conduction aphasia, as a result of a lesion to the connection between the sensory and the motor part of the language system, although not much was known about how this connection was implemented in the brain. This idea was taken up and elaborated by Ludwig Lichtheim (1885). Wernicke thought of this connection to be formed and sustained during language

acquisition and development as an important process to achieve mature language abilities.

Adapted over time and generalized beyond aphasia, the Broca–Wernicke–Lichtheim model of language implementation in the brain became the most influential model used by generations of neuroscientists to address issues of typical and atypical language processing, and it is central assumptions still provide a very useful framework (Poeppl & Hickok, 2004). Current progress in the field of neuroscience of language has provided a number of technologies for data acquisition and data processing. Today, the structural and functional neuroanatomy of the brain basis of language is accessible *in vivo*, and there is a consensus that Wernicke was correct in his assumption of a direct connection between the frontal and temporal language centers. For a long time, textbook knowledge was that a dorsal connection via the arcuate fasciculus (AF) or part of the superior longitudinal fasciculus (SLF) was the anatomical realization of this association. However, more recent work has rediscovered the importance of an independent second connection between the two language centers that probably fulfills an important role within the network (Brauer, Anwander, & Friederici, 2011; Frey, Campbell, Pike, & Petrides, 2008; Friederici, 2011; Friederici, Bahlmann, Heim, Schubotz, & Anwander, 2006; Parker, Luzzi, Alexander, Wheeler-Kingshott, Ciccarelli, & Lambon Ralph, 2005). This connection is ventrally located, running through the extreme capsule (EmC) and external capsule (EC) via the inferior fronto-occipital fasciculus (IFOF), sometimes also named extreme capsule fiber system (ECFS) (Catani, 2009; Frey et al., 2008; Friederici, 2011; Makris & Pandya, 2009; Saur et al., 2008). For a comprehensive overview on the ventral pathway's history, see Weiller, Bormann, Saur, Musso, and Rijntjes (2011).

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The dorsal and ventral information streams are assumed to each consist of several fiber bundles (Friederici, 2009). The AF and part of the SLF have been proposed to form the dorsal connection (Brauer et al., 2011; Frey et al., 2008; Saur et al., 2008). The AF connects superior temporal (Brodmann area (BA) 41, 42) and middle temporal regions (BA 21, 22, 37) to different parts of the prefrontal cortex, namely to the IFG (BA 44, 45), the middle frontal gyrus (MFG) (BA 6, 8, 9) and the precentral gyrus (PCG) (Catani, Howard, Pajevic, & Jones, 2002; Catani, Jones, & ffytche, 2005; Thiebaut de Schotten, Dell'Acqua, Valabregue, & Catani, 2012). In addition to the AF, there is the SLF, which contains three separable bundles connecting the parietal cortex to the prefrontal cortex (SLF I, II and III, Makris et al., 2005). SLF III connects the inferior parietal lobe with BA 44 in Broca's area and to BA 6. The other components of the SLF (SLF I and SLF II) are functionally less language-specific and do not connect to Broca's area but rather to BA 6, 8, 9, 32 (SLF I) and BA 6, 8, 9 and 46 (SLF II) (Makris et al., 2005; Thiebaut de Schotten, Dell'Acqua, Valabregue, & Catani, 2012).

For the ventral connection at least two bundles have been proposed, the IFOF and the uncinate fasciculus (UF). The IFOF runs through the EmC/EC and connects occipital, medial parietal, and posterior temporal areas to frontal areas (Catani et al., 2002; Martino, Brogna, Robles, Vergani, & Duffau, 2010; Thiebaut de Schotten, Dell'Acqua, Valabregue, & Catani, 2012). *Ex vivo* fiber dissection of the IFOF proposed that this bundle actually hosts two subcomponents, a superficial tract (V1) and a deep tract (V2) (Martino et al., 2010; Sarubbo, De Benedictis, Maldonado, Basso, & Duffau, 2011). The superficial tract (V1) was proposed to be involved in the language network terminating in the pars triangularis (BA 45) and pars orbitalis of the IFG, while the deep tract (V2) terminates in three frontal regions: An anterior component in the frontal pole and orbitofrontal cortex (OFC), a middle component in the middle frontal gyrus (MFG), and a posterior component in the MFG and dorsolateral prefrontal cortex (DLPFC) (Sarubbo et al., 2011). While the deep tract (V2) of the IFOF probably mainly passes through the EC, the superficial tract (V1) of the IFOF covers a more lateral part of the capsules and runs through the EmC and EC (Martino et al., 2010). The two capsules are very narrow structures separated by the claustrum that forms a thin layer of gray matter. Current image resolution in diffusion-weighted imaging (DWI) is not sufficient to clearly separate EC and EmC fibers in diffusion data. The UF was also shown to be relevant for language processing (Friederici et al., 2006; Papagno, 2011). It connects the anterior temporal lobe and the temporal pole (BA 38) to the orbitofrontal cortex (BA 10, 11, 47) and the ventro-medial located frontal operculum (Thiebaut de Schotten et al., 2012). The UF runs laterally and ventrally through the EmC to the fibers of the IFOF (Martino et al., 2010).

