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Fronto-parietal dorsal and ventral pathways in the context of different linguistic manipulations

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ABSTRACT

This study investigates structural connectivity between left fronto-parietal brain regions that were identified in a previous fMRI study which used different linguistic manipulation tasks. Diffusion-weighted images were acquired from 20 volunteers. Structural connectivity between brain regions from the fMRI study was computed using probabilistic fiber tracking. For suprasegmental manipulation, left inferior parietal lobule (IPL) and left inferior frontal gyrus (IFG), pars opercularis, were connected by a dorsal pathway via the arcuate fascicle and superior longitudinal fascicle III. For segmental manipulation, left IPL and IFG, pars triangularis, were connected by a ventral pathway via the middle longitudinal fascicle and the extreme capsule. We conclude that the dorsal pathway provides a route for mapping from phonological memory in IPL to the inferior frontal articulatory network while the ventral pathway could facilitate the modulation of phonological units based on lexical-semantic aspects, mediate the complexity of auditory objects and the unification of actor-event schemata.

1. Introduction

In recent years, *in vivo* studies on white matter connections in the human brain using diffusion tensor imaging (DTI) and various fiber tracking methods have contributed to a more detailed understanding of the anatomical connectivity between regions involved in language processing (Catani, Jones, & ffytche, 2005; Frey, Campbell, Pike, & Petrides, 2008; Glasser & Rilling, 2008; Saur et al., 2008) as well as other processing domains like vision (Lanyon et al., 2009; Staempfli et al., 2007), attention (Umarova et al., 2010) and motor cognition (Vry et al., 2012). Crucially, the studies by Frey et al. (2008) and Saur et al. (2008) have shown that, in addition to the classical dorsal language pathway via the arcuate fascicle and superior longitudinal fascicle (SLF III) fiber system, a ventral white matter pathway via the extreme capsule (EmC) connects posterior superior temporal areas with inferior frontal areas, specifically pars triangularis (BA 45/47). Recently, a lesion study with 100 patients with acute aphasia due to ischemic stroke confirmed the clinical importance of these findings by showing that task performance on auditory comprehension measures requires an interaction between temporal and prefrontal brain regions mediated by the ventral pathway via the extreme capsule (Kümmerer et al., 2013).

In the study by Saur et al. (2008), the functional magnetic resonance imaging (fMRI) condition for eliciting basic phonological mapping processes via the dorsal pathway was repetition of aurally presented pseudo-words and real words. This repetition task was hypothesized to represent a prototypical routine for mapping phonological information from auditory association cortex in posterior superior temporal regions (Binder et al., 2000; Uppenkamp, Johnsrude, Norris, Marslen-Wilson, & Patterson, 2006; Wise et al., 2001) to frontal articulatory networks (Hickok & Poeppel, 2007; Vigneau et al., 2006) via a dorsal pathway. Interestingly, however, the repetition task did not yield extensive activation in inferior parietal areas, a region which has consistently been shown to be involved in important aspects of phonological processing,

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specifically phonological memory (Jacquemot & Scott, 2006; Muller & Knight, 2006; Paulesu, Frith, & Frackowiak, 1993; Ravizza, Delgado, Chein, Becker, & Fiez, 2004; Smith, Jonides, & Koeppe, 1996; Vigneau et al., 2006; Zurowski et al., 2002).

Apart from language processing, left (and right) parietal regions especially in the anterior and posterior inferior parietal lobule (IPL) seem to play an important role in sensory integration and mapping across a variety of processing domains. This has been demonstrated for visual and tactile sensations (Avillac, Deneve, Olivier, Pouget, & Duhamel, 2005), attention and learning (Bucci, 2009), working memory (Olson and Berryhill, 2009; Baddeley, 2003; Owen, 2004; Ravizza et al., 2004; Rawley & Constantinidis, 2009) as well as in the context of mapping auditory input to articulation with which the present study is concerned primarily (see references above). In addition, evidence from lesion studies suggests that damage to the left inferior parietal area may produce deficits in phonological short-term storage (Shallice & Vallar, 1990; Vallar, Di Betta, & Silveri, 1997). In a meta-analysis on functional imaging studies of language processing, Vigneau et al. (2006) found that most clusters for phonological processing were located in superior temporal (for phonological as well as phonetic de- and encoding) and inferior frontal areas. Parietal clusters in supramarginal gyrus were by trend more likely to be activated by tasks requiring phonological short-term memory.

Based on the evidence reviewed above, it seems that left IPL (LIPL) primarily supports memory of phonologically (and possibly phonetically) specified units for further processing.

In order to functionally define the brain networks involved in differential aspects of phonological processing, the results from an fMRI experiment investigating the neural correlates of phonological manipulation processes based on differentially manipulating suprasegmental (i.e. a shift of stress placement) and segmental (i.e. a vowel shift) information at the pseudo-word level were used. In that fMRI study brain networks involved in naturally occurring phonological processes requiring phonological manipulation with low short-term storage demands were investigated (Peschke, Ziegler, Eisenberger, & Baumgaertner, 2012).

