

**Developmental Changes in Auditory-Evoked Alpha Activity Underlie  
the Increasing Precision with Which Infants Link  
Language and Cognition**

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## ABSTRACT

Although communication is ubiquitous throughout the animal kingdom, the power and precision with which we link language to cognition is uniquely human. By 3-4 months of age, infants have already begun to establish this link: simply listening to human language facilitates infants' success in fundamental cognitive processes including object categorization. This link derives from an initially broader set of signals that at 4 months includes the vocalizations of both humans and non-human primates (but not backwards speech), but by 6 months has been tuned to include only human language. This tuning is adaptive: infants increasingly focus in on the signals (language) that will ultimately constitute the foundations of meaning. But it remains unknown how these signals exert their cognitive advantage, and how infants' responses become tuned within the first 6 months of life. The researchers propose that this early link between acoustic signals and cognition may be guided by a system that directs infants' attention towards (or away from) key elements in their environment. To identify neurocognitive markers of infant attention, they collected EEG activity from 4- and 6-month-olds in response to three types of acoustic signals (infant-directed speech, backwards speech, and non-human primate vocalizations) to assess changes in alpha power, as alpha-band activity is a well-established index of infant attentional engagement. In 6-month-olds, alpha activity was modulated by both infant-directed speech and non-human primate vocalizations, the two signals that initially support cognition, but not by backward speech, a signal that fails to support cognition at any age. Moreover, human and nonhuman vocalizations modulated infants' alpha activity in inverse ways, suggesting that infants draw upon attentional mechanisms either to sustain (for human speech) or to sever (for nonhuman primate vocalizations) their links between these signals and cognition.

### **Developmental Changes in Auditory-Evoked Alpha Activity Underlie the Increasing Precision with which Infants Link Language and Cognition**

Well before infants begin to speak, listening to language enhances the core cognitive capacities that serve as their foundations for learning. For infants as young as 3- and 4-months of age, listening to language boosts the ability to form object categories – to identify commonalities among otherwise distinct objects, and to use these as a basis for reasoning about new objects (Ferry, Hespos, & Waxman, 2010; Fulkerson & Waxman, 2007). Moreover, listening to language supports infant object categorization in a way that other acoustic signals, such as sine-wave tone sequences and time-reversed (“backwards”) speech, do not (Ferry et al., 2010; Ferry, Hespos, & Waxman, 2013; Fulkerson & Waxman, 2007). Still, language is not the only signal that exerts this precocious cognitive advantage: listening to vocalizations of non-human primates (e.g., blue-eyed Madagascar lemur, *Eulemur macaco flavifrons*) offers 3- and 4-month-old infants the same advantage as listening to spoken language (Ferry et al., 2013). But in contrast to the advantage that listening to a native language provides for cognition, which persists across infancy, the link between non-human primate vocalizations and cognition fades: by 6 months of age, this signal no longer supports infant cognition. Thus, a link between language and object categorization, evident by 3-months of age, derives from a broader template that seems initially to encompass the vocalizations of both humans and non-human primates, and is subsequently tuned to include only human language (Ferry et al., 2013).

By what mechanism(s) do these initially privileged acoustic signals (human and non-human primate vocalizations) exert their cognitive advantage, and how does this link become tuned to human language? Certainly by 12 months, listening to language initiates a search to discover a word's meaning (Carey, 2011; Waxman & Markow, 1995). But in the first few

months of life, when infants cannot yet reliably glean distinct words from the ongoing stream of speech (Jusczyk, 1999; Saffran, Aslin, & Newport, 1996) nor have they begun to infuse acoustic representations of words with meaning (Bergelson & Swingley, 2012; Tincoff & Jusczyk, 2012), a different, perhaps coarser mechanism must be at play. One possibility is that for very young infants, listening to human and non-human primate vocalizations engenders heightened attention, effectively highlighting the objects and events in their current surroundings and, in this way, supports performance on fundamental cognitive tasks including object categorization.

Attention is a multifaceted set of processes, which can be difficult to measure and disentangle even in adults. The challenge is even greater for infants, for whom attentional capacities are largely rudimentary, but rapidly developing (for reviews, see (Gomes, Molholm, Christodoulou, Ritter, & Cowan, 2000; Oakes & Amso, 2018)). Here, we suggest that certain acoustic signals are able to solicit early, rudimentary components of attention that are in place in early infancy. Evidence in support of this hypothesis comes from findings in non-human species that certain privileged sounds heighten juveniles' arousal and promoting adaptive behaviors. For example, when crocodile embryos are exposed to the vocalizations of a nearby embryo on the verge of hatching, their own behavior is altered in ways that promote hatching (Vergne & Mathevon, 2008). Similarly, when gull embryos are exposed to the calls of predators, they emit vibrations which are perceived by nestmates (who were unexposed to the predators' calls), altering prenatal and postnatal phenotypes of these neighboring embryos in ways that increase arousal (e.g., higher levels of DNA methylation and stress hormones, reduced growth and numbers of mitochondria) and increase behaviors that reduce the threat of predation (e.g., reduced vocalizations, rapid crouching) (Noguera & Velando, 2019).

To investigate the developmental tuning of the set of signals that engage infants' attention, the current study examined developmental changes in electrophysiological measures of attention, which provide a more objective measure of the brain's automatic capabilities. Here, electroencephalographic (EEG) activity of healthy, full-term 4- and 6-month-olds (N=17 per group) was recorded as they were presented with 3-second recordings of human speech (infant-directed speech; IDS), non-human primate vocalizations (LEMUR), and backwards speech (BW-IDS) over a single 20 minute session. Three different tokens of each signal type (all matched for mean frequencies and duration; see Figure 1 for exemplar tokens of each signal type; see Figure S1 and Table S1 for details on all nine tokens) were presented in a pseudo-randomized order (such that no two recordings of the same signal type were presented successively). If attention is modulated by these signals, then at 4-months human and non-human primate vocalizations should elicit similar neural markers of increased attention, but at 6-months, when infants no longer link non-human primate vocalizations to cognition, neural markers of attention should decrease in response to non-human primate vocalizations.

