Cortical Representations Sensitive to the Number of Perceived Auditory Objects Emerge between 2 and 4 Months of Age: Electrophysiological Evidence

Nicole A. Folland, Blake E. Butler, Jennifer E. Payne, and Laurel J. Trainor

Abstract

■ Sound waves emitted by two or more simultaneous sources reach the ear as one complex waveform. Auditory scene analysis involves parsing a complex waveform into separate perceptual representations of the sound sources [Bregman, A. S. *Auditory scene analysis: The perceptual organization of sounds*. London: MIT Press, 1990]. Harmonicity provides an important cue for auditory scene analysis. Normally, harmonics at integer multiples of a fundamental frequency are perceived as one sound with a pitch corresponding to the fundamental frequency. However, when one harmonic in such a complex, pitch-evoking sound is sufficiently mistuned, that harmonic emerges from the complex tone and is perceived as a separate auditory object. Previous work has shown that the percept of two objects is indexed in both children and adults by the object-related negativity component of the ERP derived from EEG recordings [Alain, C., Arnott, S. T., & Picton, T. W. Bottom–up and top–down influences on auditory scene analysis: Evidence from event-related brain potentials. *Journal of Experimental Psychology: Human Perception and Performance, 27,* 1072–1089, 2001]. Here we examine the emergence of object-related responses to an 8% harmonic mistuning in infants between 2 and 12 months of age. Two-month-old infants showed no significant object-related response. However, in 4- to 12-month-old infants, a significant frontally positive component was present, and by 8–12 months, a significant frontocentral object-related negativity was present, similar to that seen in older children and adults. This is in accordance with previous research demonstrating that infants younger than 4 months of age do not integrate harmonic information to perceive pitch when the fundamental is missing [He, C., Hotson, L., & Trainor, L. J. Maturation of cortical mismatch mismatch responses to occasional pitch change in early infancy: Effects of presentation rate and magnitude of change. *Neuropsychologia, 47,* 218–229, 2009]. The results indicate that the ability to use harmonic information to segregate simultaneous sounds emerges at the cortical level between 2 and 4 months of age. ■

INTRODUCTION

Many listening environments contain multiple sound-producing objects. These sound waves arrive at the cochlea as a single, complex waveform. The auditory system is tasked with separating this complex waveform into individual representations that correspond to the sound sources. This is referred to as auditory scene analysis (Bregman, 1990) and relies on complex spectrotemporal processing beginning with the pattern of action potentials in auditory nerve fibers (e.g., Ibrahim & Bruce, 2010) and involving processing in multiple brainstem nuclei as well as auditory cortex (e.g., Krishnan, Gandour, & Bidelman, 2012).

Pitch-evoking stimuli are typically comprised of energy at a fundamental frequency, and integer multiples of that frequency, called harmonics. Four-month-old infants integrate harmonics into a single pitch percept in a manner that is qualitatively adult-like (He & Trainor, 2009). Harmonic structure provides one cue for identifying components of a complex signal that should be grouped together into a single sound (i.e., those that fit a harmonic template). Indeed, when one harmonic of a pitch-evoking sound is mistuned, adult listeners report hearing the mistuned harmonic as a second object (Lin & Hartmann, 1998; Hartmann, 1996; Goldstein, 1978). Behaviorally, young adults detect mistunings of less than 1% in a single harmonic (Folland, Butler, Smith, & Trainor, 2012; Alain, Arnott, & Picton, 2001). However, children (aged 8–13 years; Alain, Theunissen, Chevalier, Batty, & Taylor, 2003) and the elderly (Alain & McDonald, 2007; Alain, McDonald, Ostroff, & Schneider, 2001) are less able to use mistuning to determine the number of sound sources, reporting fewer instances of hearing out a mistuned harmonic across all degrees of mistuning.

Although auditory scene analysis is essential for the development of auditory function, language acquisition, and musical processing, little research has addressed its development. Moreover, the majority of existing literature focuses on the segregation of sequentially presented stimuli (e.g., Sussman, Čeponienė, Shestakova, Näätänen, & Winkler, 2001; McAdams & Bertoncini, 1997; Demany,

McMaster University, Hamilton, Ontario, Canada

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1982), with less research addressing the important issue of segregating simultaneously presented sounds. Folland et al. (2012) demonstrated behaviorally that 6-month-old infants are able to discriminate 4% but not 2% mistunings in the third harmonic of a six-harmonic complex sound. However, it remains unclear whether infants perceive the mistuned harmonic as a separate auditory object in the way that adults do or whether their discrimination is based on other perceptual features (e.g., differences in timbre).

