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Oscillatory Dynamics Underlying Perceptual Narrowing of Native Phoneme Mapping from 6 to 12 Months of Age

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During the first months of life, human infants process phonemic elements from all languages similarly. However, by 12 months of age, as language-specific phonemic maps are established, infants respond preferentially to their native language. This process, known as perceptual narrowing, supports neural representation and thus efficient processing of the distinctive phonemes within the sound environment. Although oscillatory mechanisms underlying processing of native and non-native phonemic contrasts were recently delineated in 6-month-old infants, the maturational trajectory of these mechanisms remained unclear. A group of typically developing infants born into monolingual English families, were followed from 6 to 12 months and presented with English and Spanish syllable contrasts varying in voice-onset time. Brain responses were recorded with high-density electroencephalogram, and sources of event-related potential generators identified at right and left auditory cortices at 6 and 12 months and also at frontal cortex at 6 months. Time-frequency analyses conducted at source level found variations in both θ and γ ranges across age. Compared with 6-month-olds, 12-month-olds' responses to native phonemes showed smaller and faster phase synchronization and less spectral power in the θ range, and increases in left phase synchrony as well as induced high- γ activity in both frontal and left auditory sources. These results demonstrate that infants become more automatized and efficient in processing their native language as they approach 12 months of age via the interplay between θ and γ oscillations. We suggest that, while θ oscillations support syllable processing, γ oscillations underlie phonemic perceptual narrowing, progressively favoring mapping of native over non-native language across the first year of life.

Key words: infant; oscillations; perceptual narrowing; phonemic mapping; source localization; time-frequency analyses

Significance Statement

During early language acquisition, typically developing infants gradually construct phonemic maps of their native language in auditory cortex. It is well known that, by 12 months of age, human infants move from universal discrimination of most linguistic phonemic contrasts to phonemic expertise in their native language. This perceptual narrowing occurs at the expense of the ability to process non-native phonemes. However, the neural mechanisms underlying this process are still poorly understood. Here we demonstrate that perceptual narrowing is, at least in part, accomplished by decreasing power and phase coherence in the θ range while increasing activity in high- γ in left auditory cortex. Understanding the normative neural mechanisms that support early language acquisition is crucial to understanding and perhaps ameliorating developmental language disorders.

Introduction

To acquire language, typically, developing infants construct phonemic representations of the specific sounds of their native lan-

guage across auditory cortex. In the first months of life, human infants readily discriminate most phonemic contrasts across languages via detailed acoustic analysis. By the end of their first year, however, infants gradually narrow their perceptual abilities to become expert processors of native phonemic contrasts; that is, they evolve into automatized “linguistic” processors (Shafer et al., 2011; Strange, 2011), although they decline in their ability to discriminate non-native phonemic information (Werker and Tees, 2005; Gervain and Mehler, 2010; Kuhl, 2010). Phonemic perceptual narrowing, a developmental process that establishes preference for characteristic features of the infant's native language (Pons et al., 2009; Werker et al., 2012; Maurer and Werker, 2014; Gervain, 2015), occurs in a well-defined hierarchical progression. Initially, infants favor processing of suprasegmental

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prosodic features of their native language (Mehler et al., 1988; Hayashi et al., 2001; Jusczyk, 2002; Friederici et al., 2007), followed by preference for the characteristic information comprised in native vowels (Khul et al., 1992; Cheour et al., 1998; Shafer et al., 2011; Moon et al., 2013; Tsuji and Cristia, 2014); and finally, the focus is on the segmental sublexical elements contained in native consonants (Best et al., 1995; Rivera-Gaxiola et al., 2005; Tsao et al., 2006; Ortiz-Mantilla et al., 2013). Significant delays in the time course of phonemic narrowing (maintaining the ability to process non-native phonemes without establishing a clear native language preference) could negatively impact efficient language acquisition (Kuhl et al., 2005; Jansson-Verkasalo et al., 2010).

Phoneme recognition requires precise sensitivity to the specific spectrotemporal acoustic features that characterize each phoneme. One such feature is voice-onset time (VOT: time interval between the onset of the release burst and the onset of the voicing), which allows discrimination between stop consonants that share the same place of articulation (Lisker and Abramson, 1964). Human and animal studies have revealed evidence of cortical encoding of phonemic acoustic features in primary auditory cortex as neurons respond to the distinctive acoustic features that identify a given phoneme (Steinschneider et al., 2005; Mesgarani et al., 2008; Edwards et al., 2009; Leonard and Chang, 2014). The posterior superior temporal lobe has been proposed as the primary substrate where sound representation of speech is constructed (Hickok and Poeppel, 2000; DeWitt and Rauschecker, 2012) and may play a role in the early categorical phonetic analysis of speech stimuli (Blumstein et al., 2005; Chang et al., 2010). Recently, based on electrocorticographic (ECoG) recordings in epilepsy patients, the superior temporal gyrus (STG) (Mesgarani et al., 2014) and particularly, STG posterolateral region (PL-STG) (Steinschneider et al., 2011), were identified as the critical area responsible for the temporal representation of the acoustic features associated with VOT. Increases in event-related high- γ power (75–150 Hz), the only frequency range examined, were seen in left and right PL-STG when consonant-vowel syllables varying in VOT were passively presented.

In a previous study, we found selective enhancement of induced low- γ oscillations in frontal cortex during discrimination of a native phonemic VOT contrast, suggesting that, at 6 months, the infant brain is already processing native phonemes differently from non-native ones (Ortiz-Mantilla et al., 2013). However, it is still not known whether, by the end of the first year of life when phonemic maps are thought to be firmly established, infants, like adults, show an increase in high- γ power in auditory cortex, thus signaling neural representation of phonemic mapping and native language specialization at the phonemic level. As noted, it has been suggested that an increase in high- γ power in PL-STG indicates acoustic mapping of VOT features. Consequently, we might expect that both native and non-native syllables would elicit a high- γ oscillatory response. On the other hand, if enhancement of high- γ power in PL-STG is a marker for “language-specific” phonemic mapping, we might anticipate that, by 12 months of age, high- γ activity would be exclusively elicited by native syllables.

Materials and Methods

Participants. The present study includes a subset of 36 typically developing infants, born to monolingual English families that participated in a large developmental study. From this group, 29 (9 females) infants participated at 6 months of age, and 28 (10 females) at 12 months of age.

Data from the 6 month infants were previously reported (Ortiz-Mantilla et al., 2013), and the present study reports on the prospective, longitudinal follow-up of these infants at 12 months of age. Twenty-one infants (7 females) have good data at both age points. All infants had uneventful prenatal and perinatal circumstances and were born healthy, full-term (mean gestational age: 39.84 weeks, SD: 1.36 weeks), and at normal birth weight (mean: 3554.6 g, SD: 409.4 g) into middle to upper-middle socioeconomic class families (Hollingshead, 1975). Infants were recruited from urban and suburban communities in New Jersey and had no family history of specific language impairment, autism, hearing loss, no repeated episodes of otitis media, or other medical or neurological disorders. Parents received compensation for their time, and infants were given a toy after the visit. The study was conducted in accordance with the Declaration of Helsinki, and informed consent approved by our university’s Human Subjects Institutional Review Board was obtained before inclusion in the study.

