

Cortical Plasticity in 4-Month-Old Infants: Specific Effects of Experience with Musical Timbres

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Abstract Animal models suggest that the brain is particularly neuroplastic early in development, but previous studies have not systematically controlled the auditory environment in human infants and observed the effects on auditory cortical representations. We exposed 4-month-old infants to melodies in either guitar or marimba timbre (infants were randomly assigned to exposure group) for a total of ~160 min over the course of a week, after which we measured electroencephalogram (EEG) responses to guitar and marimba tones at pitches not previously heard during the exposure phase. A frontally negative response with a topography consistent with generation in auditory areas, peaking around 450 ms, was significantly larger for guitar than marimba tones in the guitar-exposed group but significantly larger for marimba than guitar tones in the marimba-exposed group. This indicates that experience with tones in a particular timbre affects representations for that timbre, and that this effect generalizes to tones not previously experienced during exposure. Furthermore, mismatch responses to occasional small 3% changes in pitch were larger for tones in guitar than marimba timbre only for infants exposed to guitar tones. Together these results indicate that a relatively small amount of passive

exposure to a particular timbre in infancy enhances representations of that timbre and leads to more precise pitch processing for that timbre.

Keywords Cortical plasticity · Auditory · Learning · Timbre · Music · Development · Infancy

Introduction

Cortical plasticity resulting from specific auditory experience has been demonstrated in both animal and human models (see Eggermont 2008; Ohl and Scheich 2005). For example, training at a particular sound frequency changes cortical tonotopic maps in animals (e.g., Buonomano and Merzenich 1998; Recanzone et al. 1993; Rutkowski and Weinberger 2005) and modifies auditory cortical responses in humans (Bosnyak et al. 2004; Gander et al. 2010). Although plasticity is present across the lifespan, the degree of plasticity likely changes with development, and somewhat different mechanisms may be expressed at different ages. Consistent with this view, animal studies show that auditory deprivation or hearing damage has particularly devastating effects during early cortical development, setting up abnormal tonotopic maps that cannot be rectified even if normal sound experience is restored after a sensitive period (Kujawa and Liberman 2006; Norena et al. 2003; Zhang et al. 2001). Similarly in humans who were congenitally deaf, basic event-related potential responses to sound remain immature in some respects after cochlear implantation if the period of deafness is more than about 3 years (Ponton and Eggermont 2001; Sharma et al. 2005). Despite these findings, few studies have examined the effects of experience on cortical representation with an experimentally controlled methodology in young human

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infants. Understanding the extent to which experience changes the immature human brain is of educational and clinical importance as well as theoretical interest. In this study, we directly manipulate the auditory experience of 4-month-old infants and show that a relatively short passive listening experience of a few hours with music played on a particular instrument (i.e., in a particular timbre) can alter sound representations in auditory cortex for tones of the experienced timbre.

Sounds can be described as having three main features: pitch, duration, and timbre (or sound quality). The perception of timbre is multidimensional in that it is affected by several features, most notably the temporal characteristics of the onset and the long-term spectral (frequency) content. Timbre is critical to everyday functioning. Speech sounds (phonemes) differ from each other in timbre, and timbre perception enables recognition of speech sounds spoken by different speakers in different pitch ranges. Timbre is important for social communication in that we recognize people by their individual voice quality. Timbre also enables identification of musical instruments by their different sound qualities. Because of its critical role in auditory perception and human communication, we expected that experience with particular timbres would cause plastic changes in auditory representations relatively quickly.

Most human studies of the effects of auditory experience during infancy are naturalistic in design. For example, phonemic categorization has been compared in infants growing up in different language environments (e.g., Curtin and Werker 2007; Kuhl 2008). While very useful, with such designs it is difficult to examine aspects of plasticity such as the minimum amount of experience needed for plastic effects to emerge or the type of experience that is most effective in eliciting plasticity. A few previous studies have directly manipulated the infants' environment. For example, Kuhl et al. (2003) gave 9-month-old English-learning infants either interactive experience with Mandarin or passive exposure to Mandarin. They found that only the former group maintained the ability to discriminate Mandarin phonemic contrasts not found in English. However, they did not measure plastic brain changes in this case.

Musical experience provides an interesting model for studying auditory plasticity because the amount and type of musical experience varies widely in the population. Studies show volumetric differences in musicians and nonmusicians across a wide network of brain regions (Schlaug 2009) including auditory cortex (e.g., Bermudez et al. 2009; Gaser and Schlaug 2003; Schneider et al. 2002), Broca's area (Sluming et al. 2002), motor regions (Bangert and Schlaug 2006; Elbert et al. 1995; Gaser and Schlaug 2003), and cerebellum (Hutchinson et al. 2003).

Furthermore, individuals with poor pitch processing show deficient white matter volume in inferior frontal regions (Hyde et al. 2006) and reduced white matter tracts between superior temporal and inferior frontal areas (Loui et al. 2009). With these studies, however, the question remains as to whether the musician/non-musician differences existed prior to the musical experience, and indeed influenced the decision to train musically, or whether the musical experiences themselves were primarily responsible for the differences.