This study uses the object-related negativity (ORN) component of the ERP derived from EEG recordings to determine whether infants' behavioral discrimination of mistuned harmonics reflects the formation of separate auditory objects and seeks to determine at what age harmonicity is employed as a cue for auditory scene analysis. In adults, the ORN component is observed when two simultaneous objects are presented, but not when one auditory object is presented (Alain, Arnott, et al., 2001). If, like adults, infants perceive the mistuned harmonic to be a second auditory object, an ORN should be elicited in response to a mistuning exceeding their perceptual threshold. If, on the other hand, infants' discrimination of mistunings does not lead to object formation, no ORN response should be produced.

METHODS

Participants

Full-term infants between 2 and 12 months of age (n = 153) participated in the study. Five age groups, each consisting of 16 infants and one age group consisting of 32 infants formed the final sample (see Table 1 for details). An additional 41 infants were not included in the analyses (13 because they fell asleep, 10 because they had an insufficient number of artifact-free trials, and 18 because of fussiness). No parent reported that their infant had a history of frequent ear infections, pressure-equalizing tubes, or familial hearing impairment. All infants weighed more than 2500 g at birth and were born between 38 and 42 weeks gestation. All infants were screened at birth to ensure no sensorineural hearing loss according to the Ontario Infant Hearing Program (Hyde, 2005). Before testing, parents gave informed written consent and were asked to fill out a brief questionnaire outlining music and language experience. All experimental procedures were approved by the McMaster Research ethics board.

Table 1. Infant Age Groups

	No. of Infants	*Mean Age (SD)*	*Analysis Group*
2 months	n = 32	2.3 (±0.18)	A
4 months	n = 16	4.5 (±0.26)	B
6 months	n = 16	6.3 (±0.22)	B
8 months	n = 16	8.2 (±0.29)	C
10 months	n = 16	10.2 (±0.15)	C
12 months	n = 16	12.1 (±0.14)	C

Stimuli

Stimuli were synthesized using Adobe Audition (6.0), with a sample rate of 44,100 Hz and 16-bit resolution. The in-tune complex tone had a pitch of 240 Hz and contained the first six harmonics (240, 480, 720, 960, 1200, and 1440 Hz) added in random phase with a 6-dB/octave roll off. The mistuned complex was identical to the in-tune complex except that the third harmonic was mistuned upward by 8% (777.6 Hz as opposed to 720 Hz). Both stimuli were 500 msec in duration, including 50 msec rise and fall times.

In adults, several factors affect the ease of segregation, including the frequency of the complex tone, which harmonic is mistuned, the sound duration, and the degree of inharmonicity. Because no previous study has elicited an ORN in response to a mistuned harmonic in infants, we chose stimulus parameters that gave rise to a clear, salient perception of two auditory objects in adults (Lin & Hartmann, 1998; Hartmann, McAdams, & Smith, 1990; Moore, Glasberg, & Peters, 1986) and which 6-month-old infants have been shown to clearly discriminate behaviorally (Folland et al., 2012).

Procedure

The infant was seated on their parent's lap in a sound attenuating room. Stimuli were presented at 70 dB(A) with a background noise level of 30 dB(A) through a WestSun loudspeaker (WestSun Jason Sound, JSIP63, Mississauga, ON, Canada) located 1 m in front of the infant. Stimuli were presented using E-Prime 1.1 software (Psychology Software Tools, Sharpsburg, PA) from a Dell OptiPlex280 computer with an Audigy 2 platinum sound card (Creative Labs, Singapore). Infants were tested in a passive listening condition in which they watched a silent movie (Baby Einstein) and were entertained by the experimenter using silent toys and puppets to minimize movement. Each infant heard a total of 500 trials (250 in-tune complex tones and 250 mistuned complex tones) lasting 13 min, presented in quasirandom order, with the constraint that no more than eight of the same tone were played in a row. The ISI was randomized between 800 and 1000 msec.

Recording and Analysis

All infants were fitted with a 124-electrode Geodesic Sensor Net (Electrical Geodesics, Inc., Eugene, OR), and electrode impedances were maintained below 50 kΩ.