Analyses were focused on an established neurophysiological index of infants' attention: neural activity in the alpha frequency band. Alpha activity is the predominant rhythm in the infant brain, is detectable as early as 3-months (Davidson & Fox, 1982; Lindsley, 1939; J. R. Smith, 1938, 1939), and is thought to be an index of infant cognitive engagement (e.g., attention (Orekhova, Stroganova, & Posikera, 2001; Stroganova, Orekhova, & Posikera, 1999; Xie, Mallin, & Richards, 2017) and working memory (Bell, 2002; Libertus, Pruitt, Woldorff, & Brannon, 2009)). Importantly, a *decrease* in alpha power is typically observed under conditions of *increased* task demands in children and adults (e.g., Berger, 1929; Klimesch, 2012; Thut, Nietzel, Brandt, & Pascual-Leone, 2006; Van Diepen, Foxe, & Mazaheri, 2019). In infants, alpha

power has been observed to decrease during conditions requiring sustained visual attention (Stroganova et al., 1999; Xie et al., 2017) but increase when infants are required to suppress attention to task-irrelevant information (Orekhova et al., 2001). Because the current design uses a passive listening task, differences between stimuli cannot be associated with cognitive demands directly, but the primary goal here is to assess how hearing more complex or meaningful sounds might have similar effects on alpha activity. Similar passive listening paradigms in children and adults report decreased alpha activity when participants were presented with the sounds of speech or musical instruments, but increased alpha activity when presented with backwards speech (Fujioka & Ross, 2008; Krause, Porn, Lang, & Laine, 1997). Based on these previous findings, we predict here that hearing signals that support infant cognition will decrease infants' ongoing alpha activity; in contrast, hearing signals that do not support cognition will either increase or exert no influence on alpha activity. Event-related potentials (ERPs) were also compared across ages and stimuli. Early components of the auditory-evoked ERP waveform have been shown to index developmental changes in neural processing of speech in infants (Dehaene-Lambertz & Dehaene, 1994; Nacar Garcia, Guerrero-Mosquera, Colomer, & Sebastian-Galles, 2018; Peña, Pittaluga, & Mehler, 2010) and are thought to reflect gains in neural maturation and experience (Kushnerenko et al., 2002). Together, these two measures provide insight into how infants' cognitive states are modulated by these acoustic signals, and how this effect changes as infants increasingly prioritize the link between language and cognition.

## Methods

**Participants.** 34 full-term infants were included in the final analyses (17 4-month-olds, range = 4.11-5.0 [6F]; 17 6-month-olds, range = 5.95-6.98 [9F]). 28 additional infants

participated but were excluded because of contributing too few trials (8 4-month-olds, 13 6-month-olds) or technical difficulties (N=7). All participants were recruited from the Chicago area. Parents completed a questionnaire about language exposure, and the average parent-estimated exposure to English was 87% (SD: 21.4%). Informed consent was obtained from legal guardians in accordance with procedures approved by the Northwestern University Institutional Review Board, and participants were compensated for their participation with either monetary payment or a children's book and t-shirt.

***Stimuli.*** Auditory stimuli consisted of 9 unique recordings (3 per stimulus type) of infant-directed speech (IDS), backward IDS, and lemur calls (recordings are available upon request; exemplar recordings are visualized in Figure 1 and all 9 recordings are visualized in Figure S1). Each IDS recording comprised two English sentences, spoken by a different native American English-speaking woman. Backward IDS (BW-IDS) recordings were the same 3 recordings of IDS, played in reverse. Lemur recordings were selected from a recordings made by Chris Mercer at the Duke University Lemur Center (see <http://musictechnology.music.northwestern.edu> for descriptions of recording methodology and sample recordings) to match the mean duration and frequency range of the IDS recordings (see Table S1 and Figure S1 for further information and analyses of all recordings). Recordings were presented with an inter-stimulus interval (ISI) of 1800-2200 ms in sound field at 65dB SPL, in a pseudorandomized order such that no two sounds of the same stimulus type (IDS, BW-IDS, or LEMUR) occurred twice in a row. Each recording was presented 24 times for a total of 216 trials (72 trials per stimuli type).

***Electroencephalography (EEG) recording parameters.*** All EEG recordings were made in a quiet room. Infants sat on a caretaker's lap facing two speakers placed 4 ft in front of the infant and 2 ft from one another. During the recording, an experimenter kept the infant calm and

engaged by blowing soap bubbles and/or silently playing with puppets in front of the infant. The study was stopped at the completion of all 216 trials, or when the infant exhibited discomfort (e.g., crying, fussiness). The total duration of the full experiment was about 25 min.

***Data acquisition and pre-processing.*** Cortical responses were recorded with a sampling rate of 250 Hz using a 16-electrode EEG system (actiCAP, Brain Products GmbH, Gilching, Germany). Seventeen Ag/AgCl active electrodes were placed according to the 10–20 system, with an additional grounding electrode at Fpz, and online referenced to the electrode at Cz. Individual electrode impedances were ascertained to be below 10 k $\Omega$  prior to commencement of recording. Recordings were amplified (V-amp, Brain Products GmbH), online band-pass filtered (high-pass cutoff: 0.05 Hz; low-pass cutoff: 100 Hz), and notch filtered (centered at 60 Hz). Electrophysiological data were preprocessed in MATLAB (The Mathworks, Inc., Natick, MA) using EEGLAB v.14.1.2 (Delorme & Makeig, 2004) and ERPLAB v.7.0.0 (Lopez-Calderon & Luck, 2014). The online reference electrode (Cz) was returned to the recording mathematically, and all electrodes were then offline re-referenced to the average of all electrodes. Continuous data were high-pass filtered at 0.1 Hz using a second order IIR Butterworth filter and segmented into -800 to 3000 ms epochs relative to stimulus onset (at 0 ms). Epochs containing artifacts such as eyeblinks or excessive noise were first detected using an automated moving 200 ms window peak-to-peak amplitude threshold of 200  $\mu$ V, and then manually inspected and confirmed before rejection. Additional artifact-contaminated epochs were manually detected, and all contaminated epochs were excluded from further analysis. Participants with fewer than 15 artifact-free epochs per stimulus type (BW-IDS, IDS, LEMUR) were excluded from analyses. See Table S2 for further information regarding accepted trials.

***Event-related spectral perturbation (ERSP).*** ERSPs reveal event-related dynamics of the EEG spectrum induced by, but not phase-locked to, the onset of the auditory stimuli (Makeig, 1993). To compute the ERSP, the EEG time series of each epoch at each electrode was convolved with a set of complex Morlet wavelets, defined as a Gaussian-windowed complex sine wave:  $e^{-i 2\pi t f} e^{\frac{-t^2}{2\sigma^2}}$ , where  $t$  is time,  $f$  is frequency (which increased from 3-55 Hz centered over 53 linear-spaced 1 Hz-wide frequency bins, centered at each single-integer frequency), and  $\sigma$  defines the width (or “cycles”) of each frequency band, beginning with 3 cycles at the lowest frequency, and increasing by a factor of 0.92, to 4.4 cycles at the highest frequency (using eeglab’s *newtimef* function). Due to the temporal width of the wavelet at the lowest frequency, the time-frequency analytical window was restricted to -242 ms to 2500 ms with respect to the stimulus onset. A pre-stimulus baseline of 242 ms was subtracted on a frequency-by-frequency basis for each trial. The power time series were normalized by conversion to a decibel (dB) scale ( $10 \cdot \log_{10}[\text{power}(t)/\text{power}(\text{baseline})]$ ) to allow for direct comparison of effects across frequency bands. Epochs were then averaged across trials and stimulus tokens for each stimulus type at each electrode, and then averaged across participants for each age group.