The aim of the study presented here was to investigate the structural white matter pathways that provide parieto-frontal connectivity between the regions involved in phonological manipulation in the fMRI study by Peschke et al. (2012) by means of a fiber tracking method which combines probabilistic fiber tracking with functionally defined networks (Kreher et al., 2008). Specifically, we asked whether anatomical connectivity between parietal and frontal areas that were identified in the fMRI study was provided by dorsal and/or ventral fiber pathway systems. In addition, we examined which functional role the fronto-parietal connections might have for phonological processing.

2. Material and methods

2.1. fMRI study design

The stimuli and task of the fMRI experiment are described in detail in Peschke et al. (2012). To summarize, the experimental paradigm was based on a 2 × 2 full-factorial design with the factors TASK and PHONOLOGICAL PROCESS. The factor TASK comprised two conditions, REPEAT and TRANSFORM, where in the REPEAT condition subjects were instructed to repeat an aurally presented stimulus (word or pseudo-word) as quickly and accurate as possible and the TRANSFORM condition required the phonological manipulation of the presented type of PHONOLOGICAL PROCESS. Because the results from the TRANSFORM condition form the basis for our tracking experiment, the two types of phonological material (termed PROS and SEGM) that the factor PHONOLOGICAL PROCESS consisted of are described in more detail below.

The PROS type of phonological material in the factor PHONOLOGICAL PROCESS consists of pseudo-"countries" like "Doga", derived from real examples in German such as "Kuba" (engl. "*Cuba*"). In the TRANSFORM condition participants had to transform this pseudo-country into its respective pseudo-language (and vice versa), for example "Doga" → "Doganisch" (analogous to "Kuba" → "Kubanisch", engl. "*Cuba*" → "*Cuban*"). Considering that Modern Standard German predominantly has a trochaic structure (Domahs, Wiese, Bornkessel-Schlesewsky, & Schlesewsky, 2008), the pseudocountries were stressed on the first syllable (e.g. /'doga/) whereas the pseudolanguages were stressed on the second syllable (e.g. /do'ganisch/). This change in stress placement is a natural process in spoken German.

The SEGM type of PHONOLOGICAL PROCESS, in turn, consisted of pseudo-nouns like "Mall", also derived from examples in German, in this case "Ball" (engl. *ball*), which were prefixed by the German definite article "der" (e.g. "der Mall"). In the TRANSFORM task these pseudo-nouns had to be transformed into the corresponding trisyllabic pseudo-diminutive prefixed with the German definite article "das", for example "der Mall" → "das Mällchen" (engl. "*the stroom" → "*the stroomlet" in analogy to "the stream" → "*the streamlet*"). Note that this manipulation from a noun to a diminutive in standard German typically requires a shift from a back or open vowel (/u/, /o/ or /a/) to a corresponding front vowel ("umlaut"), e.g. "der Mall" → "das Mällchen"). The change from vowel to *umlaut* in the transformation of a pseudo-noun into a pseudo-diminutive is a naturally occurring process in German and was named "segmental manipulation" (SEGM) as it operates at the level of speech sound segments.

Both types of stimuli (PROS and SEGM) consisted of two sets of 36 bisyllabic and 36 three-syllable items. Mean duration of the PROS material was 824 ms (range 544–1136 ms; SD: 177 ms) and mean duration of the SEGM material was 954 ms (range 639–1288 ms; SD: 170 ms). There was a significant difference in duration between both speech stimuli groups with a significantly longer duration for the SEGM material ($t = -4.49$; $DF = 142$; $p < 0.0001$). This difference may be a result of the short pause between the definite article and the noun in the segmental condition ("der [pause] Mall") and/or the dissimilar phonetic structure of both stimuli.

The experiment in the scanner consisted of two runs of the REPETITION task of the PHONOLOGICAL PROCESS material (i.e. PROS and SEGM) and two runs of the TRANSFORM task. The factor PHONOLOGICAL PROCESS remained constant within each run, such that subjects did not have to switch between PROS and SEGM stimuli. Every run consisted of 36 trials with a length of about 5.5 min each. The sequence of tasks and phonological processes was pseudorandomized, with the restriction that maximally two runs of one task or phonological process could occur in a row and that each run appeared almost equally often in all positions across subjects. The order of the pseudowords within a run was also pseudorandomized, in such a way that maximally three mono- or bisyllabic words occurred in succession with the intention of changing the direction of manipulation (pseudo-country → pseudo-language and pseudo-language → pseudocountry) in order to make the experiment less predictable. The trial sequence was fixed within runs for all subjects. The experiment in the scanner ran for approximately 50 min for each participant.

2.2. Definition of seed points from the fMRI study

For our tracking experiment only the peak coordinates from the random effects (2nd level) fMRI analysis of the contrast TRANSFORM (either PROS or SEGM) minus REPETITION were used