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Development from childhood to adulthood increases morphological and functional inter-individual variability in the right superior temporal cortex

Milene Bonte [a,*], Martin A. Frost [a], Sanne Rutten [a], Anke Ley [a,b], Elia Formisano [a,1], Rainer Goebel [a,c,1]

[a] Department of Cognitive Neuroscience and Maastricht Brain Imaging Center, Faculty of Psychology and Neuroscience, Maastricht University, P.O. Box 616, 6200 MD, Maastricht, The Netherlands
[b] Department of Medical Psychology and Neuropsychology, Tilburg University, Tilburg, The Netherlands
[c] Netherlands Institute for Neuroscience, Institute of the Royal Netherlands Academy of Arts and Sciences (KNAW), Amsterdam, The Netherlands

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ABSTRACT

We study the developmental trajectory of morphology and function of the superior temporal cortex (STC) in children (8–9 years), adolescents (14–15 years) and young adults. We analyze cortical surface landmarks and functional MRI (fMRI) responses to voices, other natural categories and tones and examine how hemispheric asymmetry and inter-subject variability change across age. Our results show stable morphological asymmetries across age groups, including a larger left planum temporale and a deeper right superior temporal sulcus. fMRI analyses show that a rightward lateralization for voice-selective responses is present in all groups but decreases with age. Furthermore, STC responses to voices change from being less selective and more spatially diffuse in children to highly selective and focal in adults. Interestingly, the analysis of morphological landmarks reveals that inter-subject variability increases during development in the right – but not in the left – STC. Similarly, inter-subject variability of cortically-realigned functional responses to voices, other categories and tones increases with age in the right STC. Our findings reveal asymmetric developmental changes in brain regions crucial for auditory and voice perception. The age-related increase of inter-subject variability in right STC suggests that anatomy and function of this region are shaped by unique individual developmental experiences.

Introduction

The human superior temporal cortex is a relevant cortical site for many auditory and language functions. In the adult brain, its morphology is highly asymmetric between hemispheres and highly variable across individuals. It includes one of the most commonly observed anatomical asymmetries of the brain, i.e. a larger planum temporale (PT) in the left as compared to the right hemisphere, which has been often related to a left hemispheric specialization for language (Geschwind and Levitsky, 1968; but see Dorsaint-Pierre et al., 2006; Eckert et al., 2006). Albeit less well-known, an opposite asymmetry is consistently observed in the superior temporal sulcus (STS), whose depth is greater in the right when compared to the left hemisphere (Ochiai et al., 2004; Van Essen, 2005). Both PT and STS asymmetries are already present in infants (Dubois et al., 2010; Glasel et al., 2011; Hill et al., 2010a), suggesting an underlying genetic component.

Characteristic functional asymmetries include enhanced left hemispheric responses to linguistic speech information in the posterior and/or anterior superior temporal cortex (Binder et al., 2000; Kilian-Hütten et al., 2011; Obleser et al., 2007; Scott et al., 2000) and enhanced right hemispheric responses to human voices, especially toward the anterior STS (Belin et al., 2000; Formisano et al., 2008; von Kriegstein et al., 2003). Interestingly, 3-month-old infants show a relatively strong left lateralization of the superior temporal activity to speech and speech-like sounds (Dehaene-Lambertz et al., 2002, 2010). Furthermore, by 3 to 7 months, infants show a strong lateralization of neural responses to voices as compared to non-vocal sounds in the right anterior STS (Blasi et al., 2011) or right posterior superior temporal cortex (Grossmann et al., 2010). Paralleling language development, the neural systems for speech perception continue to refine throughout childhood and adolescence (Bonte and Blomert, 2004; Parviainen et al., 2011). Less is known on the developmental trajectory of voice selective activity in the superior temporal cortex and its lateralization, which is a focus of the present study.

Morphologically, the superior temporal cortex shows inter-individual variability in the number of transverse gyri of Heschl (HG), including incomplete and complete HG duplications in the left

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* Corresponding author. Fax: +31 43 3884125.
E-mail address: m.bonte@maastrichtuniversity.nl (M. Bonte).
[1] These authors have equal contribution.

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and/or right hemisphere (Campain and Minckler, 1976; Leonard et al., 1998). Other sources of inter-individual variability include the size and form of the planum temporale (Shapleske et al., 1999) and the folding pattern of the STS (Im et al., 2010; Ochiai et al., 2004). Inter-individual variability in morphology has been related to expertise in music (Schneider et al., 2002) and speech analysis (Golestani et al., 2011), and to language dysfunctions in dyslexia (Leonard et al., 2006) and schizophrenia (Shapleske et al., 1999). Surprisingly little is known about developmental changes in normal morphological variability. Studying these developmental changes can further our understanding of regionally specific maturation and learning-induced plasticity.

In the present study, we investigated structural and functional development of the superior temporal cortex by analyzing hemispheric asymmetry and inter-individual variability of cortical surface landmarks and fMRI responses to voices and control sounds in children, adolescents and young adults. We assessed morphological and functional asymmetries by calculating hemispheric differences in anatomical landmarks and fMRI activity in individual subjects and subsequently comparing them to their age group means. Furthermore, we examined morphological variability by projecting individual anatomical landmarks on a group surface for each age group and computing inter-subject distances, and functional variability by calculating inter-subject overlap of fMRI responses after minimizing macro-anatomical differences by means of cortex-based group alignment (Frost and Goebel, 2012; Goebel et al., 2006).

