

Infant speech perception activates Broca's area: a developmental magnetoencephalography study

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Discriminative responses to tones, harmonics, and syllables in the left hemisphere were measured with magnetoencephalography in neonates, 6-month-old infants, and 12-month-old infants using the oddball paradigm. Real-time head position tracking, signal space separation, and head position standardization were applied to secure quality data for source localization. Minimum current estimates were calculated to characterize infants' cortical

activities for detecting sound changes. The activation patterns observed in the superior temporal and inferior frontal regions provide initial evidence for the developmental emergence early in life of a perceptual–motor link for speech perception that may depend on experience. *NeuroReport* 17:957–962 © 2006 Lippincott Williams & Wilkins.

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Introduction

Infants' speech perception skills have been well documented, not only behaviorally, but using neural measures [1–5]. Moreover, there is consensus on the developmental timeline of language-specific speech perception and language-specific speech production; both emerge towards the end of the first year of life [1,2,6,12].

In comparison to our detailed knowledge of the development of infant speech perception and production, considered independently, very few developmental studies explore the link between the two. What does exist is behavioral in nature; no investigations to date employ neural methods to examine a perceptual–motor link for speech in infants. Behavioral evidence of the emergence of a perceptual–motor link early in development can be adduced from studies showing that by 20 weeks of age (but not at 12 or 16 weeks), infants are capable of imitating vowels that are presented auditorily [7]. By 20 weeks of age, infants also show behavioral recognition of the correspondence between an auditory presentation of a vowel sound and the sight of a person producing that vowel, indicating that, by 20 weeks, infants can relate auditory and articulatory instantiations of speech [8].

Theorists have long argued that speech perception is mediated by the underlying motor representations of speech. The Motor Theory of speech perception, for example, held that the perception of speech sounds relies on a neural motor system that is innately present (see [9–11]

for discussion). Some developmental theorists have also argued that the transition in infants' perception of speech, occurring between 6 and 12 months, relies on their knowledge of articulatory organs and gestures [12].

At issue is whether the brain mechanisms underlying speech perception and those controlling speech motor systems are linked intrinsically or emerge over time as a function of experience. Work in this laboratory has led to the view that the connection between speech perception and speech production is forged developmentally through perceptual experience and vocal imitation [1,7]. A test of the hypothesis is provided by developmental data that indicate when in infancy the pure *perception* of speech syllables activates brain regions specialized for speech *production*.

Renewed interest in the link between perceptual and motor systems for speech has been fueled by the discovery of a 'mirror neuron' system in monkeys [13]. In human adults, activation of the left frontal motor (Broca's) area when listening to speech is thought to reflect articulatory and/or phonological coding during phonetic perception [14–17]. In monkeys, mirror neurons exist in a homologous area to Broca's area, prompting theoretical speculation that mirror neurons play a role in the neurological and evolutionary basis of language [10,13].

The aim of the present study was to investigate neural activation in infants when listening to speech and non-speech signals. We employed magnetoencephalography

(MEG) to examine the perceptual-motor link for speech at three ages in the first year of life: newborns, 6-month-old infants, and 12-month-old infants. The feasibility of infant MEG has been demonstrated in infants in this age range; previous studies have elicited the mismatch field (MMF) in infants, an automatic change detection response that, in adults, is sensitive to tone and phonetic changes [18–22]. To tease apart effects that are specific to speech sounds, we examined the neural generators of MMF in infants using speech and nonspeech signals varying in their resemblance to speech. We hypothesized that detection of a change in both speech and nonspeech stimuli should lead to significant activation in the superior temporal (ST) cortex, the brain region responsible for auditory analysis, but that inferior frontal (IF) activation, involved in speech motor analysis, would be unique to speech stimuli and nonspeech stimuli resembling speech, and, furthermore, would emerge only at later ages. A unique feature of our infant MEG measurements was the use of a continuous head position monitoring system that allowed us to calibrate infants' head position during the recordings [18].

