



Adult-like processing of naturalistic sounds in auditory cortex by 3- and 9-month old infants



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A B S T R A C T

Functional neuroimaging has been used to show that the developing auditory cortex of very young human infants responds, in some way, to sound. However, impoverished stimuli and uncontrolled designs have made it difficult to attribute brain responses to specific auditory features, and thus made it difficult to assess the maturity of feature tuning in auditory cortex. To address this, we used functional magnetic resonance imaging (fMRI) to measure the brain activity evoked by naturalistic sounds (a series of sung lullabies) in two groups of infants (3 and 9 months) and adults. We developed a novel analysis method – inter-subject regression (ISR) – to quantify the similarity of cortical responses between infants and adults, and to decompose components of the response due to different auditory features. We found that the temporal pattern of activity in infant auditory cortex shared similarity with adults. Some of this shared response could be attributed to simple acoustic features, such as frequency, pitch, envelope, but other parts were not, suggesting that even more complex adult-like features are represented in auditory cortex in early infancy.

Introduction

In their first months, human infants show surprisingly sophisticated auditory perception, with a predisposition to listen to speech (Vouloumanos and Werker, 2004, 2007) and the ability to discriminate subtle phonetic contrasts in native (Trehub and Rabinovitch, 1972; Trehub, 1973; Eimas, 1975) and in non-native languages (Werker and Tees, 1984). They can discriminate between the voices of different speakers, such as their mother's and a strangers' voice (DeCasper and Fifer, 1980), and even generalize speech sounds across talkers (Kuhl, 1979; Jusczyk et al., 1992). It is surprising that young infants can perform these complex feats, considering that the cortical auditory system – the network of brain regions that supports complex auditory processing in adults, and its afferent connections – is immature at the time of birth, and it is not until 4.5–6 postnatal months that the differentiation of cortical layers and the myelination of thalamocortical projections are visible in auditory cortex (Moore and Guan, 2001; Moore and Linthicum, 2007). From these observations, some researchers have suggested that early auditory abilities are facilitated mostly by subcortical auditory processing (Moore, 2002; Eggermont and Moore, 2012). This seems unlikely given that functional neuroimaging has

shown cortical responses evoked by sound in fetuses (Moore et al., 2001; Draganova et al., 2005; Holst et al., 2005; Eswaran et al., 2007; Jardri et al., 2008), infants born very prematurely (Mahmoudzadeh et al., 2013, 2016), newborns (Cheour-Luhtanen et al., 1995a; Cheour et al., 1998a; Anderson et al., 2001; Peña et al., 2003; Kotilahti et al., 2010; Perani et al., 2010, 2011; Baldoli et al., 2014) and 3-month olds (Dehaene-Lambertz et al., 2002, 2006, 2010; Blasi et al., 2011a). What has not been established, however, is the functional role of developing auditory cortex – the auditory features it represents, and the maturity of these responses, which remain unclear.

Some studies have asked whether the immature auditory cortex of very young infants is capable of speech-specific processing. They have found that responses differ in magnitude between speech and non-speech sounds (Dehaene-Lambertz et al., 2002, 2010; Peña et al., 2003; Homae et al., 2011; Minagawa-Kawai et al., 2011; Perani et al., 2011; Sato et al., 2011; Shultz et al., 2014), or between different kinds of speech sounds, such as different phonemes (Cheour-Luhtanen et al., 1995b; Cheour et al., 1998b; Mahmoudzadeh et al., 2013, 2016; Kuhl et al., 2014), or languages (Minagawa-Kawai et al., 2011; Sato et al., 2011; Vannasing et al., 2016). However, the conclusion that these differences in responses reflect speech specificity is confounded by the

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fact that different sounds differ in their basic acoustic features such as acoustic envelope, pitch, and frequency. Adult auditory cortex is known to be exquisitely sensitive to these simple features (Giraud et al., 2000; Hall et al., 2002a; Patterson et al., 2002; Nourski et al., 2009; Linke et al., 2011a; Kubanek et al., 2013), and so neuroimaging researchers of adult speech perception often go to great lengths to create well controlled acoustic stimuli (Scott et al., 2000; Remez et al., 2001; Sohoglu et al., 2012; Wild et al., 2012a). Because of poor auditory control in infant studies (e.g., forwards vs. backwards speech, or even speech vs. silence), or presentation of a very few sounds in a highly stereotyped sequence (e.g., a train of ‘/ga’ with the occasional ‘/ba’), we still cannot determine which acoustic features drive cortical responses in very young brains. Do these responses reflect differences in simple acoustic features, more complex auditory representations (e.g., phonemes), or tuning to a variety of auditory features?