EEG and MEG studies also show musician/non-musician differences in musical processing (Besson and Faita 1995; Fujioka et al. 2006; Fujioka et al. 2004, 2005; Koelsch et al. 2002; Pantev et al. 1998; Roberts et al. 2004; Shahin et al. 2003; Shahin et al. 2004; Shahin et al. 2008; Tervaniemi et al. 2001; Trainor et al. 1999). The event-related potential (ERP) response to a discrete sound consists of a number of positive and negative deflections reflecting stages of processing and can be measured in EEG or MEG recordings. For example, musicians show larger N1 (obligatory frontally negative component peaking around 100 ms after sound onset) and P2 (obligatory frontally positive component peaking around 170 ms after sound onset) components to musical tones (Pantev et al. 1998; Shahin et al. 2003; Shahin et al. 2004), particularly for tones in the timbre of their instrument of practice (Pantev et al. 2001). N1 and P2 originate in secondary auditory cortex and appear to mark the individuation of auditory events, as they increase in amplitude the farther apart successive events are in time (Picton et al. 1999; Picton et al. 2000). One ERP component of particular interest with respect to this study is the mismatch negativity (MMN). MMN occurs when an occasional sound (deviant) is changed in an ongoing stream of standard sounds. MMN manifests as an increased negativity peaking between 100 and 250 ms after deviant onset, depending on the particular type of change (Näätänen et al. 2007; Picton et al. 2000) and reflects auditory expectations that are dependent on the immediate past sound environment (Trainor and Zatorre 2009). MMN can be measured in response to a change in a sound feature such as pitch or timbre as well as to a change in sound category. The MMN appears to localize anatomically to Heschl's gyrus (Ha et al. 2003) although the exact location appears to depend to some extent on the particular feature of the stimulus that changes (Alho 1995; Frodl-Bauch et al. 1997; Schairer et al. 2001). The mismatch may also invoke the activation of a separate frontal or front-temporal source reflecting the activity of an involuntary attention-switching mechanism (Alho 1995; Doeller et al. 2003; Frodl-Bauch et al. 1997; Kasai et al. 1999). Adult musicians show larger MMN to occasional deviant notes in a melody (e.g., Fujioka et al. 2004; Tervaniemi et al. 2001) and deviant notes in

polyphonic contexts (more than one simultaneous melody) (Fujioka et al. 2005). When EEG recordings are analyzed in the frequency domain, musicians also show larger gamma band responses to musical tones compared to non-musicians (Shahin et al. 2008; Trainor et al. 2009). Although these studies again cannot definitively indicate whether the differences are caused by musical experience, studies showing enhanced processing for tones in the timbre of the musician's instrument suggest that experience plays a role (Pantev et al. 2001; Shahin et al. 2003; Shahin et al. 2008). The unlikely alternative postulate would be that genetically driven differences give certain timbres larger cortical representations in some individuals.

The most direct studies of cortical plasticity for music in adults involve laboratory training studies. N1 and P2 components of the ERP have been shown to increase in amplitude after auditory discrimination training (Bosnyak et al. 2004; Menning et al. 2000; Tremblay et al. 2001; van Wassenhove and Nagarajan 2007) although simple repeated exposure to a stimulus may be sufficient to induce plastic changes in P2 responses (Sheehan et al. 2005). Acoustic experience also modifies properties of the 40 Hz auditory steady-state response (Gander et al. 2010) which localizes to primary auditory cortex (A1). MMN is also amenable to experiential change. Lappe et al. (2008) showed increases in MMN amplitude to deviant notes in a musical excerpt after experience with that excerpt. Furthermore, learning to play the excerpt on a keyboard resulted in larger changes in MMN responses compared to training on the same excerpt that involved only perceptual judgments.

Studies in preschool children also reveal differences between those training musically and those not. For example, Shahin et al. (2004) found that 4- to 5-year-old children in Suzuki lessons showed P2 responses similar to non-musician children 2–3 years older, but because participants were not randomly assigned, it cannot be definitively determined whether these differences were preexisting or the result of the training. Fujioka et al. (2006) measured MEG responses to musical tones in children four times over the period of a year, and found that the N2 component, which is associated with memory and attentional processes, changed more rapidly in children taking music lessons compared to those not training musically, suggestive of a causal effect of musical training. Similarly, Shahin et al. (2004) measured children twice, once at 4 years and again at 5 years of age, and found that none of the children showed significant oscillatory gamma band responses to musical tones at the outset, but that the induced gamma band response emerged by 5 years in those taking music lessons but not in those not training musically. Again, these studies suggest that musical training affects brain development, but causality cannot be definitively determined.

Auditory ERPs change dramatically during infancy and early childhood (e.g., Ceponiene et al. 2002; Choudhury and Benasich (2011); Fujioka et al. 2006; He et al. 2007, 2009a, b; He and Trainor 2009; Ponton et al. 2000; Trainor et al. 2003; Trainor et al. 2001), although fully mature evoked responses to a single tone are not achieved until the late teenage years (Ponton et al. 2000; Shahin et al. 2004). Unlike in adults and older children, infant ERPs evoked by tones are dominated by frontally positive slow waves, and obligatory components of the adult tone-evoked ERP are so small in infants that they are difficult to measure (Trainor and He 2010). The MMN response appears comparatively robust in early development, already being present in newborn infants, although with a different morphology than the adult response (Alho et al. 1990). In contrast to adults who show a negative MMN response to occasional changes in a sound stream, young infants show a frontally positive slow wave response that tends to be left lateralized (Friederici et al. 2002; Friedrich et al. 2004; He et al. 2007, 2009a, b; He and Trainor 2009; Leppanen et al. 2004; Morr et al. 2002; Novitski et al. 2007; Ruusuvirta et al. 2004; Trainor et al. 2003; Trainor et al. 2001; Winkler et al. 2003). The mature fast negative mismatch response emerges at different ages for changes in different sound features (Trainor 2008). Previous studies have shown that for pitch changes of a semitone (1/12th octave, approximately 6%) or larger, the negative response typically emerges between 2 and 4 months of age (He et al. 2007, 2009a, b), but for changes in one note of a melody, the immature slow positive response remains past 6 months (Tew et al. 2009). In the adult literature there is some controversy as to whether mismatch responses reflect memory-based processes or a modulation of the N1 response (May and Tiitinen 2010). However, it should be noted that both the fast negative and slow positive responses to a pitch change can be seen at the same time in the same infants, suggesting that these two mismatch components have different physiological bases.