Materials and methods

Subjects

Forty-three healthy full-term infants were tested, including eighteen newborns (eight boys, mean age 5.1 days), seventeen 6-month-olds (ten boys, mean age 6.6 months), and eight 12-month-olds (five boys, mean age 10.9 months). Informed consent was obtained from parents before the study.

Stimuli

Three types of stimuli were used: pure tones (tones), harmonic chords (harmonics), and speech syllables (syllables). The three types of stimuli were selected to range from nonspeech signals that did not resemble speech (tones) to nonspeech signals that resembled speech (harmonics), to speech itself (syllables). Previous studies have shown that these stimuli elicit sizable mismatch negativity (MMN) responses in neonates and older infants [18–24]. Tones were 100 ms long and differed in frequency – a 1000 Hz tone was used as the standard and a 1200 Hz tone as the deviant. Harmonics were three-sinusoidal partials of 500, 1000, and 1500 Hz and differed in duration – 100 ms was used as the standard and 40 ms as the deviant. The syllables were /ta/ (standard) and /pa/ (deviant), computer synthesized to be equivalent in all respects except the critical acoustic cues (formant transitions) that distinguish the two sounds. The syllable duration was fixed at 350 ms. The standard to deviant ratio was 85:15. The onset-to-onset interstimulus interval was 800 ms for tone and harmonics and 1200 ms for syllables.

Magnetoencephalography measurement

Infants' brain activities were measured using a 306-channel whole-head MEG system (Vectorview, Elekta Neuromag Oy, Helsinki, Finland) in a magnetically shielded room of the BioMag Laboratory at the Helsinki University Central Hospital. Although the system was designed primarily for adult measurements, infants' auditory responses have been successfully recorded in several studies [18,20,21].

All infants wore caps equipped with both Head Position Indicator coils and two nonmagnetic earphones; the stimuli

were delivered to both ears at approximately 65 dB. The infant's head location and orientation with respect to the device's coordinate system were recorded every 167 ms by a continuous head position monitoring system. During the measurement, newborns were laid with the left hemisphere facing downwards over a part of the MEG helmet that corresponded to the adult occipital region. The 6- and 12-month-old infants were seated in a safety seat and tested while an assistant was playing in front of them with toys. Mothers sat on infants' right side within their view.

For the nonspeech stimuli (tone and harmonics), epochs of 900-ms duration were digitized at 600 Hz (analog filter pass band 0.1–172 Hz; 100 ms prestimulus baseline). For syllables, the epoch duration was extended to 1300 ms. The presentation orders for the three types of stimuli were counterbalanced for each infant group. Sessions typically lasted approximately 50 min.

Analysis

On the basis of measurements from the real-time head-position tracking system, we rejected epochs that had head locations, at any point within the epoch, farther than 7 mm from the mean position of the epoch. Given that the side length of each sensor is 28 mm, this approach confirmed that at least half of the area of each sensor coil received the brain magnetic signal from the same head surface area within an epoch. We registered this mean head position as the head position for the entire epoch. Then, we applied the signal space separation method both to virtually move the infant's head position to the standardized position and to eliminate artifacts arising from sources outside the sensor array such as the heartbeat, limb movements, and other ambient magnetic disturbances. After rejecting undesirable trials, we converted the head position registered for each epoch into a virtual unified (standardized) position within the MEG sensor helmet for averaging across epochs. Considering the fact that the infants had different head sizes, in our standardized head location, the infant's left surface of the auditory region was moved to the same position and orientation across all ages. As we did not record MEG responses from the newborns' right hemisphere, we analyzed responses from the left hemisphere at all three ages. After signal space separation method processing, the averaged data were digitally lowpass filtered at 20 Hz; then direct-current offset during the prestimulus baseline was removed. Infants with fewer than 24 accepted epochs for the deviant or standard stimuli were eliminated from further analysis. To achieve an equivalent number of averages for the standard and the deviant, only the standards immediately before the deviant were used in averaging.