***Event-related potential (ERP).*** Changes in scalp-recorded voltage over time that reflect the sensory, cognitive, and affective processes elicited by the auditory stimulus are depicted in the ERP. Artifact-free epoched responses were averaged across stimuli, baseline corrected to a pre-stimulus period of 200 ms, low-pass filtered at 20 Hz, then averaged across participants for each age group, and visualized using ERPLAB (Figure 4). A large early component was observed at ~400 ms for both ages: an anterior positivity and a posterior negativity. Following prior work (Nacar Garcia et al., 2018; Peña et al., 2010), electrodes over central-anterior (F3, Fz, F4) and central-posterior (P3, Pz, P4) regions were selected *a priori* as spatial regions of interest

(ROIs) for further comparisons. ERPs were then re-averaged separately for each stimulus type at each electrode for each participant, baseline corrected to a pre-stimulus period of 200 ms, and low-pass filtered at 20 Hz. Stimulus-specific averages were then averaged across electrodes of each ROI, and then averaged across participants for each age group. The mean amplitude of the ERP component was computed for each ROI over the 200-600 ms time window.

*Statistical analysis.* Time-frequency permutation t-tests were computed in EEGLAB. Within- and across-subject comparisons were computed using *R* v.3.5.2 (R Core Team, 2018). While the comparison of a number of electrodes and frequencies imposes a problem of correction for multiple comparisons, due to the strong correlation of activity in adjacent electrodes and frequency bins, the application of such a correction would greatly inflate the probability of false negative results. Therefore, statistics are reported on averaged electrodes and frequency bins in the main results section with uncorrected p-values. Statistics for comparisons of individual, 1 Hz, frequency bins can be found in Figure 3B and Table S3. Statistical analyses and figures from a single electrode (Pz) are also presented in the supplemental materials. The mean amplitude of the early ERP component was submitted to statistical comparisons using one-way ANOVA.

## Results

*Identifying the alpha response in 4- and 6-month-old infants.* While the canonical alpha band activity in the adult brain lies between 8-12 Hz, neural activity in the infant brain is predominantly at lower ranges. For infants in the first year of life, there is little consensus regarding the precise frequency cutoffs for discriminating alpha from lower (theta) and higher (beta) activity. This is because the alpha EEG rhythm, which first emerges at 3- or 4-months, undergoes substantial changes in its frequency range with development: from ~3-5 Hz in 3-4

month-olds to ~6-10 Hz by 12-months (Lindsley, 1939; Marshall, Bar-Haim, & Fox, 2002; Saby & Marshall, 2012; Stroganova et al., 1999). Therefore, to assess alpha activity across this dynamic developmental period, in 4- and 6-month-olds, we take a liberal approach in defining infant alpha, by comparing the average activity across a comprehensive range: 4-9 Hz. Posterior activity in this range is considered alpha in infants (Lindsley, 1939; J. R. Smith, 1939, 1941), so analyses were based on the average of the two midline centroparietal electrodes, Cz and Pz. Visual inspection of event-related spectral perturbation (ERSP) plots confirmed that power within this frequency band was largely similar for each stimulus type over the majority of the response period (0 – 2500 ms), so subsequent analyses were computed on the average power over the entire time window of the response.

***Developmental changes in alpha power.*** Alpha power differed as a function of age (4-month-olds; 6-month-olds) and stimulus type (BW-IDS; IDS; LEMUR) (RMANOVA interaction:  $F_{(2,31)} = 4.282$ ,  $p = 0.023$ ,  $\eta_p = 0.216$ ). Follow-up comparisons of changes in alpha power in response to each stimulus revealed that at both ages, alpha power did not change in response to BW-IDS, the signal that does not support object categorization, relative to pre-stimulus baseline (4mos:  $M = 0.038$ ,  $SD = 0.945$ ; one-sample t-test:  $t(16) = 0.165$ ,  $p = 0.871$ ; 6mos:  $M = -0.202$ ,  $SD = 1.138$ ; one-sample t-test:  $t(16) = -0.733$ ,  $p = 0.474$ ), nor was there a change in power in response to BW-IDS across age groups (unpaired t-test:  $t(31) = 0.669$ ,  $p = 0.509$ ). In 4-month-olds, there were also no significant differences in alpha power in response to IDS ( $M = 0.155$ ;  $SD = 0.972$ ) or LEMUR ( $M = -0.199$ ;  $SD = 0.965$ ; paired t-test:  $t(16) = 0.939$ ,  $p = 0.362$ ).

However, in 6-month-olds, alpha power did differ significantly in response to IDS and LEMUR ( $t(16) = 3.297$ ,  $p = 0.005$ ,  $d = 0.799$ ; Figure 3A). In response to IDS, there was a

*decrease* in alpha power ( $M = -0.629$ ;  $SD = 0.941$ ) relative to both pre-stimulus baseline (one-sample t-test:  $t(16) = 2.757$ ,  $p = 0.014$ ) and relative to 4-month-olds (unpaired t-test:  $t(16) = 2.390$ ,  $p = 0.023$ ,  $d = 0.820$ ). In response to LEMUR, there was an *increase* in power ( $M = 0.584$ ;  $SD = 0.984$ ) relative to both pre-stimulus baseline (one-sample t-test:  $t(16) = 2.445$ ,  $p = 0.026$ ) and to 4-month-olds (unpaired t-test:  $t(16) = 2.342$ ,  $p = 0.026$ ,  $d = 0.803$ ). Permutation t-tests were also performed at each time-frequency point to further visualize which time-frequencies regions best captured differences in EEG power between the responses to IDS and LEMUR stimuli at each age (Figure 2D; masked to plot only  $p < 0.05$ ). Follow-up comparisons of power at each 1 Hz, integer-centered, frequency bin revealed that the effect was consistent for the duration of the signal across the entire 4-9 Hz frequency region (Figure 3B and Table S3).

***Developmental changes in the event-related potential (ERP).*** Previous studies of 3- to 9-month-old infants' ERPs responses to speech sounds describe a positive anterior peak (~200-300 ms) and a negative posterior (~240 ms) peak (Nacar Garcia et al., 2018; Peña et al., 2010). Here, the large initial peak occurred slightly later, around 400 ms, over both anterior (F3, Fz, F4; Figure 4B) and posterior (P3, Pz, P4; Figure 4F) regions. The mean amplitude of this peak (averaged over 200-600 ms) differed as a function of stimulus type only for the posterior ROI (RMANOVA:  $F_{(2,64)} = 6.420$ ;  $p = 0.003$ ,  $\eta_p = 0.167$ ), and follow-up comparisons of each stimulus type at each age revealed a developmental effect only for the response to IDS, such that the amplitude of this peak decreased in negativity (ANOVA:  $F_{(1,32)} = 4.443$ ,  $p = 0.043$ ) from 4- ( $M = -6.456$ ,  $SD = 3.267$ ) to 6-months ( $M = -3.744$ ,  $SD = 4.178$ ). This developmental reduction in amplitude differentiated the response to IDS from the other two signals in 6-month-olds (IDS vs BWS:  $t(16) = 1.940$ ,  $p = 0.070$ ,  $d = 0.470$ ) IDS vs LEMUR:  $t(16) = 3.361$ ,  $p = 0.004$ ,  $d = 0.815$  which was not present at 4-months.