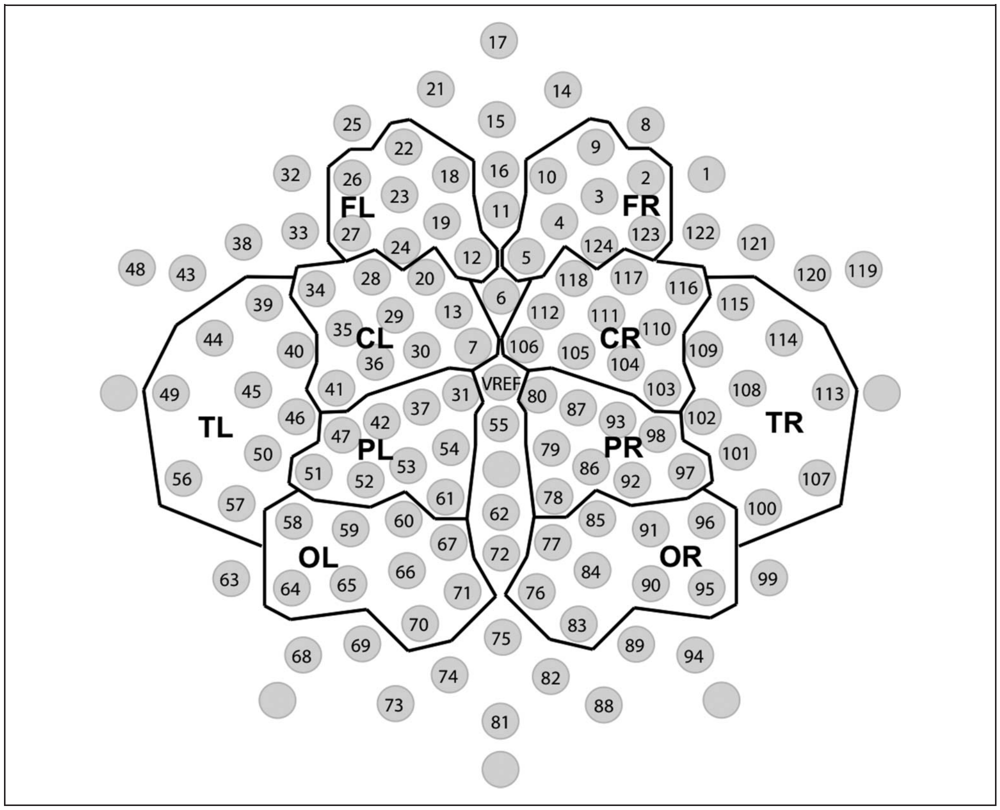

Figure 1. Electrode groupings (see Methods for details). Ninety of 124 electrodes were divided into five regions (frontal, central, parietal, occipital, and temporal) for each hemisphere. Each region contained between 16 and 20 electrodes that were averaged to represent EEG responses from that scalp region. The remaining channels around the perimeter of the net were excluded from analysis to avoid artifacts resulting from muscle activity in the face and neck, and channels along the midline were removed to allow for comparison between hemispheres.

EEG data were recorded continuously using NetStation (Eugene, OR), 4.3.1 software. Electrodes were referenced to the vertex (Cz), and a 0.1–400 Hz hardware filter was used during recording. The data were filtered offline between 0.5 and 20 Hz and were resampled at 200 Hz. Artifacts such as those arising from head movements, eye blinks, and ocular movement were blocked using a procedure described previously (Fujioka, Mourad, He, & Trainor, 2011; Mourad, Reilly, de Bruin, Hasey, & MacCrimmon, 2007). Data were then segmented into 700-msec epochs including a 100-msec prestimulus baseline. Responses to the in-tune and mistuned complexes were averaged separately and re-referenced using an average reference. Finally, difference waves for each infant were created by subtracting the response to the in-tune complex tone from the response to the mistuned complex tone. Grand averages of the in-tune, mistuned, and difference waveforms were created by averaging across all of the infants in each age group. For statistical analysis, 90 electrodes were selected and divided into five regions for each hemisphere, representing frontal, central, parietal, occipital, and temporal scalp regions (see Figure 1). Within each region, the waveforms were averaged across electrodes. Peripheral electrodes were excluded to reduce the impact of muscle artifacts from the eyes, face, and neck. Midline electrodes were excluded to allow for comparisons between hemispheres. If the mistuning of the third harmonic evoked an object-related response, a significant difference would be expected between the mistuned (two objects) and in-tune (one object) waveforms.