To obtain MMF source activity, we first performed minimum current estimation (Elekta-Neuromag MCE Version 1.4, an implementation of the minimum L1-norm estimate) based on the selected region of interests, in which 30 singular values were employed for regularization purposes [25,26]. The minimum current estimate analysis requires no a priori assumptions about the nature of the source current distribution and is considered to be more appropriate when the activity distribution is poorly known. Because the MRIs for the individual infants were not available, we used sphere head models of three sizes depending on infant age. For each infant, the source

estimates were calculated separately for the standard and the deviant stimuli at each time point. The MMF source estimates obtained by subtracting sources generated by standards from those by deviants were then averaged across infants. Therefore, activations for the auditory discriminative responses were derived from the subtraction of source activities rather than from the source estimation using the subtracted waveforms.

Results

Infants at all three ages showed significant activation when detecting sound changes for all stimuli (Figs 1a and 2a), and, as predicted from adult MEG studies on speech discrimination [22], the MMF generators were localized in the ST region.

Consistent with previous MEG studies [18,20,21], newborns exhibited no IF activation (Figs 1b and 2b). Intriguingly, however, we observed IF activities in the older infants.

Six-month-old infants showed activation at an early latency for the harmonics and at a late latency for the syllables (Fig. 2b). Twelve-month-old infants had early activations for the tones and harmonics and late activations for the harmonics and syllables. It is noteworthy that there was a coupling of late IF activation with late ST activation for speech but not for nonspeech (Fig. 2a and b).

Discussion

The present MEG results provide initial evidence for a left IF contribution to speech-sound discrimination starting as early as 6 months of age, and indicate a developmental trend toward stronger activation dependent on the type and complexity of stimuli. The speech activation patterns observed in the present study fit the timeline of the onset of imitation and canonical babbling, which begin around 5-6 months of age, both of which rely on the development of the connection between auditory cortical areas responsive to