## Discussion

These results add to a growing body of evidence documenting the rapid organization of cortical networks in the infant brain for processing language, extending the well-established evidence that infants increasingly favor language, to consider the more abstract problem of how infants link sounds, with increasing specificity for language, to cognition. Recent neuroimaging studies have described distinct areas of the infant brain that are activated by spoken language, and not by non-linguistic signals such as scrambled speech, backwards speech, sine-wave contours, tones, or monkey calls (Dehaene-Lambertz, Dehaene, & Hertz-Pannier, 2002; Minagawa-Kawai et al., 2011; Peña et al., 2003; Perani et al., 2011; Shultz, Vouloumanos, Bennett, & Pelphrey, 2014). Although the infant brain has already developed specialized networks for processing language within the first few months, the infant brain remains sensitive to the vocalizations of other species: in 4-month-olds, non-human primate vocalizations elicit greater neural activation than speech does in brain regions (i.e., bilateral anterior superior temporal gyrus (Minagawa-Kawai et al., 2011)) that are later recruited to specialize in speech (Fecteau, Armony, Joannette, & Belin, 2004). This outcome, which indicates that there may be a protracted period in human infancy during which infants remain sensitive to non-human primate vocalizations, converges well with the evidence that in 4-month-olds, both human and non-human primate vocalizations support cognitive performance (Ferry et al., 2013), and that these non-human primate vocalizations continue to boost cognitive abilities in 6-month-olds who are briefly exposed to these sounds (Ferry et al., 2013; Perszyk & Waxman, 2016).

The current study reveals that by 6-months, only the signals that are part of this initial set that support early cognition—human speech and non-human primate vocalizations—modulate infants' alpha activity. Moreover, speech and non-human primate vocalizations modulate alpha

activity in distinct ways, suggesting that infants draw upon attentional mechanisms either to sustain (for human speech) or to sever (for non-human primate vocalizations) their initial links between these signals and the objects they encounter.

The reduction in infants' alpha power in response to speech may reflect (a transition to) a cognitive state that is primed for learning. Previous investigations of infant object learning have revealed reduced alpha activity during moments of joint attention between infant-adult dyads (Hoehl, Michel, Reid, Parise, & Striano, 2014; Lachat, Hugueville, Lemaréchal, Conty, & George, 2012). Simply listening to speech may heighten infants' attention to the objects around them (e.g., to the visual images presented in the categorization task). In adults, alpha activity is also reduced when familiar speech tokens are presented during a memory task (Krause, Lang, Laine, Kuusisto, & Pörn, 1995). This suggests that a reduction in alpha activity might also index speech-specific learning and memory processes.

The increase in alpha power, relative to baseline, in response to non-human primate vocalizations in 6-month-olds may reflect disengagement from this once-privileged signal that supported cognition at 4-months, but whose role has since been neutralized or modified. An increase in alpha activity is thought to be a neural signature of inhibition and disengagement of task-irrelevant cortical areas (Klimesch, 1996; Pfurtscheller, 2003). Increased alpha activity has been identified in cortical regions processing irrelevant or distracting information during attention-related tasks, thought to be acting to suppress stimuli or stimulus features that are to be ignored (for review, see (Foxy & Snyder, 2011)).

In contrast, backwards speech, a signal that does not support cognition at any age, did not modulate alpha power. This suggests that infants may not need to suppress their attention to this signal. This is intriguing, as 6-month-olds' behavioral responses to non-human primate

vocalizations and backwards speech are identical: both fail to support object categorization. However, their neural responses to these signals differ, revealing a possible neural trace for the once-supportive signal. This suggests that infants may preserve a trace of the connection between non-human primate vocalizations and cognition, perhaps in the event that the signal proves meaningful. This might occur by means of exposure; non-human primate vocalizations continue to boost cognition in 6-month-olds who were previously exposed to these vocalizations (Perszyk & Waxman, 2016). The reduction in alpha activity may reflect how exposure guides infants to specify which signals they link to cognition. Active, enriched interaction with human language may lead to the reduction in alpha activity observed in the 6-month-olds. Future work is necessary to test whether alpha modulation may help to identify signals for which the link to cognition remains accessible via exposure, and if exposure to a signal decreases alpha activity.

The reduction in amplitude of the posterior N400 ERP component in response to language observed in 6-month-olds likely reflects an additional influence of exposure on the neural processing of acoustic signals. This component was selectively reduced in response to speech, both in relation to the response evoked by the same speech stimuli in 4-month-olds, and in relation to the responses evoked by the other two signals (backwards speech and non-human primate vocalizations). This may reflect the predictability of speech sounds, since reduced amplitude of ERP components are typically associated with inputs that elicit less surprise. Between 4- and 6-months, the infant brain increasingly gains familiarity with speech and likely processes these more frequent stimuli more efficiently, recruiting fewer neural resources to process a signal that carries important communicative cues that infants begin to link to higher order cognitive tasks, and subsequently, meaning. Previous work has described changes in latency of an early large component, similar in morphology, occurring around 240 ms (Nacar

Garcia et al., 2018; Peña et al., 2010). Nacar Garcia *et al.* observed only a latency difference in this peak for native- compared to non-native languages for monolingual 4-month-olds, but for the latter it remains unknown whether there were stimulus-related differences in the latency or amplitude of this peak. Although the component we observe here occurs later than in this prior work, this effect could be due to the inclusion of signals that were produced either artificially or by non-humans. Moreover, the reduction of the amplitude of this component in response to speech is consistent with evidence that this component may be modulated by familiarity with a signal; in infants, the amplitude of the visual-evoked central negative component (Nc; 400-800 ms) is reduced when a visual stimulus is more familiar (Wahl, Marinović, & Träuble, 2019). Together, these findings suggest that similar neural generators may be involved in the discriminative process that selectively favors speech over other signals to support cognition.

Despite these clear differences in the neural responses of 6-month-olds, several compelling questions remain. For example, the mechanism by which human speech and non-human primate vocalizations exert their cognitive advantage in 4-month-olds remains elusive. The failure to detect changes in alpha power in response to these signals among 4-month-olds, or a difference in the ERP morphology for signals that do and do not boost their cognition, may stem from limitations in methodology: additional work may be required to identify which neural measures, if any, are sensitive enough to detect differences in the neural responses that support the behavioral differences observed in 4-month-old infants. Alternatively, there may be true developmental differences in these responses. Perhaps at 4 months, listening to these signals does not yet draw upon attentional resources to facilitate cognitive performance, but engenders instead some other, more basic, mechanism. Differences may emerge at earlier levels of auditory processing, which could be revealed by comparisons of processing at earlier stages (e.g., the

brainstem's frequency-following response to these signals). Another possibility is that these neural responses are the product of distinct functions at different developmental timepoints. For example, longitudinal assessment of 5-month-olds' silent ("resting") state EEG relative power in this frequency range (6-9 Hz) has been demonstrably distinct from activity in the same band at later ages (10- to 51-month-olds) (Marshall et al., 2002).

