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Bilateral dorsal and ventral fiber pathways for the processing of affective prosody identified by probabilistic fiber tracking

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ABSTRACT

Dorsal and ventral pathways for syntacto-semantic speech processing in the left hemisphere are represented in the dual-stream model of auditory processing. Here we report new findings for the right dorsal and ventral temporo-frontal pathway during processing of affectively intonated speech (i.e. affective prosody) in humans, together with several left hemispheric structural connections, partly resembling those for syntacto-semantic speech processing. We investigated white matter fiber connectivity between regions responding to affective prosody in several subregions of the bilateral superior temporal cortex (secondary and higher-level auditory cortex) and of the inferior frontal cortex (anterior and posterior inferior frontal gyrus). The fiber connectivity was investigated by using probabilistic diffusion tensor based tractography. The results underscore several so far underestimated auditory pathway connections, especially for the processing of affective prosody, such as a right ventral auditory pathway. The results also suggest the existence of a dual-stream processing in the right hemisphere, and a general predominance of the dorsal pathways in both hemispheres underlying the neural processing of affective prosody in an extended temporo-frontal network.

Introduction

Cortical auditory processing involves several perisylvian regions, which are interconnected by different fiber pathways. Recent studies (Friederici et al., 2006; Rauschecker and Scott, 2009; Saur et al., 2008) have predominantly identified left hemispheric processing pathways within a dual-stream model of auditory processing (Hickok and Poeppel, 2007). They include ventral pathways from anterior superior temporal gyrus (STG) to the anterior inferior frontal gyrus (IFG) and dorsal pathways, which project to the posterior IFG via the posterior STG (Hickok and Poeppel, 2007; Rauschecker and Scott, 2009). Especially the dorsal pathway seems strongly left lateralized (Hickok and Poeppel, 2007). The ventral pathways convey sound-invariant meaning (Belin and Zatorre, 2000b; Rauschecker and Scott, 2009), such as speech semantics (Hagoort, 2005). The dorsal pathways serve sound-to-motor mapping (Saur et al., 2008) and the processing of temporal auditory sequences (Belin and Zatorre, 2000b; Rauschecker and Scott, 2009), which are also necessary for the understanding of speech syntax (Friederici et al., 2006). Compared to a predominant role of the left brain for syntacto-semantic processing (Specht, 2014), the emotional intonation in speech, that is the affective prosody, strongly, but not exclusively, activates regions in right STG and IFG (e.g. Alba-Ferrara et al., 2011; Beaucousin et al., 2007; Ethofer et al., 2006; Fruhholz et al., 2012). Thus, investigating the neural basis of affective prosody processing provides an ideal paradigm to investigate right hemispheric auditory pathways using diffusion-weighted imaging techniques together with functional magnetic resonance imaging.

These temporo-frontal pathways for affective prosody processing have been rarely studied (Ethofer et al., 2012; Glasser and Rilling, 2008), mainly pointing to a right dorsal pathway (Gharabaghi et al., 2009; Glasser and Rilling, 2008), but also providing evidence for the possibility of a right ventral pathway (Ethofer et al., 2012). However, these studies explored pathways, first, only for circumscribed temporal regions, second, without specifying frontal target regions, third, without quantifying the architecture of these pathways, and therefore without dissociating the different possible functional roles of these pathways (Ethofer et al., 2012; Glasser and Rilling, 2008). Taken together, these critical points might have led to a considerable underestimation of the importance and complexity of the temporo-frontal white matter pathway connectivity. Ventral and dorsal pathways, for example, are supposed to originate in multiple STG seed regions (Friederici, 2011; Fruhholz et al., 2012). Furthermore, these pathways probably terminate in the anterior as well as in the posterior IFG (Fruhholz and Grandjean, 2013b), serving to evaluate (Schirmer and Kotz, 2006) and to categorize

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vocalizations (Romo et al., 2004), respectively. Thus, especially the use of multiple temporal and frontal seed and target regions might help to more comprehensively describe the extended structural temporo-frontal neural network underlying the processing of affective prosody.

Accordingly, using high-resolution fMRI we previously described several subregions in the bilateral IFG and in STG, which were differentially responsive to emotional compared to neutral prosody (Fruhholz et al., 2012). Especially, affective prosody elicits brain activity in several distributed subregions in right STG (Fruhholz and Grandjean, 2013a; Fruhholz et al., 2012) and right IFG (Fruhholz and Grandjean, 2013b), but these subregions have functional differences (Fig. 1). Especially, they show enhanced sensitivity to emotional compared to neutral prosody depending on the attentional focus *toward* (explicit attention) or *away from* (implicit attention) emotional cues in affective prosody. The right compared with left IFG showed a sensitivity to speech prosody during implicit attention, while left IFG subregions responded to affective prosody during both attentional conditions. All STG subregions showed a sensitivity to speech prosody both for the explicit and implicit attention condition, but right mid STG (mSTG) and left anterior STG (aSTG) showed stronger sensitivity during the explicit attention condition, whereby the latter regions showed a general main effect for the explicit compared with the implicit task, and thus might reflect a rather general evaluation of voices independent of the emotion. Furthermore, regions in the right posterior STG (fundus of the posterior superior temporal sulcus (fpSTS), posterior STG (pSTG)) and all left STG subregions were sensitive to the pitch and intensity variations in affective prosody, which are one of the main acoustic features of affective prosody (Banse and Scherer, 1996; Patel et al., 2011).