In this study, we test whether randomly assigning 4-month-old infants to one of two groups exposed to tones with different timbres leads to plastic changes in the brain's response to those timbres. We do this by presenting infants once a day for a week with a 20 min CD of children's melodies in either the guitar or marimba timbre. We then measure their brain responses to occasional changes in the pitch of a guitar tone and to occasional changes in the pitch of a marimba tone. Because MMN amplitude increases with the size of the pitch change near threshold, responses to small pitch differences are most likely to show plastic effects. We therefore measured responses to a small quarter tone (1/24th octave, 3%) change in pitch, a size of change not previously tested with MMN in infants.

Materials and Methods

Subjects

Thirty-eight healthy, full-term 4-month-old infants with no known hearing deficits were assigned alternately (as they were scheduled) to either the guitar timbre exposure or marimba timbre exposure group. Thirteen infants were excluded from the final sample as they failed to produce a minimum of 500 artifact-free standard trials and 100 artifact-free deviant trials in each condition, leaving a final group of 25 (mean age = 4.6 months, range = 4.2–4.9 months, 15 females), 13 of whom were in the guitar timbre exposure and 12 in the marimba timbre exposure group. Informed written consent was obtained from parents of all subjects prior to the experiment. The number of hours that infants heard music of all kinds in an average week as reported by parents was not significantly different between groups ($P = 0.33$), with a mean of 9.8 (SD = 5.2) hours for the guitar group and 12.8 (9.2) hours for the marimba group.

Stimuli

Stimuli for the Exposure Phase

Thirty-one common children's songs with a total duration of approximately 20 min were synthesized (Cakewalk Pro Audio 9 software) in two versions, one using an acoustic nylon string guitar timbre and the other using a marimba timbre. The guitar version of the songs was recorded onto one CD and the marimba version on another. These timbres were chosen to be relatively pleasant to listen to and to have distinct spectra and amplitude envelopes (Fig. 1). In particular, it can be seen that the guitar timbre has a more abrupt onset and faster decay than the marimba timbre. As well, the guitar timbre has relatively more energy at higher harmonics compared to the marimba timbre. All songs were transposed into either C or G major and contained notes within a two-octave range between G_3 (196 Hz) and G_5 (784 Hz).

Test Stimuli

All infants completed two conditions, one using tones in the guitar timbre and the other using tones in the marimba timbre. In each condition, standard trials consisted of a 400 ms A-flat₄ (415 Hz) tone and trial-to-trial SOA was 800 ms. Tones on deviant trials were raised a quarter-tone (approximately 3%) to 428 Hz. Neither of these two tones appeared in any of the stimuli heard during the musical exposure phase.