Additionally, while it is clear that initially-privileged signals modulate alpha activity in 6-month-olds, and that such influences on alpha activity have been linked to levels of attentional engagement in infancy (Orekhova, Stroganova, & Posikera, 2001; Stroganova, Orekhova, & Posikera, 1999; Xie, Mallin, & Richards, 2017), further research is necessary to explicitly identify whether the cognitive processes involved here are attentional, or reflect other cognitive processes, such as memory. Furthermore, it will be important to determine which aspects of the broader domain of attention tunes infants' behavioral responses to acoustic signals. In very young infants, this process is likely automatic, as the rudimentary components of attention slowly emerge; over the first few months infants must first develop the ability to attain and maintain an alert state. Once an optimal level of arousal has been established, novel or salient stimuli elicit an orienting response, which shifts infants' attention towards salient features of their environment and allows for the inhibition of attention to distractors (for reviews, see (Gomes et al., 2000; Oakes & Amso, 2018)). Although the responses investigated here were to the sounds alone, without the additional dimension of the visual images as in the object categorization task, it is reasonable to assume that cognitive processing in one modality may influence perception and performance in other modalities. While auditory and visual attention are thought to have different developmental trajectories, direct comparisons of these trajectories of these processes are sparse (with the earliest longitudinal assessment occurring at age 7 years

(Günther et al., 2014)), and it remains unknown how these processes intersect and support one another in multimodal tasks such as object categorization in infancy. Future work is necessary to directly assess how auditory attention influences visual attention processes in infancy, and specifically how these processes interact to support cognitive processes in the context of tasks such as categorization.

Finally, another open question is which acoustic features of these signals engage infants' attention in such a way as to boost cognition. Mammalian vocalizations share many acoustic properties and are coded similarly in the human auditory system (Altmann, Doehrmann, & Kaiser, 2007; E. C. Smith & Lewicki, 2006). In the current study, the non-human primate tokens were selected to match the mean frequency and duration of the human speech tokens. Acoustic differences do, however, remain. For example, the frequency composition differs between signals, as the speech tokens have more concentrated energy in the 3-4 Hz band than do the more broadband non-human primate tokens (see Figure S1 for further depiction of acoustic features). However, previous work has failed to find any correlational relationships between infants' listening preferences and acoustic properties (e.g., pitch, perceived loudness, signal complexity, and amplitude variation) of speech or macaque vocalizations (Shultz & Vouloumanos, 2010).

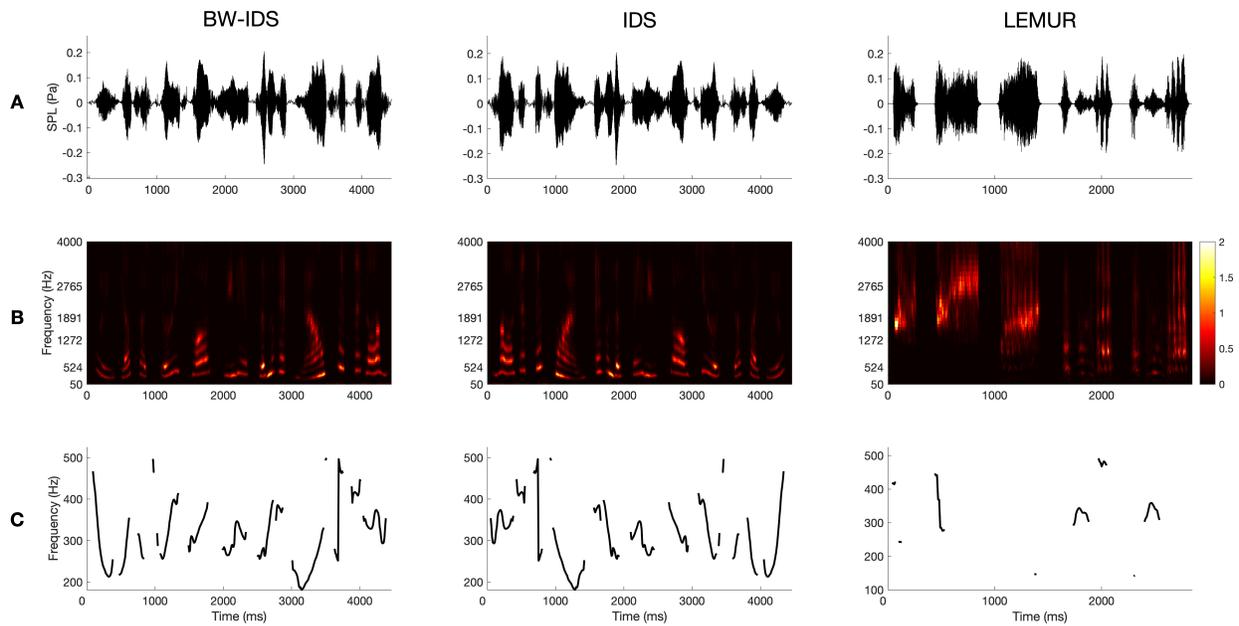
Moreover, differences in infants' responses to these signals cannot be attributed entirely to low-level acoustic features such as signal complexity, spectral composition, or the spectrotemporal modulation structure. The backwards speech tokens used here and in the behavioral studies are identical in acoustic complexity and spectral composition to speech tokens but elicit strikingly different behavioral and neural responses. Of course, reversal of the speech signal results in an envelope profile that is not compatible with a sound naturally produced by a vocal tract. The difference between possible and impossible sounds may be encoded early in the

auditory pathway (Galbraith et al., 2004; E. C. Smith & Lewicki, 2006), and may contribute to an early distinction between the signals that do and do not support cognition at an early age. Therefore, it remains an open question whether the signal's origin (natural versus artificially produced) may explain one aspect of the difference in behavior and the modulation of alpha power observed in 6-month-olds. Whether alpha was reduced or increased might be dictated by acoustic aspects of the stimulus, such as its source (human or non-human vocal tract), its biological origin (conspecific versus heterospecific), or its linguistic content. Future work will be necessary to investigate whether the neurophysiological modulation in infants observed here extends to all human-produced vocalizations (e.g., do non-linguistic, human-produced sounds like humming or laughing also support cognition and reduce alpha power?) or if this effect is specific to stimuli with putative linguistic content.