RESULTS

The morphology of the ERP waveforms changed dramatically between 2 and 12 months of age. To reflect this, infants were divided into three groups: 2-month-olds, 4- to 6-month-olds, and 8- to 12-month-olds. This produced groups with similar waveform morphology across participants (Figures 2–4).

In-tune (one auditory object), mistuned (two auditory objects), and difference waveforms for 2-month-old infants are shown in Figure 2. In-tune and mistuned waveforms are dominated by a frontally positive slow wave, which reverses at posterior sites, consistent with a source in auditory cortex. To assess whether in-tune and mistuned responses were significantly different in the absence of a clear peak, the waveform for each 2-month-old was divided into 100-msec segments, and the mean amplitude across each segment was measured. One-sample t tests on the mean amplitude in each electrode region revealed that the response did not differ significantly between in-tune and out-of-tune responses for any 100-msec segment. After correcting for multiple comparisons, all p values were $>.05$.

For the older two age groups, two components were seen in the difference waves, one a frontally negative component peaking around 230 msec and the other a frontally positive component peaking around 350 msec, both accompanied by reversals at occipital sites (Figures 3 and 4). The first of these corresponds to the ORN component seen in adults in response to the presence of two auditory objects. The second likely reflects an immature response to the presence of two objects, as discussed below. The amplitude of each component was measured for each infant by taking the average amplitude across a 50-msec time window centered at the time of each peak in that age group's grand-averaged difference waveform. Separate one-sample t tests were performed for each component in each age group to determine whether the mean amplitude was significantly different from baseline in any electrode region. These components invert in polarity between frontal and occipital electrode sites, resulting in near zero recordings at parietal electrodes. Thus, the parietal electrode region was not included in statistical analyses.

The early negativity did not approach significance in any electrode region in the 4- to 6-month-old infants (all ps > .5), but the late positive component was significant in the left frontal ($t[31] = 5.77$, $p < .001$), right frontal ($t[31] = 3.30$, $p = .008$), and left central ($t[31] = 3.59$, $p = .004$) electrode regions, after correcting for multiple comparisons.

The 8- to 12-month-old group showed a larger early negative deflection than the 4- to 6-month-old group, particularly in the frontal and central regions of the right hemisphere (Figure 4). The average amplitude in the right frontal area failed to reach significance after adjusting for multiple comparisons (adjusted $p = .19$), but there was a trend for significance at the right central region ($t[47] = 2.49$, adjusted $p = .06$). The late positive component reached significance at the frontal (right: $t[47] = 5.49$, adjusted $p < .001$; left: $t[47] = 5.94$, adjusted $p < .001$), central (right: $t[47] = 3.59$, adjusted $p < .001$; left: $t[47] = 5.83$, adjusted $p < .001$), and occipital (right: $t[47] = 4.41$,