Procedure: event-related potentials (ERPs). Stimuli: Three consonant-vowel (CV) syllables varying in VOT were used in this study. The standard stimulus (STD) was a CV syllable phonetically relevant in both English and Spanish, unaspirated voiceless /ta/ (VOT: 12 ms) heard as “da” by native English speakers and heard as “ta” by native Spanish speakers. The native deviant (ND) syllable was voiceless aspirated/ta/ (VOT: 46 ms) heard as “ta” by English speakers and the non-native deviant (NND) syllable was voicing-lead Spanish /da/ (VOT: –24 ms) heard as “da” by both Spanish and English speakers (the Spanish contrast /da/-/ta/ represent a single phonemic category in the English language and both syllables are perceived by English speakers as English /da/). Each CV syllable was 230-ms-long and had a fundamental frequency of 180 Hz. The stimuli were presented in a passive oddball paradigm that contained 800 STD syllables, 100 ND syllables, and 100 NND syllables for a total of 1000 stimuli. The stimulus onset-to-onset interval was 930 ms (for a more detailed description of these stimuli and the paradigm used, see Rivera-Gaxiola et al., 2005, 2007, 2012; Ortiz-Mantilla et al., 2012, 2013). Auditory stimuli were matched for intensity and presented binaurally in a sound-attenuated free field environment at 69 dB SPL.

EEG recording and data processing. EEG/ERP recordings were acquired while participants were seated in their parent’s lap, watching a silent movie or entertained with silent toys (for a more detailed description of the methods used, see Musacchia et al., 2015). EEG was recorded using a 62 Ag/AgCl channel EGI sensor net (Electrical Geodesics) with the vertex electrode (Cz) used as the online reference, a sampling rate of 250 Hz, and high/low pass filters between 0.1 and 100 Hz. Eye blinks were removed from the raw data using Brain Electrical Source Analysis (BESA) software’s automatic correction algorithm (principal component analysis method). ERPs were processed off-line with BESA software using a bandpass filter of 1–15 Hz and rereferenced to an average reference. For EEG segmentation, 300 ms prestimulus and 930 ms poststimulus time was used, and 100 ms before stimulus onset was defined as baseline. After segmentation, three types of epochs were available according to stimulus type (STD, ND, NND); epochs with signals exceeding $\pm 300 \mu\text{V}$ from the baseline were excluded. To be included in ERP averaging, a minimum of 70% artifact-free epochs was required for each stimulus (6 months: average for STD: 78 trials [71–90], for ND: 80 trials [72–89], for NND: 79 trials [71–90]; 12 months: average for STD: 78 trials [72–86], for ND: 80 trials [74–89], for NND: 79 trials [71–86]). To ensure similar signal-to-noise ratio between responses to standard and deviant contrasts, only the standard epochs that preceded the ND were included in the averaged standard response.

MRI. Structural T-1weighted 3D SPGR images were acquired on a GE 1.5 T Echospeed scanner for a subset of nonsedated, naturally sleeping infants (for a detailed explanation of the scanning procedures, see Raschle et al., 2012). MRI brain templates for 6 and 12 months were created by affine transform of 19 (6 months) and 9 (12 months) MRI images into the MRI space of an infant with the median age of the sample and combined into an average image. The original individual and average (template) MRIs were processed with Brain Voyager QX software and imported into BESA Research 5.3 for source localization of the ERP generators. Age-appropriate parameters were calculated for thickness (6 months: skull: 1.5 mm; scalp: 2.5 mm; subarachnoid space: 1.7 mm; 12

months: skull: 2.0 mm; scalp: 2.5 mm; subarachnoid space: 1.5 mm) and skull conductivity (6 months: 0.0581; 12 months: 0.0527) of the infant structures to be used during source localization (for a detailed description of the technique used, see Hämäläinen et al., 2011; Ortiz-Mantilla et al., 2012).

Source localization of ERP generators. To gain a deeper understanding of the neural dynamics that support ERPs obtained using traditional EEG analyses, source localization techniques were applied to identify the neural generators of the ERP responses. Scalp surface EEG recordings are not informative as to where in the brain responses are generated, as each electrode location captures overlapping information and thus does not represent activity from neural tissue below any specific electrode (Ponton et al., 2002; Hoehstetter et al., 2004; Michel et al., 2004; Cosandier-Rimélé et al., 2008). A dipole model based on activity recorded using a dense array of sensors (Michel et al., 2004) gives a more robust representation by providing maximal separation of the sources of activation from different brain regions that normally overlap at the scalp surface. Thus, modeling generators of the ERP responses allows identification of areas of activation (Hari and Salmelin, 1997) and, further, may reveal hidden sources of activation not always obvious with surface sensors (David et al., 2011). Generators of the ERP responses were investigated by mapping ERP data onto the individual or average MRI using BESA and Brain Voyager QX software programs (Scherg et al., 2010a). The standard electrode positions were fitted onto their corresponding MRI for 16 infants at 6 months and 12 infants at 12 months. Infants, for whom individual MRIs were not available, had the electrode positions fitted onto the age-appropriate MRI template. Peaks for responses to STD, ND, and NND were identified from the grand average and from the individual ERP waveforms at each age. Before conducting dipole modeling, ERP peak amplitudes were confirmed to be significantly different from zero baseline using one-sample *t* tests ($p < 0.001$). Then, equivalent current dipole sources were fitted (Scherg and Von Cramon, 1985) using a 4-shell ellipsoidal head model, and a confirmatory distributed source model calculated using Classic LORETA Recursively Applied (CLARA) method (Hoehstetter et al., 2010); a time window of ± 20 ms around the selected peak was used for dipole fitting, which allowed the best signal-to-noise ratio. Peaks for each condition and source at each age were identified, and amplitude, latency, and source coordinates submitted to statistical analyses (for further description of the method, see Ortiz-Mantilla et al., 2012).

Time-frequency analyses. Spectrotemporal changes during perception of native and non-native stimuli were examined in source space. The raw 62-channel recording was processed as follows: a fixed spatial filter (source montage) from each individual's source model (created from the averaged ERP data) was applied to the corresponding raw data, thus transforming the ongoing EEG into a 3-channel source space. This montage separates activity from different brain regions (i.e., left auditory cortex [LAC], right auditory cortex [RAC], and frontal cortex at the level of the anterior cingulate cortex [ACC]). Next, using complex demodulation, each single trial was transformed into the time-frequency domain (for detailed information of this methodology, see Scherg et al., 2010b). To compare the 6 month with the 12 month data, parameters for time-frequency analysis were kept similar to those previously reported for the 6 month data (Ortiz-Mantilla et al., 2013) with two minor changes: (1) The noise level in infant ERPs is often higher than that typically observed in adult ERP recordings, thus introducing more error variance into source localization results. More noise was evident for the 12 month data compared with the 6 month, as older infants tend to be more active than at 6 months. To preserve as much of the frequency information as possible while at the same time controlling for low-frequency activity, a low cutoff of 0.5 Hz (90.5% of the data) and of 1 Hz (9.5% of the data) was applied to the raw EEG (Scherg et al., 2010b) at both ages. The 0.5 Hz high-pass filter was used for most children, but this was adjusted to 1 Hz in cases where prominent slow-wave activity was present. (2) As infants grow older, a developmental shift is seen toward greater power in higher frequencies and less power in lower frequencies (Koroleva et al., 2002; Marshall et al., 2002; Orekhova et al., 2006; Cragg et al., 2011). To examine an extended frequency range of the γ band, a higher frequency range of 2–90 Hz was used at both ages, instead of the 2–50 Hz previously used