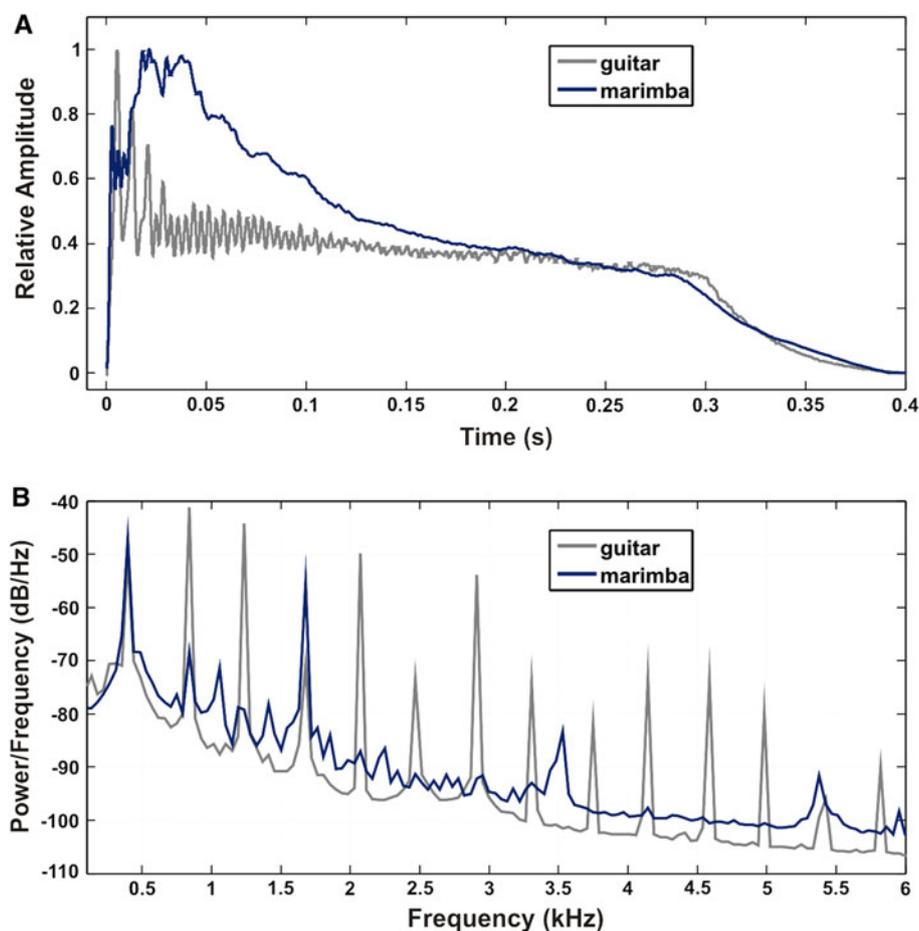
Procedure

Infants were randomly assigned to either the guitar-exposed or the marimba-exposed group. Parents were mailed a package containing an instruction sheet, a log sheet, and a CD in either the marimba or the guitar timbre. Parents were instructed to play the CD in its entirety for their infant at least once per day for at least seven consecutive days, with a provision for up to three additional days of listening to allow for scheduling of the EEG testing session. Parents were further instructed to refrain from playing the music while there were competing sounds in the environment (e.g., television), and were encouraged to play the CD more than once a day. They reported on the provided log sheet the number of times and context in which the CD was played each day. On average, infants in the guitar group heard the CD 8.38 times (SD = 1.61, range = 7–13) and infants in the marimba group 8.92 times (SD = 1.31, range = 7–11) prior to test.

The EEG testing session was scheduled immediately following the training period. During testing, each infant was seated on his or her parent's lap in a sound-attenuated room. The tones were presented from a central speaker placed at eye level one meter in front of the subject in a single experimental session lasting approximately 25 min. A passive listening protocol was used in which infants watched a silent animated movie while the experimenter silently entertained the infant with toys, puppets and bubbles. Infants were permitted to suck on pacifiers or drink from their bottle if necessary in order to keep them still and silent. The experiment was stopped if infants became fussy. Subjects from both the guitar-exposed and the marimba-exposed groups were tested with both the guitar and marimba test tones. 2,000 trials were presented in ten blocks of 200, with blocks alternating between the guitar and marimba timbres (order counterbalanced across subjects).

Within each block, tones of the same instrument were presented in an oddball paradigm with 85% standard and 15% deviant trials in a pseudo-random order such that at least two standard trials needed to occur between deviant trials. Stimuli were presented using E-prime version 1.2 software through an Audigy 2 platinum sound card. The stimuli were matched for intensity and presented at 70 dB(A) over a noise floor of 29 dB(A) measured at the position of the participants' heads. After the experiment, infants were presented with a certificate and a bath toy as a token of gratitude for participation. All study procedures were approved by the McMaster University Research Ethics Board which follows the Canadian Tri Council policy statement on ethical conduct for research involving humans.

Fig. 1 a Amplitude envelopes for stimuli: The guitar and marimba tone (415 Hz standards shown) waveforms were rectified and low-pass filtered (50 Hz) to show the amplitude envelopes. Both tones had sharp initial onsets, rising to within 60% of full amplitude within 5 ms. The guitar tone rose to full amplitude within 10 ms while the marimba took approximately 20 ms to reach full amplitude. **b** Power spectra of the 415 Hz standard tones. Spectra were taken using Welch's spectral density estimation method, not including the first 25 ms of tone onset. The guitar tone contained all harmonics while the marimba tone contained primarily the fundamental and fourth harmonics