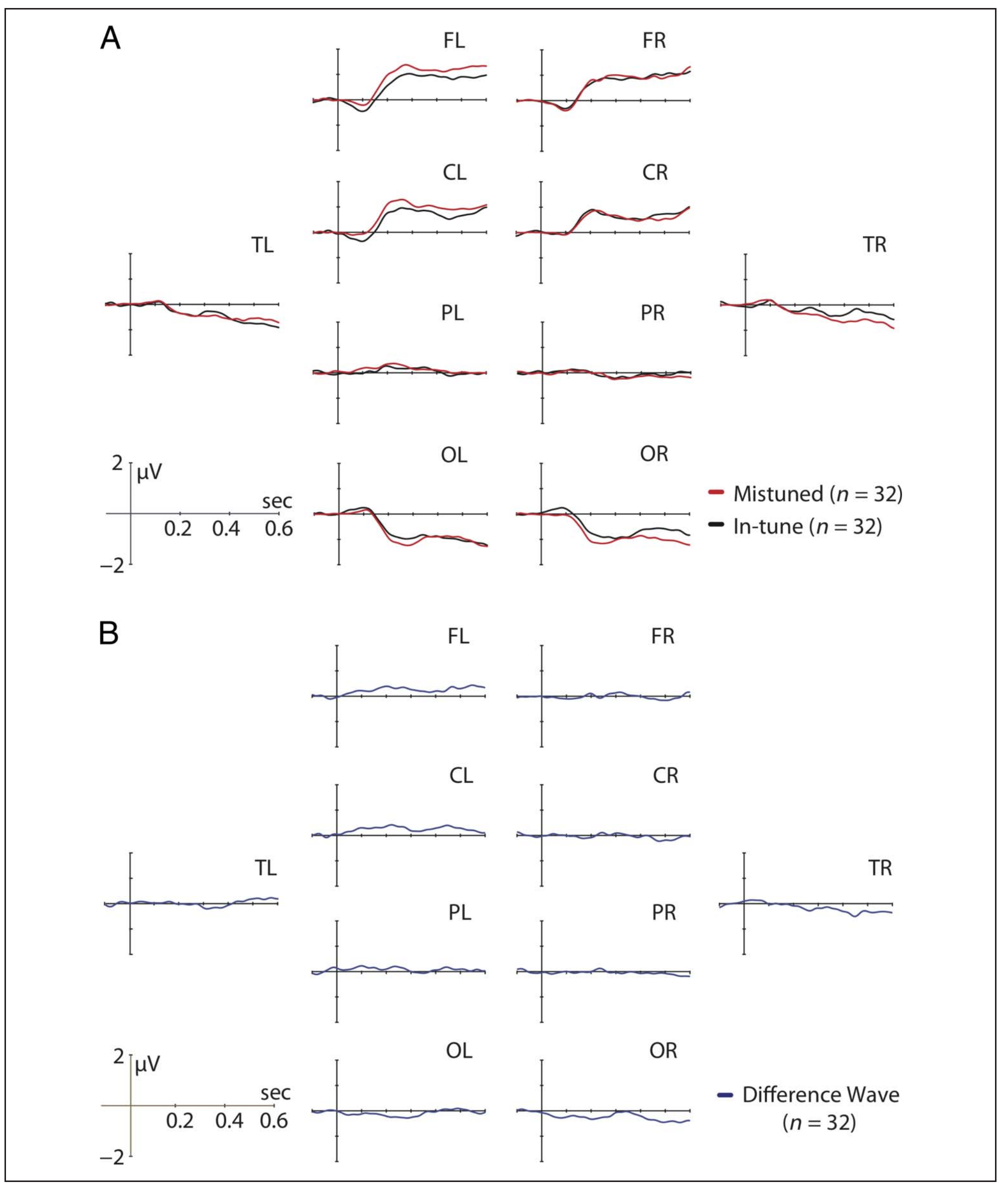

Figure 2. Two-month-olds: A shows the grand-averaged responses of 2-month-old infants to the in-tune (black) and mistuned (red) tones. B shows the grand-averaged difference waveforms (mistuned − in-tune). In each case, responses from each of the 10 electrode regions are presented.