(Ortiz-Mantilla et al., 2013). A complex demodulation method with 1-Hz-wide frequency bins and 50 ms time resolution, from -300 to 930 ms in the frequency range of 2–90 Hz was then used for decomposing the 6 and 12 month single-trial EEG data into time-frequency representations. Temporal spectral evolution (TSE) was used to examine event-related changes in amplitude (power) of the different frequency bands relative to the baseline (Tallon-Baudry et al., 1996; Hari et al., 1997; Tallon-Baudry and Bertrand, 1999). The TSE value is comprised of induced (random-phase/non-phase-locked) and evoked (phase-locked) changes in amplitude of oscillatory activity related to stimulus presentation. The intertrial phase locking (ITPL) value measures how consistently the phase at different frequency bands locks to stimulation presented across trials; a value of 0 indicates random phase across trials, and a value of 1 corresponds to perfect intertrial phase alignment (Tallon-Baudry et al., 1996; Tallon-Baudry and Bertrand, 1999). TSE and ITPL measurements were obtained at the three sources previously identified (i.e., LAC and RAC and frontal at the level of ACC), for each of the three stimuli (STD, ND, NND) that were presented at each age to the infants. The TSE and ITPL measures of each individual generated for each source and stimulus at each age were exported to MATLAB R2012a (The MathWorks) for plotting graphics across subjects.

Statistical analyses. The statistical analyses were conducted using BESA Statistics 1.0 (BESA) for permutation testing and cluster analysis and SPSS Statistics 21 (SPSS) for the repeated-measures ANOVA. The source strength and latency were examined separately using source \times stimulus \times age repeated-measures ANOVAs. Source coordinates (*x*: medial–lateral; *y*: anterior–posterior; and *z*: superior–inferior) were examined separately for each direction also using repeated-measures ANOVAs. For time-frequency analysis, statistics were conducted in two steps (Kriegeskorte et al., 2009): First, we detected time-frequency regions with significant changes in the magnitude of amplitude (TSE) and phase coherence (ITPL) using BESA Statistics 1.0 software. BESA Statistics uses a parameter-free permutation testing on the basis of Student's *t* test (Maris and Oostenveld, 2007). In this study, there were no “predefined” clusters as BESA Statistics 1.0 automatically identifies clusters in time and frequency that are significantly different between 2 conditions/stimuli. Results are considered corrected for multiple comparisons as only those clusters will be identified that have higher cluster values than 95% of all clusters derived by random permutation of data (a more detailed description of the methods can be found in BESA Statistics website: <http://www.besa.de/products/besa-statistics/brochures/>). The mean of each cluster was calculated, and then, the same cluster parameters were used to obtain information about the third condition. In this way, we were able to identify at each age, “data clusters of significance” in the time-frequency domain. Second, repeated-measures ANOVAs (Source \times Stimulus \times Age), using the mean of each significant cluster, were conducted to examine age \times stimulus interactions in the sources. *Post hoc* tests were conducted when indicated to elucidate significant main effects. Greenhouse-Geisser correction was applied if the sphericity assumption was not met.

Results

Source analyses

At 6 and 12 months, ERP responses to STD, ND, and NND stimuli were characterized by a frontocentral-positive deflection ~ 200 ms followed by a negative deflection at ~ 400 ms (Fig. 1) similar to those described in other studies using the same paradigm (e.g., Rivera-Gaxiola et al., 2005, 2007). To examine perceptual processing of the different phonemes, sources of the first positive ERP response for each stimulus at each age were identified. At 6 months, we found that a 3-dipole model explained $\sim 96\%$ of the variance (residual variance in the grand average for STD: 4.0%, ND: 3.9%, and NND: 3.0%) with 2 dipoles located at LAC and RAC, close to the STG, and a mid-frontal dipole, placed at the level of ACC (Ortiz-Mantilla et al., 2013). At 12 months, ERP generators located at LAC and RAC explained $\sim 94\%$ of the variance (residual variance in the grand average for STD: 6.2%,

ND: 5.4%, and NND: 5.3%); however, no dipole could be modeled at the frontal level. A distributed source model (CLARA) confirmed sources of activation at each age (Fig. 2). The source waveforms at both ages were characterized by a positive deflection followed by a negative deflection (Fig. 3), and resembled the original ERP waveforms (Fig. 1). Means and SD of amplitude and latency of the positive source peaks can be found in Table 1.

The $2 \times 3 \times 2$ (Source [LAC, RAC] \times Stimulus [ND, NND, STD] \times Age [6 months, 12 months]) repeated-measures ANOVAs were conducted separately on the source latency and amplitude. As no source of activation was found at 12 months in the ACC, the ANOVA model only included LAC and RAC sources. The ANOVA for the latency of the positive response revealed a main effect of source ($F_{(1,20)} = 16.402, p = 0.001$) with the right source having a shorter latency than the left; a main effect of stimulus in which the STD stimulus had shorter latency than the ND ($F_{(2,40)} = 9.282, p = 0.000$; *post hoc* pairwise comparisons: STD/ND: $p = 0.000$) and a main effect of age ($F_{(1,20)} = 51.772, p = 0.000$) with faster processing at 12 than at 6 months of age. Statistical analysis on the source amplitude also demonstrated a main effect of stimulus: the peak amplitude for the STD stimulus was smaller than for the ND ($F_{(2,40)} = 8.589, p = 0.001$; *post hoc* pairwise comparisons: STD/ND: $p = 0.004$). This result captures the same information as a “mismatch response” and suggests that at both ages infants favor discrimination of the native contrast.

Differences in source locations across age were examined individually by $2 \times 3 \times 2$ (Source [LAC, RAC] \times Stimulus [ND, NND, STD] \times Age [6 months, 12 months]) ANOVAs for the $x, y,$ and z coordinates. A main effect of age ($F_{(1,20)} = 8.183, p = 0.01$) and a main effect of source ($F_{(1,20)} = 6.683, p = 0.018$) were found for the x and z coordinates, respectively. At 12 months, sources were more medially located compared with the 6 month sources; moreover, the sources in LAC were more inferior compared with the RAC sources. No significant differences were found for the y coordinate.

Time-frequency analyses

Cluster analyses in the 2–50 Hz frequency range

Clusters of significance in the 2–50 Hz frequency range were identified through permutation testing and cluster analyses were conducted between ND and STD in the 6 month data. The following clusters were found: (1) For TSE in the θ range, a significant cluster was identified from 4 to 6 Hz between 100 and 400 ms, showing enhanced activity for the ND compared with the STD in the LAC ($p = 0.03$); (2) for TSE in the low γ range, a significant cluster was found from 30 to 34 Hz between 100 and 400 ms, which showed more power elicited for ND than for STD in the ACC ($p = 0.018$); and (3) for ITPL in the δ - θ range, a significant cluster found from 2 to 6 Hz between 0 and 400 ms revealed larger phase coherence for ND than for STD in the LAC ($p = 0.013$), as well as in ACC ($p = 0.02$). The mean of each cluster was calculated and then, the same cluster parameters were used to obtain information about the third condition (NND) for the 6 months.