Data Recording and Analysis

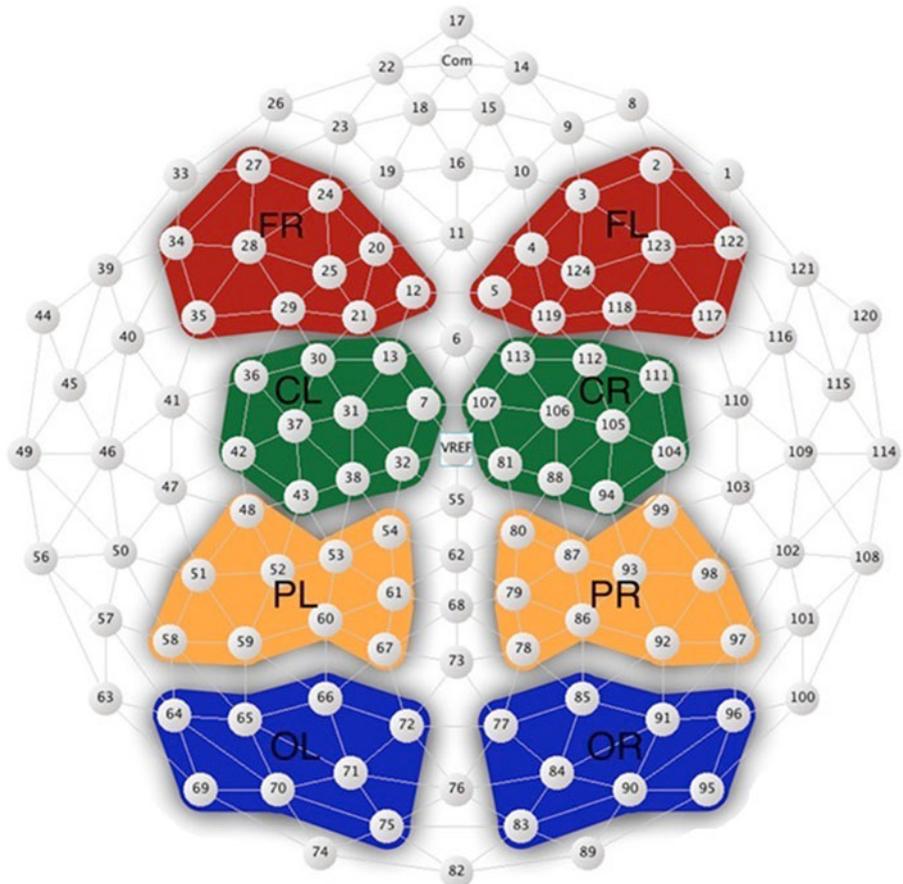
EEG was recorded from 124 scalp locations with a Geodesic Sensor net using Electrical Geodesics Inc. Netstation 4.3.1 software while infants were awake. The EEG was recorded continuously at a sampling rate of 1 kHz with Cz as the reference, was online filtered between 0.1 and 400 Hz, and impedance levels for each electrode were maintained below 50 k Ω . Recorded EEG data were filtered offline between 0.5 and 20 Hz, downsampled at 200 Hz, and run through the artifact-blocking algorithm (see Fujioka et al. 2011) using a threshold of ± 100 μ V to reduce movement-related artifacts. After artifact-blocking, electrodes were digitally re-referenced to the common average. The data were segmented into 600 ms epochs with a 100 ms baseline. The accepted trials were averaged separately into standard guitar, standard marimba, deviant guitar and deviant marimba responses. The number of accepted standard epochs across all 25 infants ranged from 505 to 700 for the standard guitar tone ($M = 666$, $SD = 58$) and 517–700 for the standard marimba tone ($M = 674$, $SD = 49$) with each standard immediately following a deviant presentation excluded from averaging. The number of accepted deviant epochs ranged from 100 to

150 for the deviant guitar tone ($M = 143$, $SD = 13$) and 101–150 for the deviant marimba tone ($M = 143$, $SD = 14$). For statistical analysis, the 124 channels were divided into ten groups representing average responses from five different locations on the scalp from each hemisphere: frontal, central, temporal, parietal and occipital (see Fig. 2). The channels in each group were averaged together for analysis. The average amplitude over the 100 ms baseline period prior to stimulus onset was subtracted from each waveform. This procedure resulted in four average waveforms (standards and deviants for the guitar tone and the marimba tone) for each subject at ten scalp regions. Difference waves were created for each subject for each timbre at each scalp region by subtracting the standard waveform from the deviant waveform. When time windows for analysis are described in the results, these analyses were performed on the average amplitude over the specified window.

Results

Standard and deviant waveforms evoked by the guitar tones are shown in Fig. 3. It can be seen that responses to

Fig. 2 Electrode groupings: For analyses, activity in groups of electrodes representing left and right frontal, central, parietal and occipital regions were averaged. Each group contained between eight and ten electrode sites as shown. Midline electrodes were excluded in order to examine hemispheric differences and peripheral electrodes were excluded to reduce noise



standards included two main components, a frontal positivity peaking between 150 and 200 ms and a negativity peaking between 400 and 500 ms. Both components were present bilaterally and reversed polarity at the back of the head, consistent with generators in auditory cortex. For the first peak analysis of the time window between 100 and 200 ms found no significant differences between groups for either the guitar tone or the marimba tone. However, for the second component, an ANOVA with the average amplitude between 350 and 550 ms as the dependent measure and group (guitar-exposed, marimba-exposed), tone (guitar, marimba), and hemisphere (left frontal region, right frontal region) as independent measures revealed a significant effect of tone (larger amplitude for guitar tone), $F(1, 23) = 5.75$, $P < 0.05$, and a significant interaction between group and tone, $F(1, 23) = 21.38$, $P < 0.001$. No significant differences were found for other regions between 350 and 550 ms. The overall larger response to guitar tones may reflect familiarity with the guitar tone and/or temporal onset and spectral features of the guitar timbre. The lack of a significant effect of hemisphere or interactions involving hemisphere suggests that tones were encoded equally strongly in both hemispheres for both group and for both timbres. The interaction was examined with separate

ANOVAs for each group, such that each ANOVA used tone and hemisphere as independent variables. For both groups the only significant effect was for tone. For the guitar-exposed group, the late component was significantly larger for the guitar compared to the marimba tone, $F(1, 12) = 12.08$, $P < 0.005$. For the marimba-exposed group, the late component was significantly larger for the marimba compared to the guitar tone, $F(1, 11) = 5.04$, $P < 0.05$. Thus, exposure to the guitar or to the marimba timbre through listening to the melodies increased the size of this component in response to tones in that timbre.