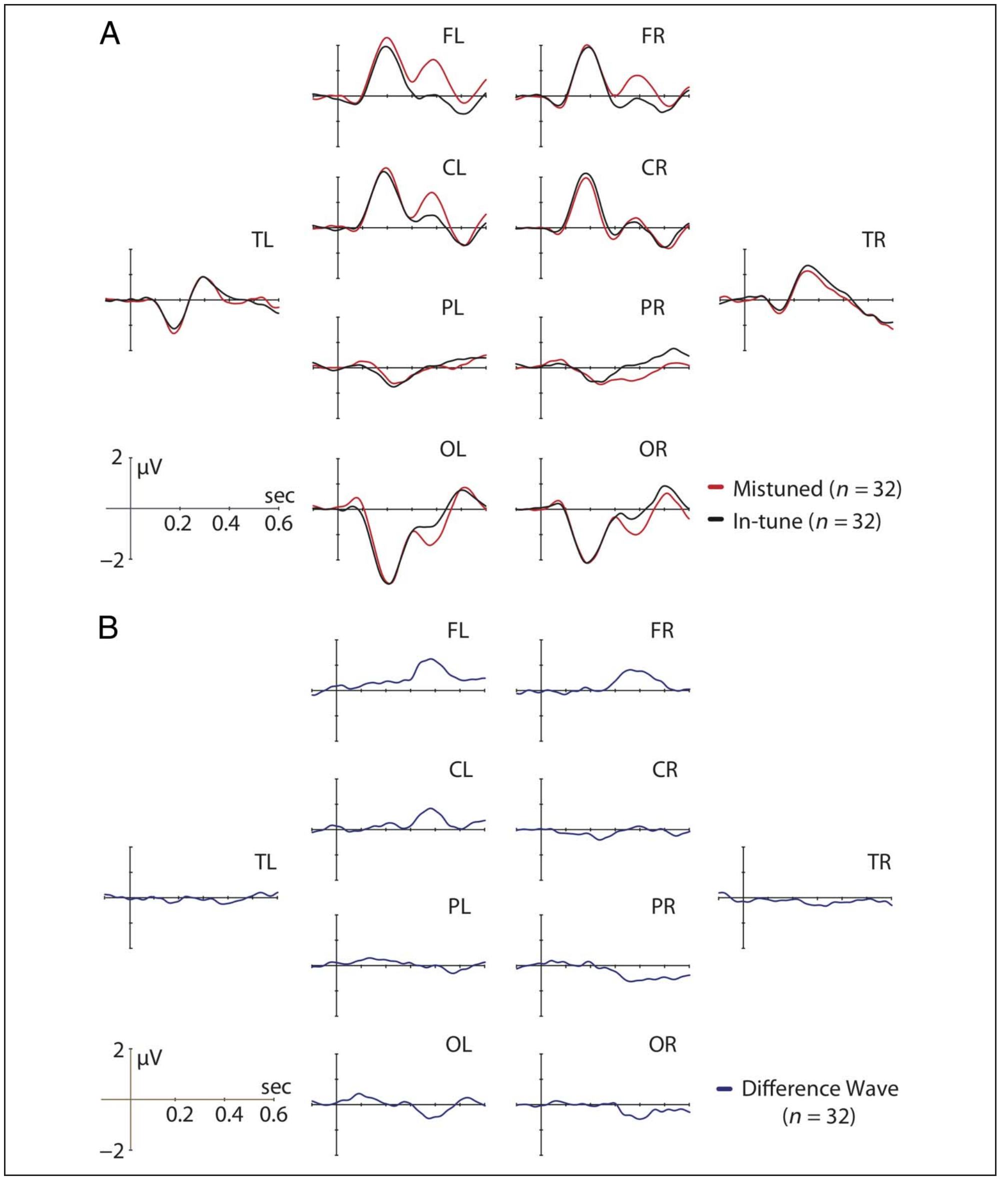

Figure 3. Four- to 6-month-olds: A shows the grand-averaged responses of 4- to 6-month-old infants to the in-tune (black) and mistuned (red) tones. B shows the grand-averaged difference waveforms (mistuned − in-tune). In each case, responses from each of the 10 electrode regions are presented.

adjusted $p < .001$; left: $t[47] = 4.87$, adjusted $p < .001$) electrode regions bilaterally and in the right temporal region ($t[47] = 3.42$, adjusted $p < .001$).

Repeated-measures ANOVAs were run separately for the early negative and late positive waveform deflections with Electrode region (frontal, central, occipital, temporal) and Hemisphere as within-subject factors and Age group (4–6 months, 8–12 months) as a between-subject factor. The polarities of recordings from temporal and occipital electrode regions were inverted before statistical analysis so that region effects would reflect differences in waveform amplitude rather than differences arising from the inversion of polarity common to responses from auditory cortex.

The early negative deflection showed a significant Region × Age group interaction ($F[3, 234] = 4.69, p = .003$). Post hoc independent sample t tests on each region revealed that the amplitude of the early negativity was greater in 8- to 12-month-olds than 4- to 6-month-olds at frontal ($t[78] = 2.41, p = .02$) and occipital ($t[78] = 2.47, p = .02$) electrode regions. No other significant effects were observed for this deflection.

The late positive deflection showed no main effect of Group. However, there was a significant effect of Electrode region ($F[3, 234] = 34.67, p \leq .001$) with the amplitude in frontal regions exceeding the amplitude in the central regions ($t[79] = 4.00, p < .001$), whereas the frontal, central, and occipital regions each exceeded the amplitude in temporal regions (all ps $< .001$). Additionally, response amplitudes in the left hemisphere exceeded those recorded in the right hemisphere ($F[1, 78] = 5.11, p = .03$).