Longitudinal analyses in the 2–50 Hz frequency range

To allow comparison of the 6 and 12 month time-frequency data, a third fixed dipole, using the frontal location coordinates iden-

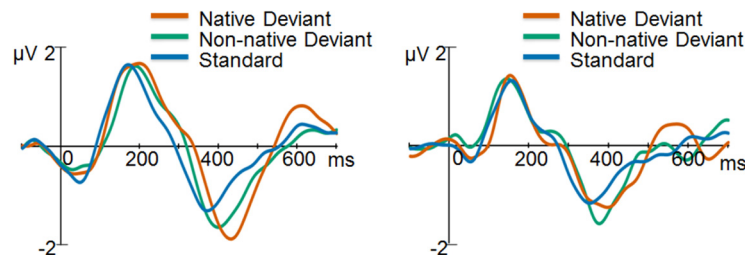


Figure 1. Grand average ERP waveforms at 6 months (left) and 12 months of age (right) are shown at the frontocentral channel. Responses: red represents ND; green represents NND; blue represents STD. Positivity is plotted up. Amplitude of the responses is given in microvolts (μV) and latency in milliseconds (ms).

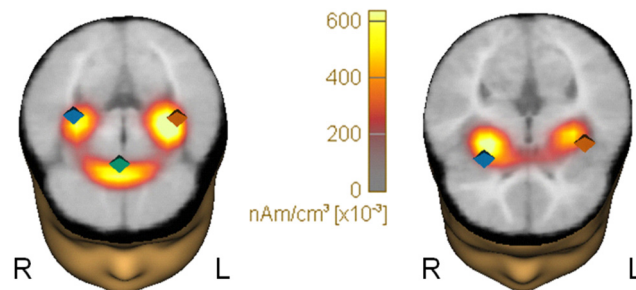


Figure 2. Source localization of the ERP generators is shown for the positive peak of the ND response, on the left for 6 months, and right for 12 months. Discrete equivalent current dipole and distributed CLARA solutions converged at left (L; red) and right (R; blue), auditory sources at both ages and at the frontal (green) ACC source at 6 months. No source of activation in the ACC was found at 12 months. Magnitude of CLARA activation is given in nanoampere meters by cubic centimeter $\text{nAm}/\text{cm}^3 [\times 10^{-3}]$.

tified at 6 months, was added to the 12 month model. To investigate changes across development, the cluster parameters (TSE θ , TSE low- γ , and ITPL θ) identified in the 6 month data were applied to the 12 month data for all three conditions (ND, NND, STD). Stimulus \times age interactions for amplitude (TSE) and phase synchrony (ITPL) were examined in source space using a repeated-measures ANOVA.

TSE θ

A $3 \times 3 \times 2$ (Stimulus [ND, NND, STD] \times Source [LAC, RAC, ACC] \times Age [6 months, 12 months]) repeated-measures ANOVA was conducted on the mean of a cluster found between 100 and 400 ms in the 4–6 Hz frequency range (Fig. 4). Results showed a main effect of source: ($F_{(1,57, 31,46)} = 9.886, p = 0.001$; *post hoc* pairwise comparisons: LAC/RAC: $p = 0.001$; LAC/ACC: $p = 0.001$) with larger power shown at the LAC source compared with the RAC and ACC sources, and a main effect of age: ($F_{(1,20)} = 5.383, p = 0.031$) with larger power elicited at 6 compared with 12 months.

TSE low- γ

At 6, but not at 12, months of age, a frontal/ACC cluster of increased oscillatory activity in the low- γ frequency range (100–400 ms, 30–34 Hz) was found for ND (Fig. 5). A 3×2 (stimulus [ND, NND, STD] \times age [6 months, 12 months]) repeated-measures ANOVA showed a stimulus by age interaction ($F_{(2,40)} = 3.66, p = 0.035$) where larger power was seen at 6 than at 12 months for the ND, whereas no difference was found for the NND and STD stimuli across age.

ITPL θ

An early increase in phase alignment was found in the δ - θ frequency band (0 and 400 ms, 2–6 Hz). A $3 \times 3 \times 2$ (Stimulus [ND,

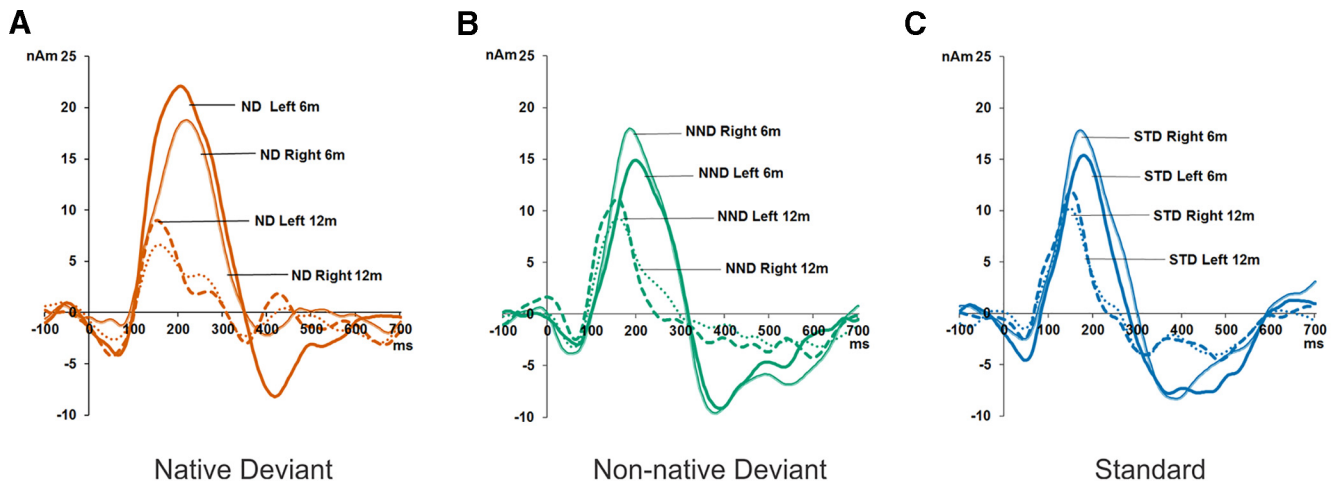


Figure 3. Grand average source waveforms of the responses to ND (A; red), NND (B; green), and STD (C; blue) are shown at the LAC as a thick solid line at 6 months and a thick dotted line at 12 months. For the RAC, a thin solid line indicates 6 month data and a thin dotted line indicates 12 month data. Positivity is plotted up; amplitude of the source dipole moment is given in nanoampere meters (nAm) and latency in milliseconds (ms).