The effect of the exposure on pitch encoding was examined by comparing responses to standards and deviants. For the guitar tones, deviants were significantly more positive between 50 and 300 ms in the left frontal group of electrodes and between 150 and 300 ms in the left central group of electrodes for the guitar-exposed group, but there were no significant differences between standards and deviants for the marimba-exposed group (Fig. 3a). This is consistent with exposure to the guitar tones during training leading to better representations for the pitch of tones with this timbre. It should be noted that deviants were more positive than standards, consistent with other studies showing a positive mismatch response in young infants. For the marimba tones,

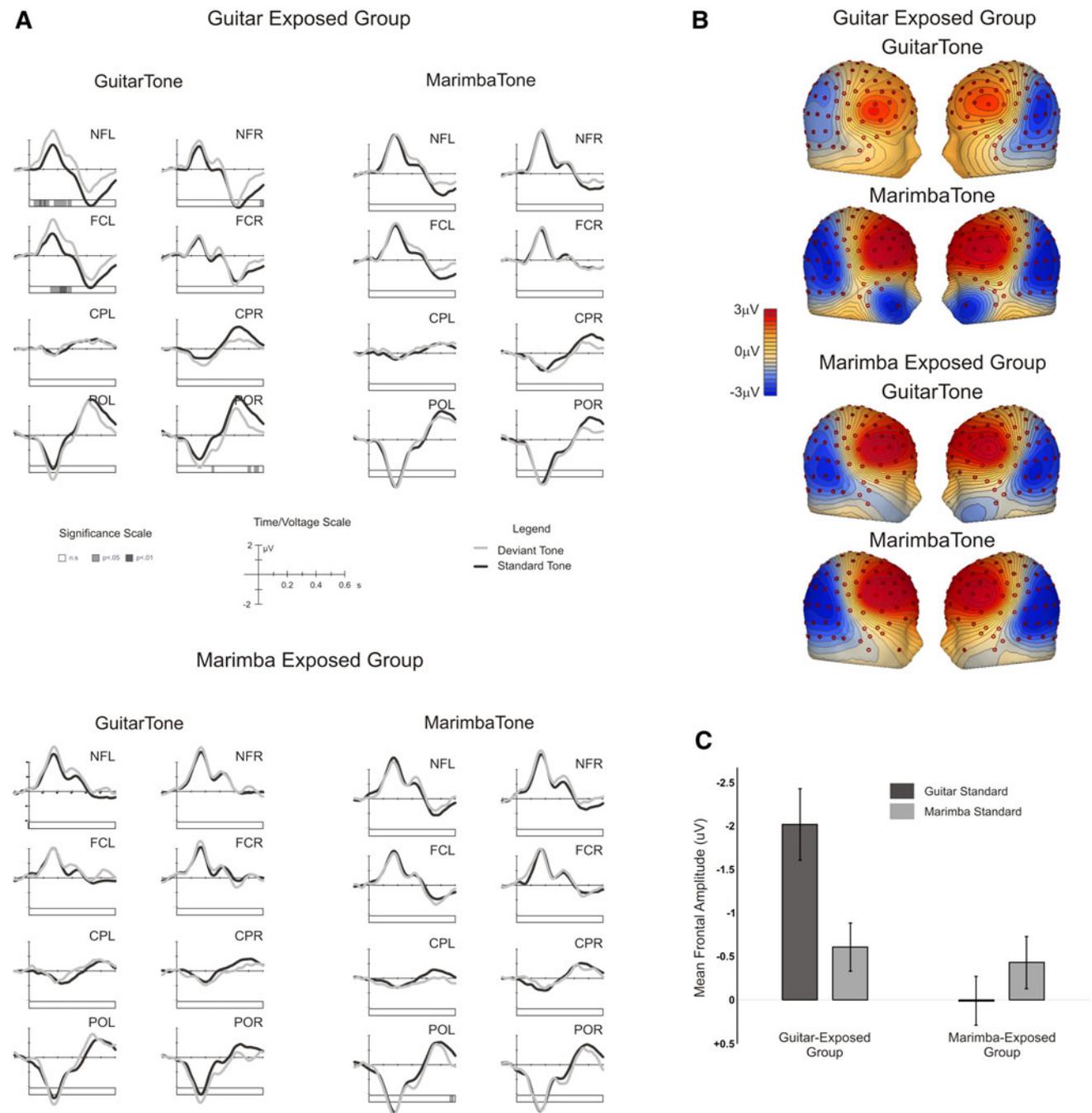


Fig. 3 a Responses to standards and deviants: Grand average waveforms of responses to standard tones (*black traces*) and deviant tones (*light gray traces*) for the eight electrode groupings shown in Fig. 2. Voltage and time scale are the same for every waveform. The guitar-exposed group (*above*) showed significant differences between standard and deviant tones in the NFL and FCL electrodes at various points during the first 300 ms. The significance value for a running *t*-test of the difference between the standard and deviant waves is portrayed in the box beneath each electrode. **b** Topographies of standard tones: As topographies for standards and deviants were virtually identical only the standards are shown. The topographies are for the frontally positive peak occurring at ~ 165 ms for both tones.

These topographies are consistent with bilateral activation in auditory cortices. **c** Analysis of the 350–550 ms window: Mean amplitudes over the time window of 350–550 ms for NFL and NFR electrode groupings revealed no main effect for laterality so amplitudes were collapsed over the left–right groupings. The significant interaction between group and tone is shown. The guitar-exposed group showed significantly larger (more negative) responses for the guitar standard than for the marimba standard tones while the marimba-exposed group showed significantly larger responses for the marimba standard than for the guitar standard tones. *Error bars* represent SE, note *negative* is up

there were no significant differences between standard and deviant waveforms for either group (Fig. 3a, right panels), suggesting that even after exposure to this timbre, fine pitch discrimination is difficult.