DISCUSSION

This study infers a cortical representation of concurrent auditory stream segregation in infant listeners. Using an experimental paradigm designed to elicit an ORN component in response to the perception of two simultaneous auditory objects, we demonstrated that, by 4 months of age, infants, like adults, are able to detect a mistuned harmonic within a complex tone based on its emergence as a separate auditory object. The ORN is thought to reflect a bottom–up process that is largely preconscious, with the segregation of frequency components that do not fit the harmonic structure of a complex sound occurring preattentively (Synder, Alain, & Picton, 2006; Alain & Izenberg, 2003; Alain, Arnott, et al., 2001). Finding an object-related response in young infants is consistent with the idea that perceptual organization occurs preattentively.

Two-month-old infants showed no object-related response to the mistuned harmonic stimulus. It is possible that a larger mistuning might elicit a response from these listeners or that their neural generators are oriented in such a way that we cannot see their activity. However, this is unlikely, as previous studies have shown that infants are easily able to perceive changes in frequency of this magnitude both with behavioral (e.g., Olsho, Schoon, Sakai, Turpin, & Sperduto, 1982) and EEG (e.g., He, Hotson, & Trainor, 2009) methods. The failure of 2-month-olds to perceive two auditory objects on the basis of harmonic cues at the cortical level is particularly interesting in that a previous study examining infants' responses to the pitch of the missing fundamental concluded that infants are first able integrate harmonic information into a single pitch percept at 4 months of age (He & Trainor, 2009). Thus, integrating harmonics into a single object with pitch and using mistuning to separate harmonics into different objects appear to emerge at the same time in development.

The object-related responses recorded from 4- to 6-month-old infants were dominated by a late, frontally positive deflection. The object-related responses recorded