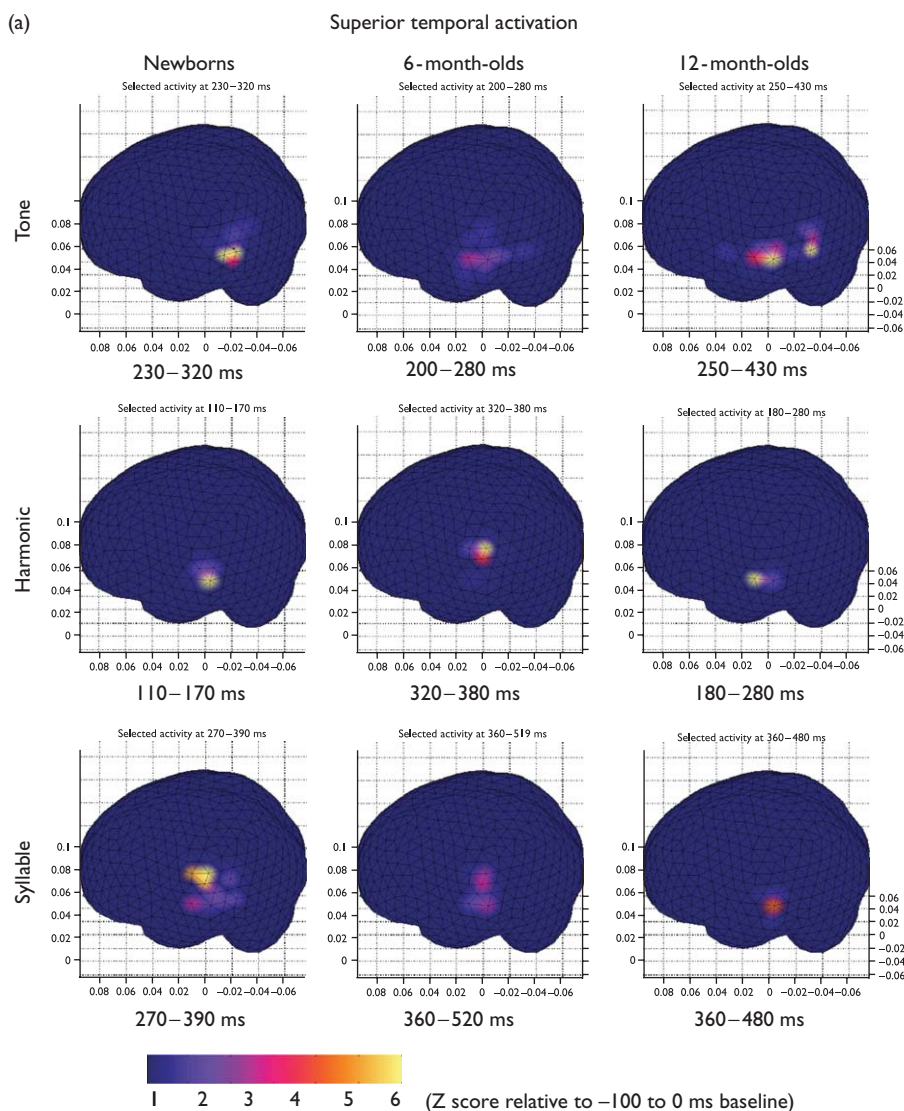


Fig. 1 Minimum current estimates for discriminative responses in regions of interest projected to the standard brain. (a) Left view of superior temporal activation. (b) Left view of inferior frontal activation. Samples from individuals are integrated, averaged, and plotted relative to the baseline for each age group and each type of stimulus. Time windows of activation are indicated underneath the standard mesh brain.