The grand average difference waveforms (deviant–standard) are shown comparing the guitar- and marimba-exposed groups in Fig. 4a for guitar and marimba tones. To avoid multiple *t*-tests, the mean amplitudes of the difference waves were calculated for each subject in 50 ms time windows between stimulus onset and 600 ms. Between group comparisons revealed that the difference wave for the left central electrode group was significantly larger for the guitar-exposed than for the marimba-exposed group during

the time intervals 100–150 ms ($P < 0.05$), 150–200 ms ($P = 0.024$), and 200–250 ms ($P = 0.038$) post stimulus onset (Fig. 4b). Figure 4c shows head maps of the difference waves for the guitar tones at 200 ms (marimba difference waves are not shown as they were not significantly different from zero). For the guitar group it can be seen that the mismatch response has a left frontal focus with posterior reversal consistent with a source in left auditory cortex. This is in contrast to the standard responses which showed no significant laterality (Fig. 3a). These topographies are consistent with bilateral activation of auditory cortices in encoding the tones, but left activation in processing pitch differences.

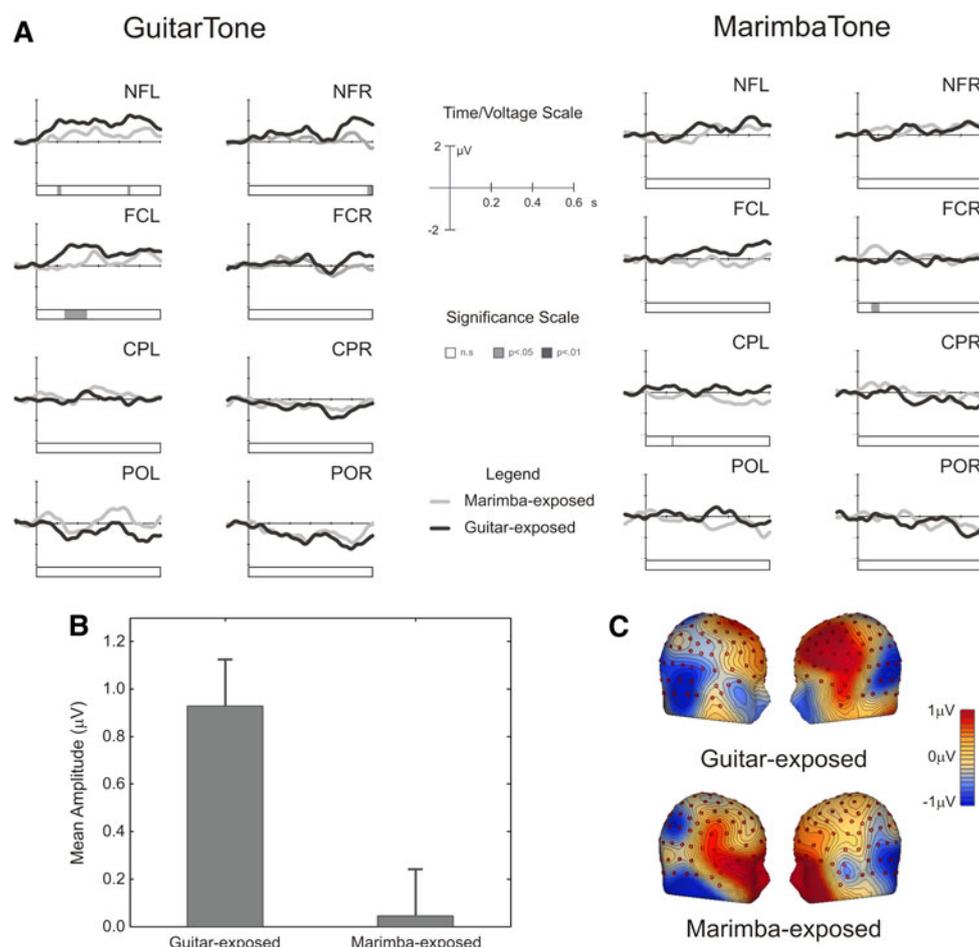


Fig. 4 **a** Mismatch responses: Grand averages of the mismatch responses, derived by subtraction of the deviant response from the standard response, to the guitar deviant tones (*left*) and marimba deviant tones (*right*) for the guitar-exposed (*dark gray*) and the marimba-exposed (*light gray*) groups. The voltage and time scale are the same for all waveforms. The significance scale below each electrode group indicates when a running *t*-test shows that the two groups differ significantly. The guitar-exposed group showed a significantly larger mismatch response in the FCL electrode group between about 130 and 240 ms. The mismatch response for marimba

deviants did not differ significantly from zero for either group at any time. **b** Analysis of 200–250 ms window: The mean amplitude of the mismatch response was calculated over the 200–250 ms window for each subject. *Error bars* represent SE. **c** Topographies of the mismatch responses: Topographies are shown for both groups at 200 ms for the guitar tone mismatch. The guitar-exposed group shows a topography consistent with activation of left auditory cortex. The response for the marimba-exposed group did not differ significantly from zero at this time

Discussion

After exposing 4-month-old infants to melodies in either guitar or marimba timbre, we compared cortical processing of those timbres by recording ERP responses to tones in both timbres at pitches that were not experienced during the exposure phase. We found that a frontally negative component between 350 and 550 ms after tone onset was sensitive to the timbre of training. Specifically, this component was larger in response to the guitar than marimba tones for infants exposed to the melodies in the guitar timbre, but larger in response to the marimba than guitar tones for infants exposed to the melodies in the marimba timbre. The topographies of the ERPs across the scalp were consistent with a generator in auditory cortex. Thus, we have demonstrated that a relatively short exposure of less than 3 h total to a particular timbre in the midst of the large variety of sounds that infants are exposed to every day, results in plastic changes in responses to timbre that generalize to pitches not previously heard in that timbre.