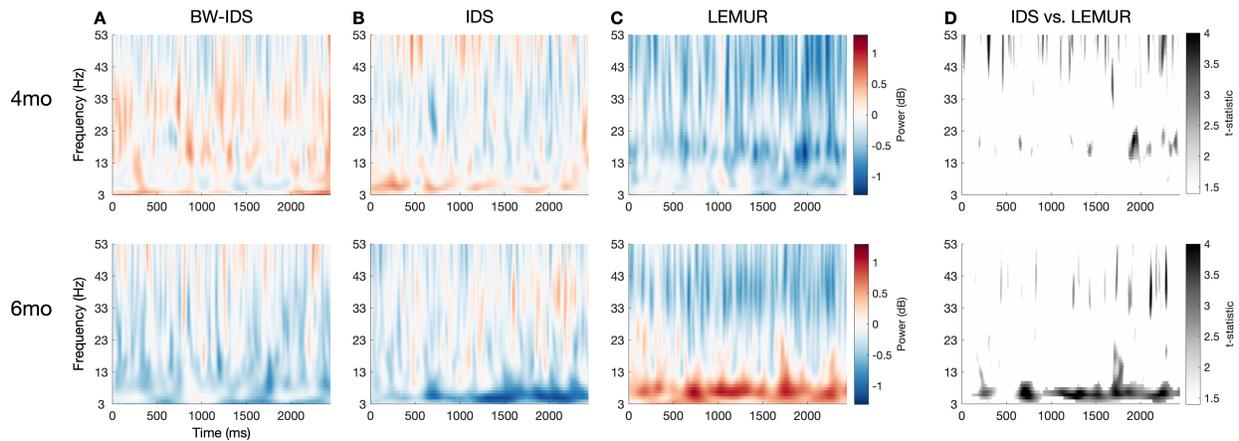
These findings shed new light on earlier behavioral results and provide novel insights into how infants begin to link the sounds they hear to the objects they encounter in their environment – well before they begin to speak or are even able to parse words from the stream of speech. The data provide a more nuanced understanding of how an initially privileged signal (non-human primate vocalizations) and a signal that is never linked to cognition (backwards speech) may have different effects on infant cognition, despite equivocal outcomes that are limited by the challenges inherent in assessing infant behavior. Furthermore, the results suggest that the origin and developmental tuning of a quintessentially human link between language and cognition may be guided by maturationally-sensitive systems of arousal and attention within the first six months of life.

## Figures

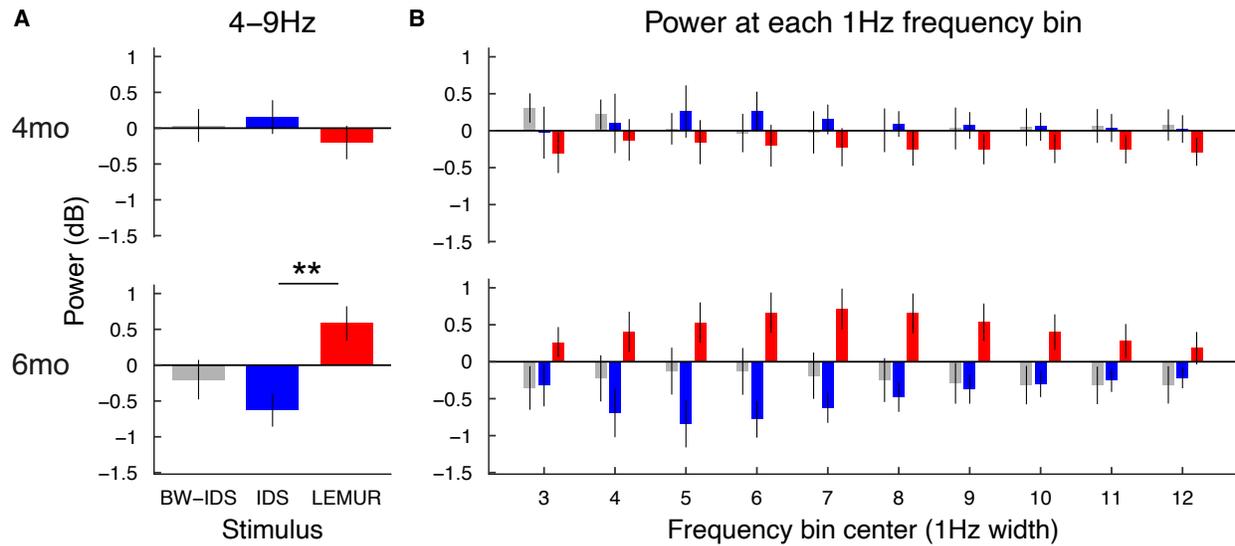
Figure 1



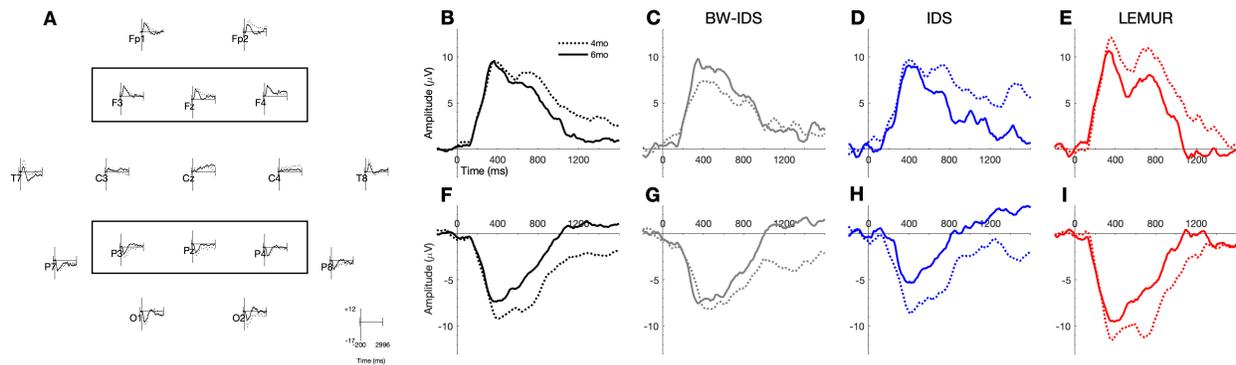
**Figure 1.** Neural responses were collected to three types of sounds: backwards infant-directed speech (BW-IDS), infant-directed speech (IDS), and non-human primate vocalizations (LEMUR). Nine different recordings were presented (3 different tokens of each stimulus type). Plotted here are example tokens of each stimulus type: (A) time-domain waveforms; (B) cochleograms revealing changes in frequency across time, extracted using *gammatonegram.m* (Ellis, 1998) to construct the weighting matrix to convert the time-frequency spectrograms into gammatone-filter approximations to match the ear's frequency sub-bands; and (C) pitch contours extracted from Praat (Boersma & Weenink, 2001). See Figure S1 for plots of all 9 stimuli tokens.

**Figure 2**

**Figure 2.** Event-related spectral perturbations (ERSPs) reveal the mean total (evoked and induced) changes in event-related EEG spectral power (in dB), in 4- (N=17; upper panels) and 6-month-olds (N=17; lower panels) elicited by (A) backwards speech (BW-IDS), (B) infant-directed speech (IDS), and (C) non-human primate vocalizations (LEMUR). ERSPs have been baseline corrected to the pre-stimulus period on a trial-by-trial basis for each frequency, such that 0 dB represents no change from baseline. ERSPs at Cz and Pz were comparable, so mean power at each time-frequency point were averaged. (D) Permutation t-tests were computed on each time-frequency point of the ERSPs elicited by IDS and LEMUR and masked to plot only significant ( $p < 0.05$ ) differences.