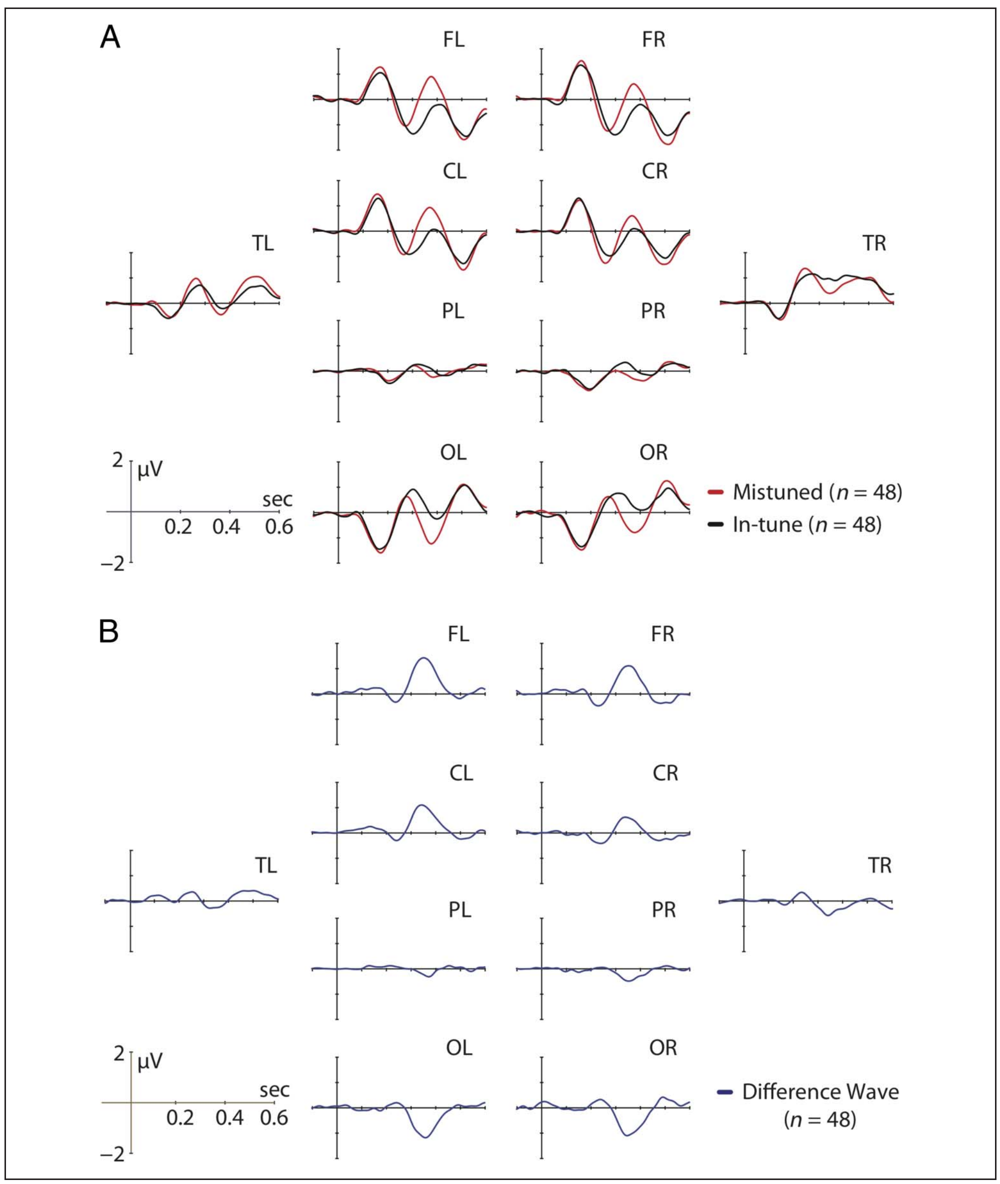

Figure 4. Eight- to 12-month-olds: A shows the grand-averaged responses of 8- to 12-month-old infants to the in-tune (black) and mistuned (red) tones. B shows the grand-averaged difference waveforms (mistuned − in-tune). In each case, responses from each of the 10 electrode regions are presented.

from 8- to 12-month-old infants also contained this positive component but contained a shorter latency frontally negative deflection as well, resembling the ORN recorded in older children and adults. This age-dependent pattern of frontally positive responses in younger infants and the later emergence of shorter latency, adult-like frontally negative responses has been demonstrated previously for other neural components, including the MMN response (e.g., He et al., 2009; Tew, Fujioka, He, & Trainor, 2009; He, Hotson, & Trainor, 2007). This pattern of responses across age is likely related to maturational changes affecting synaptic connections occurring at this time (Trainor, 2008, 2012).

To maximize the number of artifact-free infant trials, we chose to use one in-tune stimulus and one mistuned stimulus. Consequently, we cannot say with certainty whether the object-related infant response seen here reflects the detection of mistuning independent of concurrent sound perception. Although this study is an important first step toward understanding simultaneous sound perception in infancy, we encourage future studies to manipulate stimulus properties previously shown to affect thresholds for detecting mistuning in adults, such as sound duration and the degree of mistuning (Alain, McDonald, et al., 2001).

It should also be noted that because the in-tune and mistuned stimuli were presented with equal probability in this study, neither an MMN component nor any responses related to activation of nonrefractory neurons would have been elicited. The frontally negative object-related response in the 8- to 12-month-old infants resembled the ORN recorded previously in older children and adults (Alain et al., 2003) although it was at a longer latency in the infants (peak latency of 270 msec) than in 8.5- to 12.5-year-old children (160 msec; Alain et al., 2003). This latency difference is likely because of maturational factors, although it is possible that the fact that our stimuli had longer rise times (50 msec) than those used by Alain and colleagues (10 msec) may have contributed to the latency difference (Alain et al., 2003; Alain, Arnott, et al., 2001). Previous research has demonstrated that, although the mechanisms involved in complex pitch perception first appear functional around 4 months of age (He & Trainor, 2009), even simple frequency discrimination does not reach adult levels until 10 years (Thompson, Cranford, & Hoyer, 1999; Jensen & Neff, 1993). Thus, it is likely that, as the perception of pitch improves, so too does the ability to separate auditory objects based on how well they fit harmonic structures and that this improvement is indexed by a decrease in the latency of the ORN component.

This study indicates that the ability to separate simultaneous sound sources on the basis of harmonic cues emerges between 2 and 4 months of age, the same time frame during which cortical responses emerge that reflect integration of harmonics into a pitch percept. These abilities relate to auditory scene analysis and likely contribute to linguistic, musical, and social development during this time period.

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Reprint requests should be sent to Laurel J. Trainor, Department of Psychology, Neuroscience and Behaviour, McMaster University, Hamilton, ON L8S 4B2, Canada, or via e-mail: LJT@mcmaster.ca.

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