Table 1. Amplitude and latency of the positive peak in response to the ND, NND, and STD stimuli based on individual source analyses^a

	6 months		12 months	
	Amplitude (nAm)	Latency (ms)	Amplitude (nAm)	Latency (ms)
ND LAC	31.36 (14.9)	218 (37.5)	29.54 (20.4)	159 (28.5)
ND RAC	33.19 (12.4)	206 (24.5)	25.52 (13.4)	157 (32.3)
ND ACC	20.01 (7.5)	188 (48.6)	—	—
NND LAC	30.06 (10.7)	206 (29.0)	24.68 (13.2)	156 (26.9)
NND RAC	28.31 (10.9)	196 (34.9)	23.64 (10.9)	148 (19.6)
NND ACC	23.85 (13.5)	191 (40.5)	—	—
STD LAC	23.60 (10.8)	190 (24.2)	23.08 (12.9)	149 (14.6)
STD RAC	27.58 (13.6)	182 (23.6)	19.14 (7.3)	149 (16.1)
STD ACC	14.82 (5.5)	171 (27.9)	—	—

^aData are mean (SD).

NND, STD] × Source [LAC, RAC, ACC] × Age [6 months, 12 months]) repeated-measures ANOVA revealed a source × age interaction ($F_{(2,40)} = 6.468, p = 0.004$). Theta phase coherence was larger at both LAC and RAC sources at 6 months compared with 12 months, whereas at the ACC source no change was seen across age (Fig. 6). In addition, a main effect of stimulus was found with larger phase coherence for ND than for STD ($F_{(2,40)} = 4.067, p = 0.025$; *post hoc* pairwise comparisons: ND/STD: $p = 0.007$). Larger ITPL for ND than for STD could suggest that the mismatch discrimination response is supported by phase synchrony of θ oscillations.

Close examination of the ITPL θ plots suggested longer phase synchronization at 6 than at 12 months, particularly in LAC and RAC sources (Fig. 6). To explore further this developmental timing effect, we kept the same spectral range (2–6 Hz) but divided the time range into two nonoverlapping time-windows (TWs): TW1 from 0 to 200 ms, and TW2 from 250 to 400 ms. A $2 \times 2 \times 2 \times 2$ (Stimulus [ND, NND] × Source [LAC, RAC] × Age [6 months, 12 months] × TW [TW1, TW2]) repeated-measures ANOVA conducted on the mean of the clusters revealed an age × TW interaction ($F_{(1,20)} = 12.813, p = 0.002$). In general, larger ITPL was found at 6 compared with 12 months in both TWs. However, whereas at 6 months larger intertrial phase coherence was found at TW2 compared with TW1, at 12 months, larger ITPL was found in TW1 compared with TW2 (Fig. 7).

Cluster analyses in the 50–90 Hz frequency range

As high- γ power has been suggested to index encoding of VOT features of native phonemes, and in accord with the known perceptual narrowing trajectory, both native phonemes (STD and ND) are expected to already be mapped by 12 months of age. Therefore, clusters of significance in the sources were investigated at 12 months in the 50–90 Hz frequency range using the ND and NND stimuli. The following clusters were found: (1) A significant TSE cluster was found in the high- γ range (>70 Hz), from 70 to 77 Hz between 0 and 800 ms with the ND showing more frontal power than the NND ($p = 0.016$); and (2) for ITPL in the γ range, a cluster was identified from 57 to 63 Hz between 50 and 300 ms, which showed larger phase coherence for the ND compared with the NND in the LAC ($p = 0.048$). Parameters of the 12 month TSE high- γ and ITPL γ clusters were used to obtain information about the third condition at 12 months (STD).

Longitudinal analyses in the 50–90 Hz frequency range

To investigate changes across development, the same cluster parameters (TSE high- γ , and ITPL γ) identified in the 12 month data were applied to the 6 month data in all three conditions (ND, NND, STD). Stimulus × age interactions for amplitude (TSE), and phase synchrony (ITPL) were examined in source space using a repeated-measures ANOVA.

TSE high- γ (>70 Hz)

A long burst of high- γ oscillatory activity (70–77 Hz range, 0–800 ms) was elicited at 12 months (Fig. 8) for both native conditions (ND and STD). A $3 \times 3 \times 2$ (Stimulus [ND, NND, STD] × Source [LAC, RAC, ACC] × Age [6 months, 12 months]) repeated-measures ANOVA revealed a stimulus × source × age interaction ($F_{(4,80)} = 2.918, p = 0.026$). Compared with 6 months, 12 month ND and STD elicited larger γ power in LAC and ACC sources than in the RAC source, whereas the NND showed the lowest amount of γ power in the three sources at both ages.

ITPL γ

At 12 months, a significant increase in phase coherence was seen in the γ band from 57 to 63 Hz between 50 and 300 ms. A $3 \times 3 \times 2$ (Stimulus [ND, NND, STD] × Source [LAC, RAC, ACC] × Age [6 months, 12 months]) repeated-measures

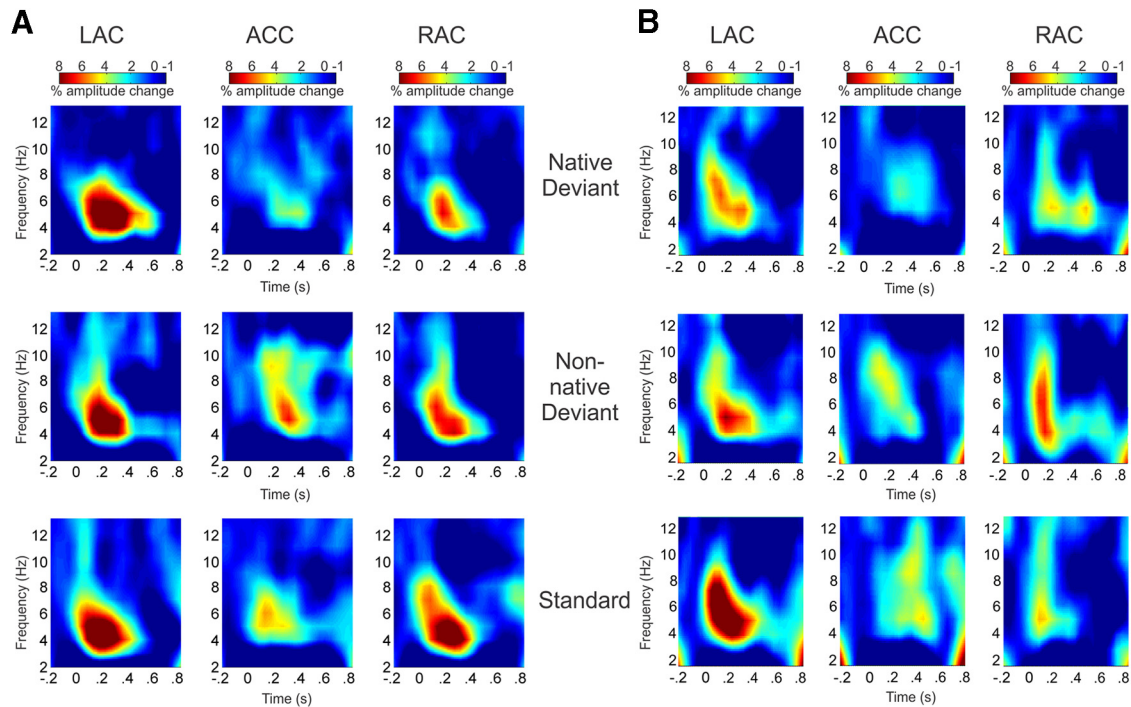


Figure 4. TSE grand average plots showing power for low-frequency oscillations in the θ range at LAC and RAC and at frontal at the level of the ACC. The TSE for 6-month-olds is shown on the left (A) and for 12-month-olds on the right (B). Top row represents TSE for ND. Middle row represents TSE for NND. Bottom row represents power elicited by the STD. Time is shown in seconds (s) on the x-axis and frequency in Hz on the y-axis.