Materials and methods

Participants

(f)MRI measurements were performed in thirty-seven healthy Dutch-speaking participants (13 children, 14 adolescents, 10 adults). Analysis was performed on 30 subjects: 10 children (8f, mean (SD) age 9.1 ± 0.7 years), 10 adolescents (8f, mean age 14.1 ± 0.6 years) and 10 adults (6f, mean age 24.1 ± 2.4 years). Data of 3 children and 4 adolescents were discarded: 2 children did not complete the measurement, 1 child moved too much during the measurements, 3 adolescents showed no significant activation to tones and/or voices and 1 adolescent was discarded due to technical problems during the measurement. For the functional analysis 2 additional children had to be excluded due to excessive movement, resulting in the inclusion of 8 out of 10 children (6f, mean age 9.1 ± 0.7 years). Adults and adolescents received a monetary reward for participation (€5 per hour), children could select a toy (e.g. car, ball, bracelet, book) after both sessions. Informed consent was obtained from all adult and adolescent participants and from parents of adolescents and children, according to the approval by the Ethical Committee of the Faculty of Psychology and Neuroscience at the University of Maastricht.

All participants were Dutch speakers with normal hearing as assessed with a pure tone audiogram (detection thresholds of frequencies from 250 to 8000 Hz at 0–20 dB). Each age group included 9 right-handed participants and 1 left-handed participant, as assessed by a handedness questionnaire adapted from Annett (1979). The adaptation consisted of replacing four less child oriented items (striking a match, using thread, using a broom, using a shovel) with child oriented items (drawing, using a spoon, using a hair comb, turning a page). All children, adolescents and adults showed normal language development and cognitive abilities as assessed by psychometric tests (see Table 1). Psychometric tests included a word reading task and a phoneme deletion task (Blomert and Vaessen, 2009), as well as the block design, similarities and digit span sub-tests of the WISC (Wechsler et al., 2000) or WAIS (Kort et al., 2005). ANOVA analyses were performed on age-appropriate t-scores (word reading, phoneme deletion; mean = 50; SD = 10) or norm scores (WISC/WAIS subtests; mean = 10; SD = 3). There were no significant age group differences, with the exception of the phoneme deletion test. The latter test showed a main effect of age group (F(2,27) = 4.2; p = 0.026) and a post-hoc difference between children and adolescents (p = 0.012) and children and adults (p = 0.033), but not between adolescents and adults (p =0.66). These differences were due to 3 children who performed just below the age-appropriate norm with t-scores of 34, 37 and 38. Importantly however, their t-scores for word reading corresponded to 53, 60 and 58 and their average WISC norm scores corresponded to 11, 9 and 10 respectively, indicating normal reading and cognitive abilities.

Table 1
Psychometric test results across age groups.

	Child	Adolescent	Adult
Word reading[a]	57.0 (3.2)	57.6 (1.5)	57.8 (1.7)
Phoneme deletion[a]	51.0 (10.8)	61.0 (3.9)	59.4 (7.5)
WISC/WAIS			
Similarities[b]	10.4 (3.0)	12.3 (3.3)	13.3 (2.8)
Block design[b]	10.5 (2.8)	10.3 (3.2)	11.5 (3.4)
Digit span[b]	11.1 (2.5)	12.1 (2.9)	11.9 (3.2)

[a] Age-appropriate t-scores, mean = 50, SD = 10.
[b] Age-appropriate norm scores, mean = 10, SD = 3.

Anatomical measurement

Brain imaging was performed with a 3 Tesla scanner (head setup, Allegra — Siemens) at the Maastricht Brain Imaging Center. Children and adolescents were acquainted to the scanning environment and trained to minimize head movement using a simulation scanner. Movement training consisted of two 6-minute blocks during which children/adolescents watched a cartoon movie that was shortly interrupted whenever head movement would exceed 3 mm. A high-resolution structural scan (voxel size, 1 × 1 × 1 mm^3) was collected for each subject using a T1-weighted three-dimensional ADNI sequence [TR, 2050 ms; echo time (TE), 2.6 ms; 192 sagittal slices].

Preprocessing and cortex based alignment

Anatomical data were analyzed using BrainVoyager QX 2.4 (Brain Innovation). The anatomical images of each participant were normalized into Talairach space. This operation included the definition of the landmarks AC (anterior commissure) and PC (posterior commissure) as well as a demarcation of the extremities of the cortex (inferior, superior, left and right most points); the defined subject-specific landmarks were then used to rotate each brain in the AC–PC plane followed by piecewise, linear transformations to fit each brain in the common Talairach "proportional grid" system (Talairach and Tournoux, 1980). The achieved brain normalization aligns global orientation and adjusts size of the brains without distorting individual brain anatomy. Thus, it is suited for the analysis of morphological features such as sulcal depth or orientation of sulci. However, with Talairach (as well as the related template-based MNI) normalization, gyri and sulci are not aligned well across brains. For fine-grained questions requiring maximal correspondence between brain anatomical locations (e.g. to study functional variability with respect to morphology), more advanced cortex-based alignment schemes have been introduced (e.g. Fischl et al., 1999; Goebel et al., 2006). For advanced alignment of gyri and sulci as well as for visualization, mesh representations of the cortical surface were created using an automatic segmentation tool (Kriegeskorte and Goebel, 2001). Curvature maps, reflecting the gyral/sulcal folding pattern, were then derived from the extracted cortical meshes for both hemispheres of each individual. To allow mesh vertices to find corresponding locations across brains, each hemisphere was inflated to a spherical representation to create a restricted space for vertex displacements (e.g. Fischl et al., 1999). While this representation is void of original morphology, information about the gyral/sulcal folding