Based on these functional differences, we assumed different white matter fiber connections, which link different subregions in right STG and right IFG, probably similar to several STG–IFG fiber pathways described for the left hemisphere (Friederici, 2011). In the present study we therefore used diffusion-weighted imaging together with a probabilistic fiber tracking approach to investigate these temporo-frontal pathways, which might connect subregions in STG and IFG, which we observed previously (Fruhholz et al., 2012). Beside some left hemispheric pathways, we especially expected to find right dorsal and ventral pathways underlying the processing of affective prosody given the extended anterior to posterior distribution of right STG subregions.

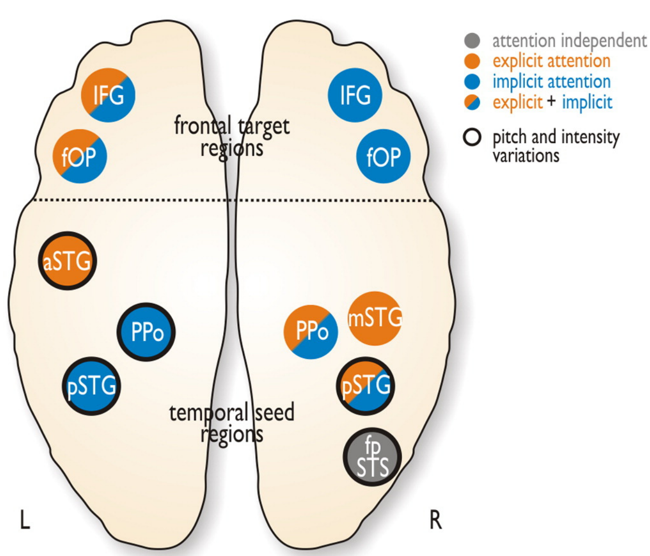

Fig. 1. Summary of the functional roles of the STG/STS and IFG subregions during the processing of affective prosody as found previously (Hickok and Poeppel, 2007). Some of these activations were found independent of the attentional focus, during both the explicit and the implicit attention condition, or were especially enhanced during the explicit or implicit attention task. Additionally, some of these regions were sensitive to pitch and intensity variations of affective prosody (encircled in black).

Materials and methods

Participants

To investigate bilateral temporo-frontal pathways for the processing of affective prosody, we recorded diffusion-weighted imaging data in participants, who listened to affective prosody in a previously described experiment (Fruhholz et al., 2012). Seventeen healthy participants took part in the experiment. Data from two participants had to be excluded from the analysis because of signal artifacts in the diffusion-weighted data. The remaining sample consisted of three males and twelve females, with a mean age of 25.12 years ($SD = 4.95$, age range 20–38 years). All participants were native French speakers, were right-handed, and reported to have normal or corrected-to-normal vision, and to have no hearing disabilities. No subject presented a psychiatric or neurological medical history. Subjects gave informed and written consent for their participation in accordance with the ethical and data security guidelines of the University of Geneva. The experiment was approved by the local ethics committee of the University of Geneva.

MRI scanning

Images were recorded on a 3T Siemens Trim Trio System (Siemens, Erlangen, Germany) equipped with a 32-channel head coil using parallel imaging (GRAPPA factor 2). First, two repetitions of monopolar diffusion-weighted images (Stejskal-Tanner; TR/TE = 8200/82 ms, vocal size 2 mm^3, 65 slices) were performed along 30 independent directions, including a b-value of 1000 s/mm^2. A reference image with no diffusion weighting ($b = 0$ s/mm^2) was also obtained during each diffusion-weighted acquisition. Second, a high-resolution, magnetization-prepared rapid acquisition gradient echo (MPRAGE) T1-weighted sequence (TR/TE/TI = 1900/2.27/900 ms, FoV 296 mm, voxel size 1 mm^3, 192 slices) was obtained in sagittal orientation to obtain structural brain images. Finally, functional images were recorded using high-resolution T2*-weighted EPI images (TR/TE/TA = 10,000/30/8250 ms, voxel size 1.5 × 1.5x2 mm, 25 slices).

Stimuli and procedure

A full description of the stimuli and the experimental setup can be found here (Fruhholz et al., 2012). In short, we presented four speech-like but meaningless words ("*molen*", "*belam*", "*nikalibam*", "*kudsemina*"), which were spoken in either a neutral or an angry tone by two male and two female actors. The same stimuli were presented during blocks, which varied according to the focus of attention. In two blocks participants were asked to make explicit prosody discriminations (*neutral* or *angry*; referred to as "explicit attention"). In another two blocks participants were asked to discriminate the gender of the voices (*male* or *female*; referred to as "implicit attention"), where the emotional intonation of words was assumed to be processed on an implicit level.

Region of interest (ROI) selection for seed regions

With the above described experimental procedure, we previously identified several subregions in the left and right superior temporal cortex (STC, consisting of STG and STS) and two subregions in the bilateral IFG resulting from the comparison of angry and neutral voices across both attention levels, but also for this comparison within each of the explicit and the implicit attention condition (Fig. 1) (Fruhholz et al., 2012). Here we used these regions as seed and target regions for probabilistic fiber tracking in order to establish the white matter connectivity between these regions. We took three subregions in the voice-sensitive cortex of the left hemisphere (pSTG [MNI *xyz* −68 −27 6], planum polare (PPo) [−50 −10 4], aSTG [−56 11 −10]), and two IFG subregions, one located more posterior in the frontal operculum (fOP; BA 44; [−51 13 14]), and one more anterior in the IFG (BA 47; [−44 29