We also measured mismatch responses to a small change in the pitch of tones in guitar and in marimba timbres. Because mismatch amplitude increases with the difficulty of the pitch discrimination primarily near threshold, we tested a pitch change of 1/24th of an octave, or about 3%, which approaches behavioural thresholds for infants of this age (Werner 2007). For the pitch change with marimba tones, no significant mismatch response was measured in infants exposed to the melodies in either the guitar timbre or in the marimba timbre. Deviants in the guitar tone, however, evoked significant mismatch responses from infants exposed to the melodies in the guitar timbre that were significantly larger than the responses from infants exposed to the marimba timbre.

Mismatch responses to pitch changes in adults are considered to be an indication of pitch representations (Näätänen et al. 2007). These results suggest, then, that exposure in infancy to tones of a particular timbre sharpens pitch representations for tones in that timbre. It should also be noted that the mismatch response did not have the frontal-negative morphology of the adult MMN, although the negative mismatch response has been reported previously in infants 4 months of age in response to a change in pitch (He et al. 2009b). The persistence of the positive mismatch response and absence of the MMN in this study is likely due to the difficulty of the small pitch change. Indeed, positive mismatch responses and the absence of MMN to pitch changes have also been reported in infants as old as 6 months with a demanding melody stimulus (Tew et al. 2009).

There are several possible reasons why a significant mismatch was not seen in response to the pitch change for tones in the marimba timbre. One is that the guitar is much

more common than the marimba in Western culture in general and children's music in particular. Thus, infants may have begun the study with a better representation for the pitch of tones with guitar compared to marimba timbre, and the short exposure period might not have been enough for fine pitch discrimination to develop for tones in the marimba timbre. Differences in the harmonic structure between the two tones may also provide an explanation; as shown in Fig. 1, there is much less energy at higher harmonics in the marimba compared to the guitar timbre. It has been shown previously in adults that pitch representations are better for timbres with additional higher harmonics present (Shahin et al. 2005). Specifically, when the higher harmonics are filtered out of tones in piano timbre, P2 responses decrease in amplitude. Thus, fine pitch representations may be easier to achieve with tones in guitar compared to the marimba timbre. Behavioural data was not collected in this study, so it remains unknown as to whether 4-month-old infants are able to hear a 3% pitch change in the marimba timbre.

The two peaks present in the standard waveforms—a frontally positive component peaking around 165 ms and a frontally negative component peaking around 450 ms—showed bilaterally similar topographies consistent with generators in right and left auditory areas. The mismatch response to the pitch change produced a frontally positive component peaking around 200 ms with a topography also consistent with a generator in auditory areas. But unlike the components in the standard waveforms, the positive mismatch response was left lateralized. The negative mismatch response in adults (MMN) tends to be right lateralized (Näätänen et al. 2007; Picton et al. 2000). The present results in infants are consistent with previous reports that show a tendency for the immature positive mismatch response to be left lateralized (e.g., He et al. 2007). The generators of the positive mismatch response are not clear, but the present results add to previous work suggesting that they are distinct from those of the more mature negative MMN response.

One interesting aspect of the results is that the effects were measured in a different context at test (pitch discrimination for a single tone) than during exposure (melodies) and for a tone at a pitch that had not been present during the exposure phase. This implies that some kind of template for the guitar or marimba timbre had been extracted rather than that the exposure enhanced representations for particular instances of the guitar or marimba tone. Furthermore, the test context occurred at least a full 24 h after the infants' last exposure to the tones in the training context, implying some stability to the exposure-induced changes. It remains for future studies to determine how long such effects might last. A second interesting aspect is that the plastic changes occurred after passive

exposure to melodies in a particular timbre and did not require active training or attention. In studies with adult animals, active training with attention often results in better learning than passive exposure (Blake et al. 2006; Fritz et al. 2007). The infant brain, on the other hand, appears to wire itself according to the linguistic input (Curtin and Werker 2007; Kuhl 2008), musical pitch input (Hannon and Trainor 2007; Trainor and Trehub 1992), and musical rhythm input (Hannon and Trehub 2005) of its environment without explicit instruction or training. It is possible that when a neural network is in a relatively unorganized state, as in the young infant brain, passive exposure is more effective compared to later in development, after the network has become specialized for particular inputs such as a specific language or musical system.

In sum, the present results show that a relatively small amount of exposure to tones in a particular timbre results in plastic changes to the general representations of that timbre in infants as young as 4 months of age. It remains for future studies to explore the limits of this plasticity in terms of the amount of exposure necessary and the sound features to which the system is most sensitive.

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