**Figure 3**

**Figure 3.** Infant alpha power was significantly different in response to human and non-human primate vocalizations in 6-month-olds, but not in 4-month-olds. Power (in dB), was averaged across the entire response time region (0-2500 ms) and across occipito-parietal electrodes (Cz and Pz), for 4- (upper panel) and 6-month-olds (lower panel). Power was (A) averaged across the literature-defined frequency range (4-9 Hz) for alpha at these ages and (B) at each frequency (1 Hz integer-centered bins) within the broader frequency region identified by the permutation tests from Figure 2D. \*\* =  $p < 0.01$ .

**Figure 4**

**Figure 4.** Event-related potentials (ERPs) were recorded in 4- (dotted line) and 6-month-olds (solid line) in response to the three signals: BW-IDS (gray), IDS (blue), and LEMUR (red). (A) Responses were averaged across stimuli (black lines), revealing a peak ~400 ms at (B-E) anterior (F3, Fz, F4) and (F-I) posterior (P3, Pz, P4) electrodes. The amplitude of this component decreased with age only in the posterior region of interest (F). Follow-up comparisons of the mean amplitude of this component (200-600 ms) for the responses to each stimulus type revealed that a this maturational reduction in the amplitude of this ERP component occurred only in response to IDS (H).

## Supplemental Information

### *Supplemental Results*

**Statistical analysis for single channels.** The statistics and figures reported in the main paper are computed on the average of the ERSPs from Cz and Pz electrodes because the responses at each of these individual electrodes were comparable. Here, the results from a single electrode (Pz) are reported.

**Developmental changes in alpha power at Pz.** In 4-month-olds, alpha (4-9 Hz) power differed as a function of stimulus type (RMANOVA:  $F_{(2,31)} = 3.159, p = 0.047$ ). Follow-up comparisons revealed that at both ages, alpha power did not change in response to BW-IDS for either age group, nor did this response change in magnitude across age groups in response to BW-IDS. In 4-month-olds, alpha activity in response to IDS ( $M = -0.133; SD = 1.50$ ) and LEMUR ( $M = -0.274; SD = 1.25$ ) also did not differ from baseline, and these responses were not different from one another. However, in 6-month-olds, alpha power differed significantly in response to IDS and LEMUR ( $t(16) = 2.281, p = 0.037, d = 0.370$ ; Figure S3A). Specifically, in response to IDS, there was a *reduction* in power in the 6-month-olds ( $M = -0.705; SD = 0.959$ ; one-sample t-test vs. pre-stimulus baseline:  $t(16) = 3.034, p = 0.008$ ) but these response magnitudes did not differ across age groups.

*Supplemental Tables***Table S1**

Recording	Duration (ms)	Pitch average (Hz)	Pitch range (Hz)
<b>IDS/BW-IDS 1</b>	3830	277.39	139.09-495.09
<b>IDS/BW-IDS 2</b>	4460	312.07	181.11-522.38
<b>IDS/BW-IDS 3</b>	4760	253.03	162.69-445.04
<b>LEMUR 1</b>	3480	334.49	75.62-446.81
<b>LEMUR 2</b>	3850	338.55	140.79-491.74
<b>LEMUR 3</b>	3320	309.49	138.45-501.75

**Table S1.** Recordings of infant-directed speech (IDS) and non-human primate vocalizations (LEMUR) were matched for stimuli parameters such as duration and average pitch. Backwards infant-directed speech (BW-IDS) were the IDS stimuli, time-reversed.

**Table S2**

Group	BW-IDS	IDS	LEMUR	TOTAL
4mos	28 (11.6)	27 (12.6)	27 ( 9.7)	83 (32.6)
6mos	30 ( 9.7)	30 (11.0)	29 ( 9.5)	89 (29.1)
<b>Total</b>	<b>29 (10.5)</b>	<b>29 (11.2)</b>	<b>28 (10.3)</b>	<b>86 (30.6)</b>

**Table S2.** Average number of artifact-free trials (M (SD)) are reported for each stimulus type, by age group. Each participant contributed at 15 least artifact-free trials of each stimulus type.

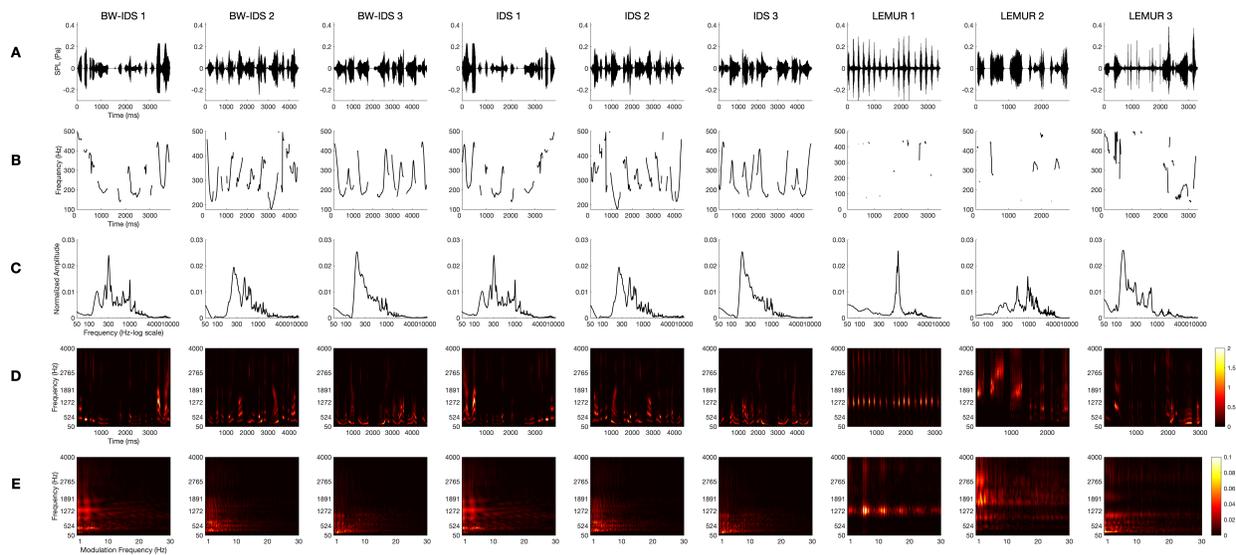
**Table S3**

Frequency (Hz)	IDS vs. LEMUR			
	4mo		6mo	
	<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>
3	0.490	0.631	1.512	0.150
<b>4</b>	0.364	0.721	<b>2.323</b>	<b>0.034*</b>
<b>5</b>	0.745	0.467	<b>2.926</b>	<b>0.010**</b>
<b>6</b>	1.035	0.320	<b>3.581</b>	<b>0.002**</b>
<b>7</b>	0.394	0.670	<b>2.669</b>	<b>0.012*</b>
<b>8</b>	1.149	0.267	<b>2.871</b>	<b>0.011*</b>
<b>9</b>	1.224	0.239	<b>2.382</b>	<b>0.030*</b>
10	0.168	0.869	0.808	0.431
11	1.095	0.290	1.579	0.134
12	1.137	0.273	1.281	0.218

**Table S3.** Paired t-test comparisons of alpha power in response to infant-directed speech (IDS) and non-human primate vocalizations (LEMUR) in 4-month-olds and 6-month-olds at each 1 Hz integer-centered frequency bin. Power was averaged across the 0-2500 ms post-stimulus onset time region and then averaged across centroparietal electrodes (Cz and Pz). Boldface and \* indicates a comparison of  $p < 0.05$  and the inclusion of that frequency band in the averaged alpha-band comparisons.