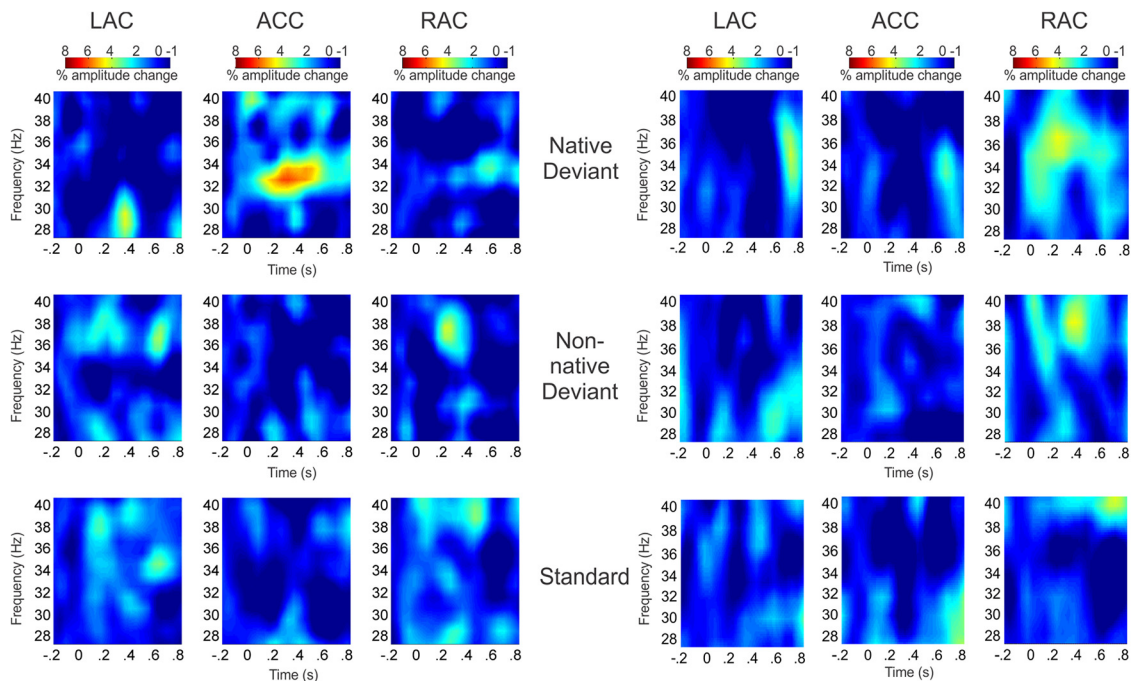


Figure 5. TSE grand average plots illustrating enhanced oscillatory activity in the low- γ range at LAC and RAC and in frontal cortex at the level of ACC. Top row represents TSE for ND. Middle row represents TSE for NND. Bottom row represents power elicited by the STD. At 6 months of age, low- γ activation is particularly evident for the ND stimulus in the ACC (second plot in the first row). The TSE for 6-month-olds is shown on the left (A) and for 12-month-olds on the right (B). Time is shown in seconds (s) on the x-axis and frequency on Hz on the y-axis.

ANOVA revealed a main effect of stimulus ($F_{(2,40)} = 3.397$, $p = 0.043$; *post hoc* pairwise comparisons: ND/NND, $p = 0.031$; ND/STD, $p = 0.027$) with larger phase coherence shown for the ND stimulus compared with the NND and STD stimuli.

Discussion

Becoming an expert processor of native language is a developmental process mediated by the interplay between maturation and experience as reflected in neuroplastic changes in the neuro-

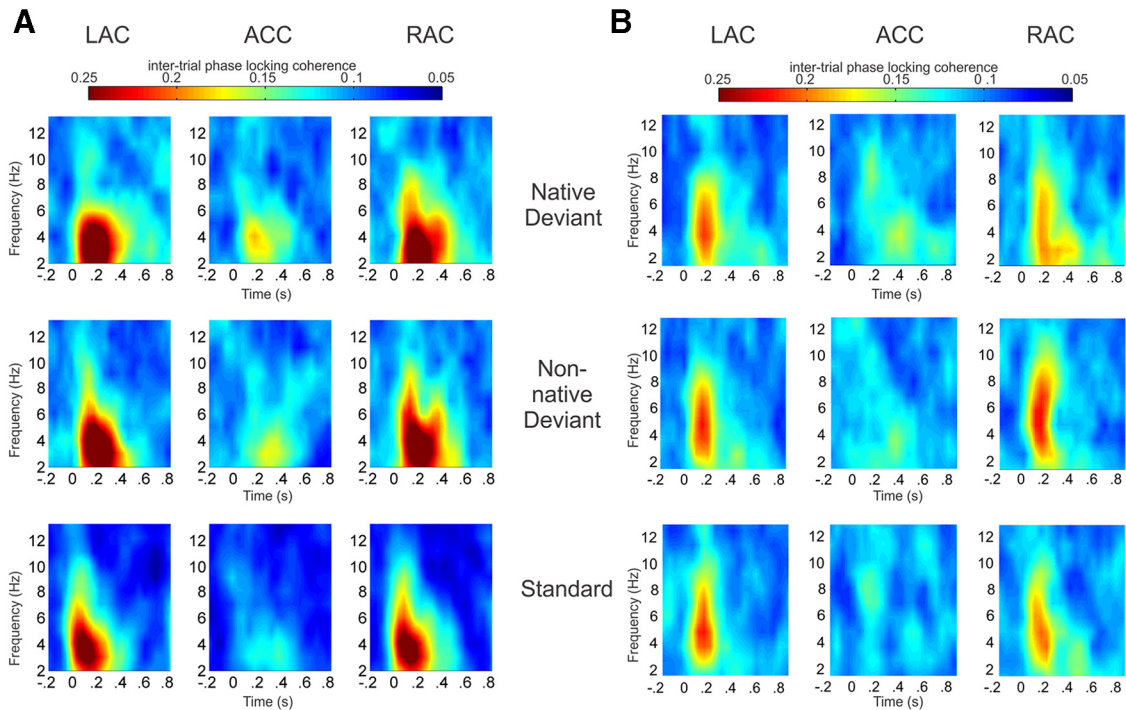


Figure 6. Grand average plots showing ITPL of low-frequency oscillations in the δ - θ range at LAC and RAC and at ACC. The ITPL for 6 months is shown on the left (A) and for 12 months is shown on the right (B). Top row represents ITPL for ND. Middle row represents ITPL for NND. Bottom row represents ITPL elicited by the STD. Time is shown in seconds (s) on the x-axis and frequency in Hz on the y-axis.