In terms of the neuroanatomical development of the language network during early ontogeny, DWI data suggest that newborn infants do not yet possess a fully matured dorsal connection from the STS/STG to the language region in the IFG (Perani et al., 2011). Rather, the newborns' dorsal connection terminates in the premotor cortex (PMC). These two different termination points of the dorsal connection, one terminating in the PMC (dorsal pathway D1), one terminating in BA 44 in Broca's area (dorsal pathway D2) have been proposed to form two distinct pathways of the dorsal connection (Friederici, 2011, 2012). Dorsal pathway D1 connecting to the PMC is already observable at birth (Perani et al., 2011) and potentially responsible for sensory-to-motor mapping (Saur et al., 2008), a function that is in place very early in language learning (Gervain, Macagno, Cogoi, Peña, & Mehler, 2008; Perani et al., 2011; Teinonen, Fellman, Naatanen, Alku, & Huotilainen, 2009). Dorsal pathway D2 connecting to BA 44 in the IFG is not yet observable by DWI in newborns. This subcomponent of the dorsal connection is probably responsible for the ability to process

complex sentence structures as observed in adults' common activation of BA 44 and STS/STG during sentence processing of more complex types (Bornkessel, Zysset, Friederici, von Cramon, & Schlesewsky, 2005; Friederici, Makuuchi, & Bahlmann, 2009). It is unknown how the two pathways of the dorsal connection that terminate in the PMC (D1) and in the IFG (D2), respectively, mature during development. However, recent findings from developmental linguistics show that the ability to process complex sentences develops at around the age of 7 years (Dittmar, Abbot-Smith, Lieven, & Tomasello, 2008; Hahne, Eckstein, & Friederici, 2004; Knoll, Obleser, Schipke, Friederici, & Brauer, 2012).

For the current analysis, we concentrated on pathways connecting the frontal language region in the IFG to the posterior language region, i.e., the dorsal pathways D1 and D2 and the ventral pathway via the IFOF including V1 and V2. The ventral superficial tract V1 as described in the adult brain (Martino et al., 2010) is evident in newborns (Perani et al., 2011). It is unknown, however, whether the deep tract (V2) of the IFOF shows the same maturation trajectory as the superficial tract (V1). If the dorsal pathway D2 terminating in Broca's area is relevant for the processing of complex linguistic structures as described above, this connection should be in place at age 7 (Brauer et al., 2011).

In order to describe the maturation of the dorsal and the ventral pathways of the language network, we compared DWI data from previously published studies including newborn infants (Perani et al., 2011), 7-year-old children, and adults (Brauer et al., 2011). The infant data were acquired at a different institution and scanner than the child and adult data. We used fiber tracking to delineate the two pathways and their components as they have been described for the adult brain and we compared their microstructural properties using the diffusion MR biomarker of fractional anisotropy (FA). The comparison of adult data with infant and child data sheds light on the structural maturation trajectory of the human language network.

2. Materials and methods

2.1. Participants

Here we reanalyzed diffusion imaging data from Brauer et al. (2011) and Perani et al. (2011). Data from 19 newborns (age 2 days, range 1–3 days), 10 children (5 girls, age 7.0 years, range 5–8 years), and 10 adults (5 female, age 27.8 years, range 24–32 years) were available. All participants or the parents of non-adult participants gave written informed consent. The studies were approved by the respective local ethics committees of the University of Leipzig (Brauer et al., 2011) and San Raffaele Scientific Institute (Perani et al., 2011).

2.2. Data acquisition

Diffusion MR images from newborns were acquired on a Philips 3 Tesla Achieva scanner (Philips Medical Systems, Best, The Netherlands) using an EPI sequence with a voxel size of $1.4 \times 1.4 \times 2 \text{ mm}^3$ covering the whole brain (40 axial slices) in 21 diffusion-encoding gradient directions, b -value 1000 s/mm^2 , and one image without diffusion weighting. Motion-affected diffusion-weighted images were individually removed. This correction was necessary for one image (out of 21 diffusion-weighted images) from five individuals, for two images from four individuals, and for three images from one individual dataset. The remaining images were corrected for motion using rigid body transformations (Jenkinson, Bannister, Brady, & Smith, 2002). The motion correction was combined with a co-registration to a newborn reference brain and resampled to an isotropic resolution of 1 mm. As reference

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