Furthermore, does the feature tuning of infant auditory cortex appear adult-like? If presented with naturalistic sounds, is the infant cortex driven by the same kinds of auditory features, and in the same way, as the mature auditory cortex? One tantalizing observation from infant functional magnetic resonance imaging (fMRI) is that the spatial distribution of auditory activity resembles that seen in adults (Dehaene-Lambertz et al., 2002, 2006; Perani et al., 2011; Shultz et al., 2014). While one can conclude that similar cortical regions process sound in infants and adults, we cannot conclude that they function similarly. For example, it is well known that the functional mismatch response (MMR) – the most common tool for studying infant perception with electroencephalography (EEG) – undergoes significant change in the first six months after birth to become more adult-like (Trainor et al., 2003; He et al., 2007a), which suggests that cortical auditory responses in early infancy are immature, and perhaps quite distinct in function. Yet, alternatively the differences in the morphology of auditory evoked responses might reflect the influence of immature physiology of the coupling between neural activity and the measured signal (Trainor et al., 2003; Eggermont and Moore, 2012), rather than underlying differences in function.

We conducted an experiment to address these unresolved questions about auditory cortex function in early infancy. What acoustic features does auditory cortex process? Is there evidence for tuning to complex in addition to simple acoustic features? Do auditory responses in infant auditory cortex resemble adult cortical responses? We used fMRI to isolate and characterize, in infants (at 3- and 9-months of age) and adults, the responses in auditory cortex evoked by rich and naturalistic sounds that are engaging to infants – sung lullabies. These infant age groups were selected because around six months after birth is considered to be a turning point in terms of auditory perception (e.g., the beginning of a shift from universal to language-specific perception, Werker and Tees, 1984) and anatomical development (e.g., myelination of thalamocortical projections, Moore and Guan, 2001). We therefore expected to see developmental differences in how auditory cortex responses to rich sounds; for example, perhaps these perceptual and anatomical changes are accompanied by more mature-like processing in auditory cortex. We developed a novel analysis technique, inter-subject regression (ISR), which specifically allowed us to answer these questions. ISR combines the hypothesis-driven general linear model (GLM) with the model-free approach of inter-subject correlation (ISC) (Hasson et al., 2004) in order to decompose brain activity into components that reflect different aspects of naturalistic auditory processing. Brain responses driven by simple acoustic features, such as amplitude envelope, pitch, and frequency, were directly modelled from the stimulus (as in a conventional GLM), whereas more complex brain responses to abstract features were identified as the component of evoked response shared by all listeners that could not be attributed to the simple features. Importantly, ISR allowed us to directly measure the similarity of the timecourse of brain

activity between infants and adults, while accounting for age-related differences in the hemodynamic response function (HRF) (Arichi et al., 2012) that would make their evoked brain responses appear to be dissimilar. We hypothesized that adult auditory cortex would be sensitive to low-level acoustic features and show coding of more complex features of the rich acoustic stimuli. We also hypothesized that, despite immature cortical anatomy, we would observe reliable tuning to these features at 3 months of age, and that these responses would be somewhat similar to adults. Furthermore, we expected to observe maturational changes in the first year, so that by 9-months, auditory responses would be even more adult-like.

Materials and methods

Subjects

Two groups of infants at different ages (3- and 9-months old) were recruited to undergo MRI scanning. These ages were chosen because they fall before and after 6-months – a time that has been proposed to be associated with increasing cortical connectivity (Moore and Guan, 2001; Moore and Linthicum, 2007) and the beginning of significant changes in auditory perception (Kuhl et al., 2008; Werker and Hensch, 2014).

Twenty-four 3-month old infants were recruited, but only six useable fMRI data sets were obtained from these volunteers (mean corrected age at scan 3.5 months, standard deviation 0.5 months; 4 females, 2 males). Similarly, sixteen 9-month old infants were admitted to the study, but only seven yielded useable fMRI data (mean corrected age at scan 9.3 months, standard deviation 1.0 months; 1 female, 6 males). All infant participants were scanned unседated during natural sleep to minimize subject motion. The seemingly low success rate (6/24 3-months, and 7/16 9-months) is a result of infants either: not falling asleep at all (and not entering the scanner); or waking before we had completed 2 fMRI sessions and at least one structural image. Of the 3-month old infants (N=6), two families were recruited from Western University's Developmental Psychology Pool, and four families were recruited from the Neonatal Intensive Care Unit (NICU) at Children's Hospital in London, Ontario. Families in the latter group were approached to participate in a larger study investigating the effects of suspected brain injury on neurodevelopmental outcomes. Similarly, four of the 9-month olds (N=7) were recruited from the Developmental Psychology Pool at Western University, and three of the families were approached in the NICU at Children's Hospital. Despite the inclusion of subjects recruited from the NICU, none of the final cohort had brain injury apparent on the structural MRI. The details of the infant participants are shown in Table 1. Parents or legal guardians gave informed consent for the infants to participate in this study, and the study protocol was examined and cleared by the Western University Health Sciences Research Ethics Board.

To characterize the response of the mature auditory system, a group of 16 adults (11 females, mean age 22 years 7 months) were recruited from the students and staff at Western University, and were paid for their participation in this study. All participants spoke fluent English, were right-handed, with no reported hearing deficits, and no known language or neurological impairments. Participants were screened for compliance with magnetic resonance imaging safety standards: they reported no prior surgeries involving metallic implants, devices, or objects. They gave informed consent according to ethical guidelines laid down by Western University.

Data acquisition

All scanning was performed on a Siemens (Erlangen, Germany) MAGNETOM Prisma 3T MRI system located at the Robart's Centre for

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