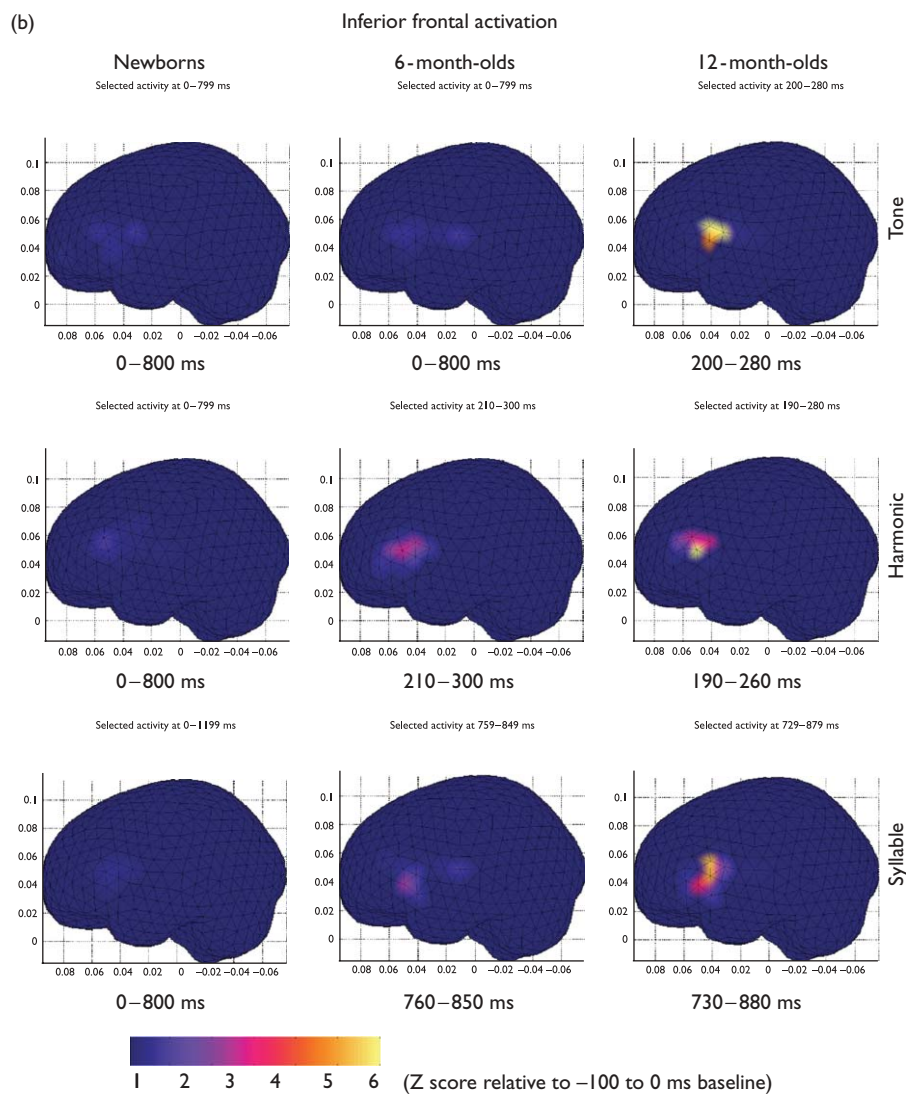


Fig. 1 – contd.

hearing speech and those responsible for speech motor movements [1,6–8]. The data also fit the timeline of the age at which developmental speech perception becomes language specific, which occurs between 6 and 12 months of age [1,2,12]. The emergence of activation in IF over time is less consistent with views that suggest that infants' initial perception of speech involves the recovery of innate articulatory gestures [9]. The results suggest that exposure to native-language speech over the first 12 months of life produces neural changes not only in auditory cortex but also in brain regions that subservise articulation, and in brain regions that allow a connection between the two systems. The emerging Broca's activation we observed in the first year of life may reflect maturation of a 'mirror neuron' system, which has been hypothesized to play a key role in the binding of action, perception, and language [10,13].

Some data exist to suggest that the IF region plays a role in the discrimination of nonspeech auditory signals that closely resemble speech; adult MEG data show IF activation for nonspeech tonal analogs of speech syllables [26]. In

infants, there is a distinction between the IF activities for speech and nonspeech – late IF activation showing temporal correspondence to ST activation is unique to speech. The development of this pattern of response with age needs further exploration with a variety of speech and nonspeech stimuli, especially nonspeech tonal analogs.

Our data point to an emerging left-hemisphere link between phonetic perception and activation of the motor system as early as 6 months of age and a strengthening of that connection as infants develop in the first year of life. We did not collect right-hemisphere data from the newborn infants, and therefore our analysis focused only on the developmental trajectory of ST and IF activations in the left hemisphere. Future studies will examine the bilateral neural substrates for speech perception as reported in many adult studies [10,14–17,26].

Conclusion

The activation patterns observed in the superior temporal and inferior frontal regions in newborns, 6-month-old