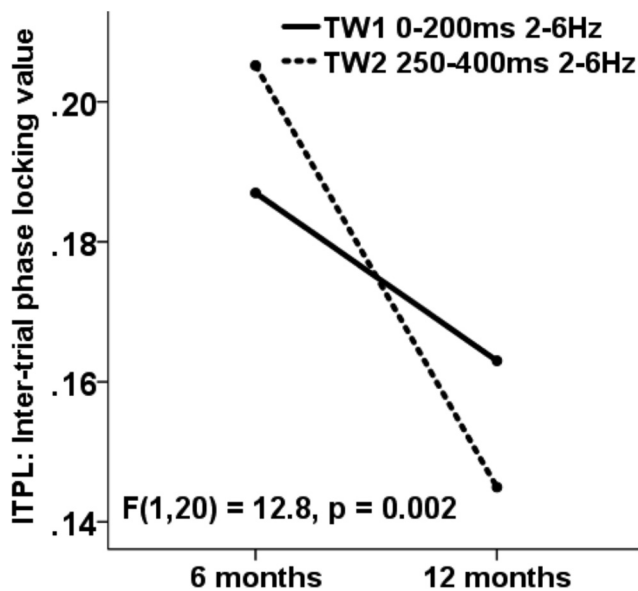


Figure 7. ITPL in the δ - θ range, showing infants’ increase in speed of processing as a function of age. Age in months is shown on the x-axis and ITPL value on the y-axis. Specifically, there was a larger ITPL value at 6 months compared with 12 months in both TWs. However, an age \times TW interaction showed that 6 month ITPL was larger in TW2 (TW2: 2–6 Hz, 250–400 ms; dashed line) compared with TW1 (2–6 Hz, 0–200 ms; solid line), whereas 12 month ITPL was larger in TW1 compared with TW2.

nal networks that support acoustic mapping (Buonomano and Merzenich, 1998). In this study, we examined the neural dynamics underlying infant processing of native and non-native phonemic contrasts at 6 and 12 months of age. We found, across age, that the response to native and non-native syllables is characterized by a general decrease in the magnitude of power elicited in

lower frequency ranges accompanied by widespread increases in high- γ power as seen in LAC and frontal areas at 12 months of age. Our results align with studies reporting that, over development, oscillatory activity at lower frequencies gradually shifts to higher-frequency bands (Koroleva et al., 2002; Marshall et al., 2002; Orekhova et al., 2006; Cragg et al., 2011). High- γ power in auditory cortex is thought to index mapping of segmental/phonemic information (Steinschneider et al., 2011). Hence, our finding of high- γ power in LAC exclusively for native phonemes strongly supports the view that, by the end of the first year, infants have narrowed their perceptual abilities and made significant progress toward mapping the distinctive characteristics of their surrounding linguistic environment. Paralleling these changes in power, less θ -phase alignment was seen at 12 than at 6 months. Furthermore, we found that phase locking in the θ range persisted over a shorter interval in older compared with younger infants, suggesting more rapid processing of syllabic information with age, particularly for discrimination of the ND stimulus. Finally, in the γ range, a significant increase in intertrial phase coherence in the LAC marked preferential processing of the ND over NND.

Role of θ and γ band activity

It is thought that low-frequency oscillations capture the activity of connected neuronal populations and may be involved in information transfer among brain areas (Wang et al., 2005; Wang, 2010; Saby and Marshall, 2012). Theta oscillations are important for perceptual and cognitive functions, such as spatial navigation and declarative and episodic memory processes (Sauseng and Klimesch, 2008; Wang, 2010; Musacchia et al., 2013) and have been proposed as the neural mechanism subserving stimulus discrimination (Ko et al., 2012; Jin et al., 2014). On the other hand, γ oscillations may represent synchronized activity of local neuronal populations during sensory and cognitive processes (Ward,

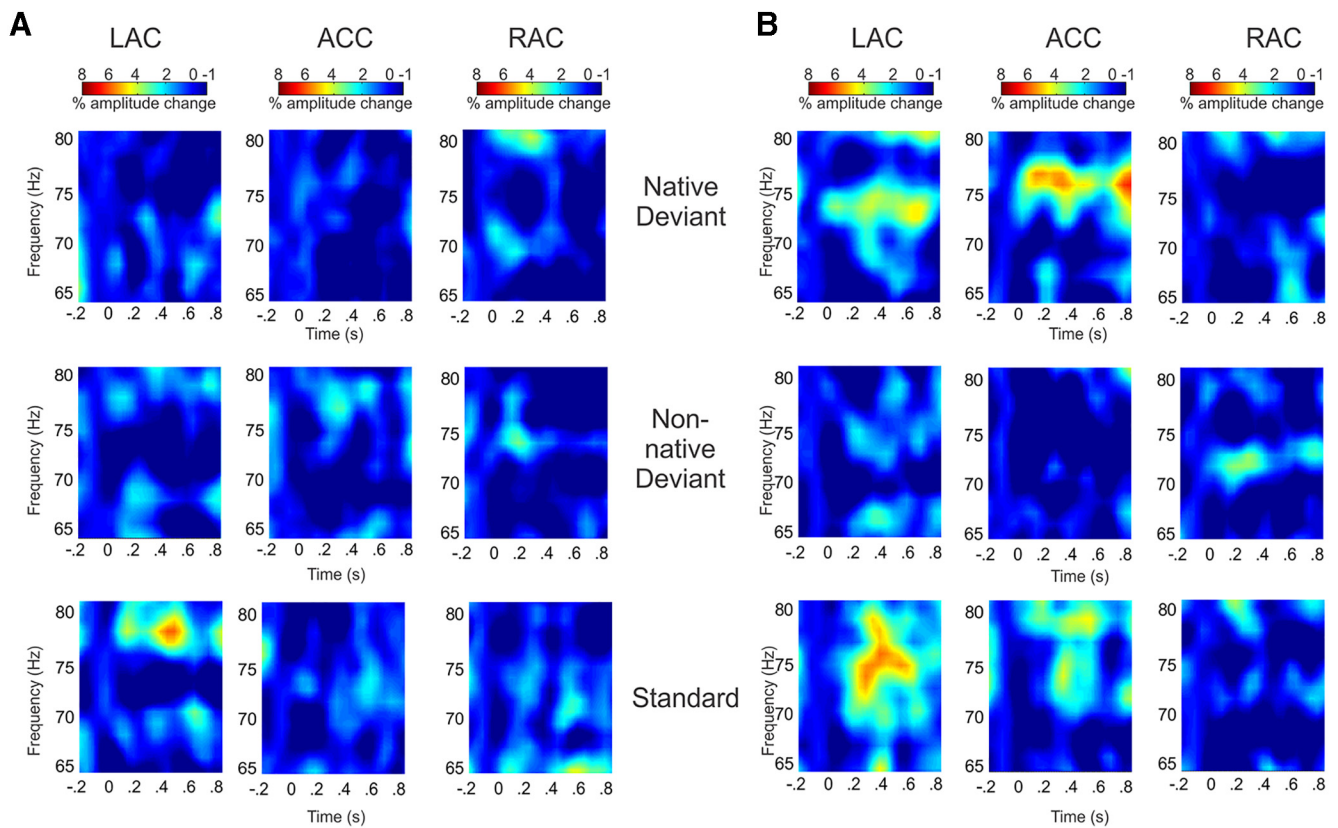


Figure 8. TSE grand average plots showing power for oscillations in the high- γ range at LAC and RAC and in frontal cortex at the level of ACC. Power elicited is shown on the left at 6 months (A) and on the right at 12 months (B). Top row represents TSE for ND. Middle row represents TSE for NND. Bottom row represents power elicited by the STD. At 6 months, a small burst of high- γ power is seen in LAC for the STD. At 12 months, enhanced oscillatory activity in the high- γ range is seen for both native syllables (ND and STD) in LAC and in ACC. Time is shown in seconds (s) on the x-axis and frequency in Hz on the y-axis.