## Supplemental Figures

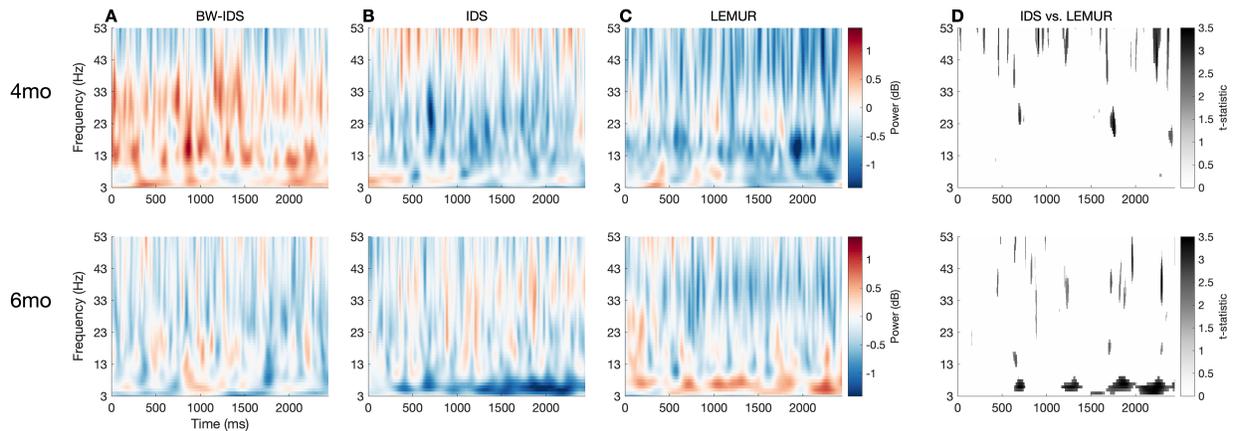
### Figure S1



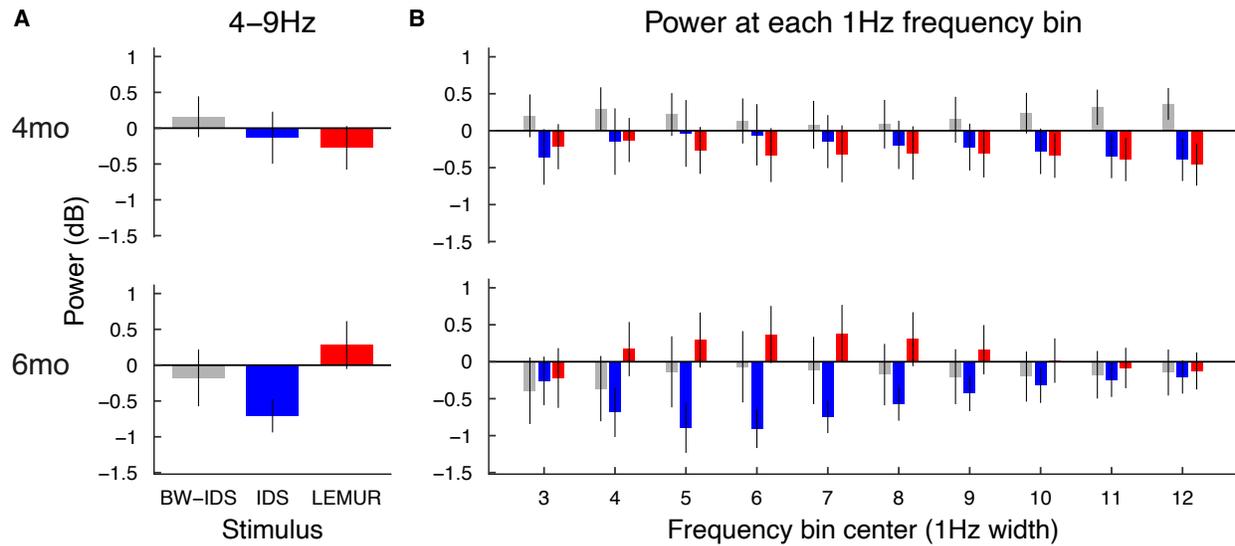
**Figure S1.** Neural responses were collected to three types of sounds: backwards infant-directed speech (BW-IDS), infant-directed speech (IDS), and non-human primate vocalizations (LEMUR). Nine different recordings were presented (3 different tokens of each stimulus type). (A) Time-domain waveforms; (B) Pitch contours extracted using *Praat* (Boersma & Weenink, 2001); (C) Amplitude spectrums; (D) Cochleograms revealing changes in frequency across time, extracted using *gammatonegram.m* (Ellis, 1998) to construct the weighting matrix to convert the

time-frequency spectrograms into gammatone-filter approximations to match the ear's frequency sub-bands; (E) Modulation spectrums at each cochlear band.

**Figure S2**



**Figure S2.** Event-related spectral perturbations (ERSPs) reveal the mean total (evoked and induced) changes in event-related EEG spectral power (in dB), in 4- (N=17; upper panels) and 6-month-olds (N=17; lower panels) elicited at electrode Pz by (A) backwards speech (BW-IDS), (B) infant-directed speech (IDS), and (C) non-human primate vocalizations (LEMUR). ERSPs have been baseline corrected to the pre-stimulus period on a trial-by-trial basis for each frequency, such that 0 dB represents no change from baseline. (D) Permutation t-tests were computed on each time-frequency point of the ERSPs elicited by IDS and LEMUR and masked to plot only significant ( $p < 0.05$ ) differences.

**Figure S3**

**Figure S3.** Infant alpha power at Pz was significantly different in response to human and non-human primate vocalizations in 6-month-olds, but not in 4-month-olds. Power (in dB), was averaged across the entire response time region (0-2500 ms), for 4- (upper panel) and 6-month-olds (lower panel). Power was (A) the literature-defined frequency range (4-9 Hz) for alpha at these ages and (B) at each frequency (1 Hz integer-centered bins) within the broader frequency region identified by the permutation tests from Figure S2D. \* =  $p < 0.05$ .

### **Author contributions**

DRP, JLV, ESN, DP, and SRW designed the study; KWC & DRP collected the data; KWC processed and analyzed the data; KWC and SRW drafted the manuscript; all authors provided input on the interpretation of the results and manuscript.

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