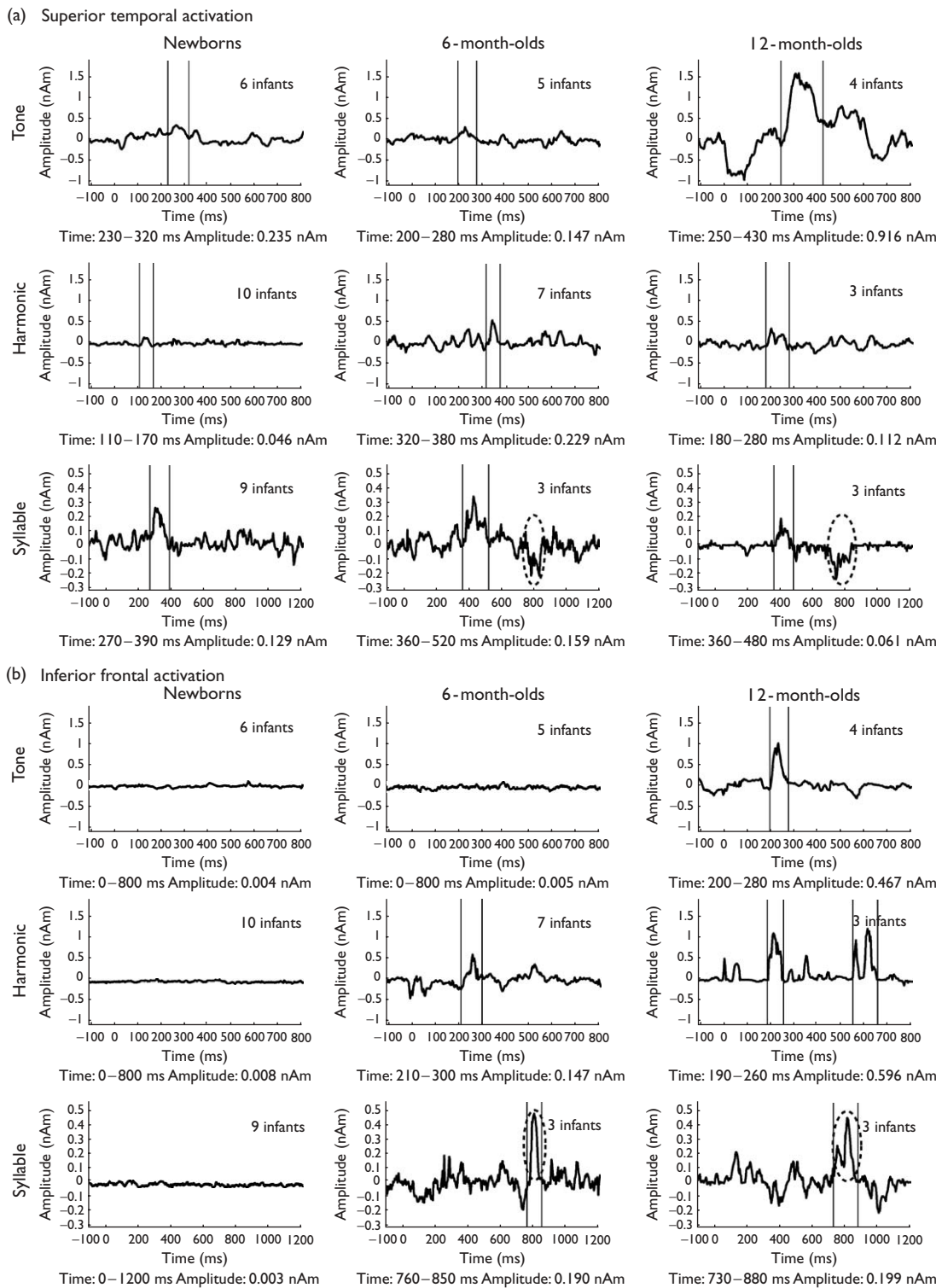


Fig. 2 Minimum current estimates (MCEs) for discriminative responses in regions of interest as a function of time. The graphs here correspond to the MCE activations in Fig. 1. The number of accepted infants in averaging is indicated above the amplitude curve for each stimulus type and each age group. Time window and mean amplitude of selected region of interest are marked under each graph. The late coupling of ST and IF activations for syllables is marked by dotted circles on the MCE amplitude curves.

infants, and 12-month-old infants provide initial evidence for an emerging perceptual–motor link for speech perception. The data suggest that speech motor areas are not

activated by the perception of speech initially, but require experience to bind perception and action in early speech development.