2003; Herrmann et al., 2004; Ribary, 2005; Buzsáki, 2006; Fan et al., 2007; Benasich et al., 2008; Uhlhaas et al., 2010; Gou et al., 2011) but may also play a role in coupling of remote cortical areas (Buzsáki and Schomburg, 2015). However, responses elicited in low- γ (~ 30 – 70 Hz) may well be functionally different from those elicited in higher- γ (>70 Hz) ranges. Low- γ oscillations appear to support object representations, temporal binding, arousal, attentional selection, and working memory (Engel and Singer, 2001; Uhlhaas et al., 2011). In contrast, high- γ activity is a prominent characteristic of early sensory processing (Steinschneider et al., 2008) and may index cortical activation, given that larger high- γ , but not low- γ responses correlate with increases in overall firing rates, particularly during attentional modulation (Crone et al., 2011; Ray and Maunsell, 2011). In humans, more consistent activations have been found in high- than in low- γ ranges within auditory (Crone et al., 2006; Trautner et al., 2006), visual (Friedman-Hill et al., 2000; Frien et al., 2000), and motor domains (Miller et al., 2007). Indeed, whereas 6-month-old infants showed low- γ enhancement to the ND in ACC, at 12 months, high- γ activity was prominent for both native syllables in LAC and ACC. We suggest that the increases in high- γ activity reflect the neural mechanism by which phonemic representations are established within auditory cortex. Simultaneous activation of presynaptic and postsynaptic neighboring neurons fosters plasticity (Hebb, 1949) by increasing synaptic strength between neurons that fire together, and thus is a useful mechanism to explain developmental processes (McClelland, 2006).

Further, cross-frequency synchrony of θ and γ oscillations may mediate temporal integration of local neuronal activity into

large-scale, coordinated, interregional networks, a crucial mechanism for cognitive, sensory, and perceptual processes (von Stein and Sarnthein, 2000; Canolty et al., 2006; Fujisawa and Buzsáki, 2011; Giraud and Poeppel, 2012; Lisman and Jensen, 2013; Doesburg et al., 2015). Interactions between ACC and auditory sensory regions have been reported in adults, with ACC activation relating to attentional modulation (Crottaz-Herbette and Menon, 2006), involuntary switching of attention (Waberski et al., 2001), and the orienting response to potentially significant auditory stimuli (Baudena et al., 1995). In consort with such studies, 6-month-old infants already demonstrate coordinated oscillatory activity across brain regions and frequency ranges. The enhanced low- γ activity observed during the period in which infants are constructing their phonemic maps could be related to involuntary switching of attention toward an increasingly relevant stimulus change as they tune into their native language. At 12 months, infants showed stronger spectral and spatial responses that favored processing of native syllables (increases in high- γ power in both ACC and LAC for both STD and ND stimuli). The fact that, at 12 months, no γ enhancement was seen for the NND suggests that phonemic mapping may already be well established at 12 months and that γ activity may indeed play an important role during infants' native language specialization (Peña et al., 2010; Ortiz-Mantilla et al., 2013).

Although EEG recordings do not have the precise anatomical specificity that ECoG recordings confer, the application of source-localization techniques allows a good estimate of the cortical areas contributing to the evoked responses. Notably, our results align with reports in adults using ECoG-array recordings

in which processing of the temporal attributes of the VOT in native phonemes elicited a high- γ response in PL-STG (Steinschneider et al., 2011; Mesgarani et al., 2014). However, as the participants in those studies were not presented with non-native phonemes, the authors could not ascertain whether the high- γ response was due to general acoustic characteristics, or to “language-specific” phonemic differences. Although we acknowledge that it is more difficult to record γ activity with scalp-recorded EEG, due to the smaller amplitude characteristic of γ activity and frequency similarities with electrical signatures for muscle activity (Crone et al., 2001; Sauseng and Klimesch, 2008), our findings are noteworthy. The fact that infants processing native and non-native VOT contrasts mounted a high- γ response only for native syllables suggests that: (1) the equivalent current dipole model used was accurate enough to capture activity from/close to the STG; (2) the high- γ power exclusively elicited for native phonemes may represent STG specificity for the processing of language-specific phonemic information varying in VOT; and (3) the increased high- γ response at 12 months to native phonemes may signal developmental progress in phonemic mapping, possibly representing the neural signature of phonemic perceptual narrowing.

Lateralization of brain responses

In adults, perception of ongoing speech is considered a multitime resolution process with cross-frequency interactions performed by both auditory cortices. Whereas synchronized oscillatory activity in the θ range is thought to resolve syllabic information, γ oscillations may resolve segmental/phonemic information (Poeppel et al., 2008; Giraud and Poeppel, 2012). Similar to adults, syllable processing in infants is resolved in a multitime fashion through synchronized activity in low- and high-frequency ranges. However, our results are also in line with previous findings in infants (Dehaene-Lambertz et al., 2002; Gervain et al., 2008; Minagawa-Kawai et al., 2011; Mahmoudzadeh et al., 2013), suggesting that speech perception during the phonemic mapping period is left lateralized. It is known that both auditory cortices respond to temporal and spectral variation; however, it is the LAC, in particular, that appears to specialize in rapid temporal processing (Zatorre and Belin, 2001) and to support discrete phonological representations (Phillips et al., 2000). Our findings are consistent with this view, as infant processing in the θ range of rapid successive changes within both native and non-native syllables was predominantly left lateralized. Given that only processing of native information elicited a left-lateralized γ response, we suggest that θ activity likely supports syllable processing at 6 and 12 months, whereas at 12 months, the switch from low to higher γ activity signals a shift to preferential processing of native language.

In conclusion, the process of linguistic perceptual narrowing is critical to the establishment of fluent and efficient native language processing and constitutes a major task across the first year of life. The creation and tuning of the acoustic maps that support this process depend on ongoing neural plasticity and keen sensitivity to environmental cues; however, the details of how this process unfolds in the developing brain are still unclear. To our knowledge, this is the first time that the evolving time-frequency dynamics supporting phonemic perceptual narrowing have been closely examined over development. Our results provide a window into the dynamic and changing patterns that occur in neural mechanisms as language-specific phonemic mapping takes place and highlight the neural substrates of linguistic perceptual narrowing across the first year. Characterizing the normative neural mechanisms that support language acquisition is crucial to understanding how these processes might go awry in some children,

and therefore will facilitate early screening for developmental language disorders and provide insights as to how one might alter the course of such impairments.

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