References

1. Kuhl PK, Conboy BT, Coffey-Corina S, Padden D, Rivera-Gaxiola M, Nelson T. Developmental phonetic perception: native language magnet theory expanded (NLM-e). *Philos Trans R Soc* (in press).
2. Werker JF, Tees RC. Cross-language speech perception: Evidence for perceptual reorganization during the first year of life. *Infant Behavior and Development* 2002; **25**:121–133.
3. Friedrich M, Friederici AD. Lexical priming and semantic integration reflected in the event-related potential of 14-month-olds. *NeuroReport* 2005; **16**:653–656.
4. Rivera-Gaxiola M, Klarman L, Garcia-Sierra A, Kuhl PK. Neural patterns to speech and vocabulary growth in American infants. *NeuroReport* 2005; **16**:495–498.
5. Mills DL, Prat C, Zangl R, Stager CL, Neville HJ, Werker JF. Language experience and the organization of brain activity to phonetically similar words: ERP evidence from 14- and 20-month-olds. *J Cogn Neurosci* 2004; **16**:1452–1464.
6. de Boysson-Bardies B, Vihman MM. Adaptation to language: evidence from babbling and first words in four languages. *Language* 1991; **67**:297–319.
7. Kuhl PK, Meltzoff A. Infant vocalizations in response to speech: vocal imitation and developmental change. *J Acoust Soc Am* 1996; **100**:2425–2438.
8. Kuhl PK, Meltzoff AN. The bimodal perception of speech in infancy. *Science* 1982; **218**:1138–1141.
9. Liberman AM, Whalen DH. On the relation of speech to language. *Trends Cogn Sci* 2000; **4**:187–196.
10. Pulvermuller F. Brain mechanisms linking language and action. *Nat Rev Neurosci* 2005; **6**:576–582.
11. Diehl RL, Lotto AJ, Holt LL. Speech perception. *Ann Rev Psychol* 2004; **55**:149–179.
12. Best CT, McRoberts GW. Infant perception of non-native consonant contrasts that adults assimilate in different ways. *Language Speech* 2003; **46**:183–216.
13. Rizzolatti G, Craighero L. The mirror–neuron system. *Ann Rev Neurosci* 2004; **27**:169–192.
14. Zatorre RJ, Evans AC, Meyer E, Gjedde A. Lateralization of phonetic and pitch discrimination in speech processing. *Science* 1992; **256**:846–849.
15. Paus T, Perry DW, Zatorre RJ, Worsley KJ, Evans AC. Modulation of cerebral blood flow in the human auditory cortex during speech: role of motor-to-sensory discharges. *Eur J Neurosci* 1996; **8**:2236–2246.
16. Gandour J, Wong D, Hsieh L, Weinzapfel B, Van Lancker D, Hutchins GD. A crosslinguistic PET study of tone perception. *J Cogn Neurosci* 2000; **12**:207–222.
17. Wang Y, Sereno JA, Jongman A, Hirsch J. fMRI evidence for cortical modification during learning of Mandarin lexical tone. *J Cogn Neurosci* 2003; **15**:1019–1027.
18. Cheour M, Imada T, Taulu S, Ahonen A, Salonen J, Kuhl PK. Magnetoencephalography (MEG) is feasible for infant assessment of auditory discrimination. *Exp Neurol* 2004; **190**:S44–S51.
19. Draganova R, Eswaran H, Murphy P, Huottilainen M, Lowery C, Preissl H. Sound frequency change detection in fetuses and newborns, a magnetoencephalographic study. *NeuroImage* 2005; **28**:354–361.
20. Huottilainen M, Kujala A, Hotakainen M, Shestakova A, Kushnerenko E, Parkkonen L, et al. Auditory magnetic responses of healthy newborns. *NeuroReport* 2003; **14**:1871–1875.
21. Kujala A, Huottilainen M, Hotakainen M, Lennes M, Parkkonen L, Fellman V, Näätänen R. Speech-sound discrimination in neonates as measured with MEG. *NeuroReport* 2004; **15**:2089–2092.
22. Näätänen R, Tervaniemi M, Sussman E, Paavilainen P, Winkler I. 'Primitive intelligence' in the auditory cortex. *Trends Neurosci* 2001; **24**:283–288.
23. Kuhl PK, Coffey-Corina S, Padden DM, Dawson G. Links between social and linguistic processing of speech in preschool children with autism: behavioral and electrophysiological measures. *Dev Sci* 2004; **7**:19–30.
24. Rivera-Gaxiola M, Silva-Pereyra J, Kuhl PK. Brain potentials to native and non-native speech contrasts in 7- and 11-month-old American infants. *Dev Sci* 2005; **8**:162–172.
25. Uutela K, Hämäläinen M, Somersalo E. Visualization of magnetoencephalographic data using minimum current estimates. *NeuroImage* 1999; **10**:173–180.
26. Zhang Y, Kuhl PK, Imada T, Kotani M, Tohkura Y. Effects of language experience: neural commitment to language-specific auditory patterns. *NeuroImage* 2005; **26**:703–720.