

Neural Substrates of Language Acquisition

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Key Words

brain measures, language development, speech perception, infants

Abstract

Infants learn language(s) with apparent ease, and the tools of modern neuroscience are providing valuable information about the mechanisms that underlie this capacity. Noninvasive, safe brain technologies have now been proven feasible for use with children starting at birth. The past decade has produced an explosion in neuroscience research examining young children's processing of language at the phonetic, word, and sentence levels. At all levels of language, the neural signatures of learning can be documented at remarkably early points in development. Individual continuity in linguistic development from infants' earliest responses to phonemes is reflected in infants' language abilities in the second and third year of life, a finding with theoretical and clinical implications. Developmental neuroscience studies using language are beginning to answer questions about the origins of humans' language faculty.

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INTRODUCTION

Language and neuroscience have deep historical connections. Neuroscientists and psycholinguists have mined the link between language and the brain since the neuropsychologist Paul Broca described his patient, nicknamed “Tan” for the only word he could utter after his devastating accident. “Tan” was found to have a brain lesion in what is now known as Broca’s area. This finding set the stage for “mapping” language functions in the brain.

Humans’ linguistic capacities have intrigued philosophers and empiricists for centuries. Young children learn language rapidly and effortlessly, transitioning from babbling at 6 months of age to full sentences by the age of 3, following a consistent developmental path regardless of culture. Linguists, psychologists, and neuroscientists have struggled to explain how children acquire language and ponder how such regularity is achieved if the acquisition mechanism depends on learning and environmental input. Studies of the infant brain using modern neuroscience techniques are providing the first glimpses of the mechanisms underlying the human capacity for language and are exam-

ining whether these mechanisms are specific to speech and to the human species.

Infants begin life with the ability to detect differences among all the phonetic distinctions used in the world’s languages (Eimas et al. 1971, Streeter 1976). Before the end of the first year they learn from experience and develop a language-specific phonetic capacity and detect native-language word forms, learning implicitly and informally (Kuhl et al. 1992, Saffran et al. 1996, Maye et al. 2002, Newport & Aslin 2004a). The goal of experiments on infants has been to determine whether the initial state and the learning mechanisms are speech specific and species specific.

Tests on nonhuman animals and in humans using nonspeech signals have examined the species specificity and domain specificity of the initial state. Animal tests on phonetic perception (Kuhl & Miller 1975) and on the learning strategies for words (Hauser et al. 2002, Newport & Aslin 2004b), as well as tests on human infants’ perception of nonspeech signals resembling speech (Jusczyk et al. 1977), suggested that general perceptual and cognitive abilities may account for infants’ initial speech perception abilities (Aslin et al. 1998, Saffran et al. 1999). These data promoted a shift in theoretical positions regarding language, one that advanced the domain-general hypothesis to describe the initial state more strongly than had been done previously (Jusczyk 1997, Kuhl 2000, Saffran 2003, Newport & Aslin 2004a,b).

Theoretical attention is increasingly focused on the mechanisms that underlie language learning. Experiments showed that infants’ initial learning from speech experience involves computational skills that are not restricted to speech or to humans (Saffran 2003, Newport & Aslin 2004a). However, there is new evidence to suggest that social interaction (Kuhl et al. 2003) and an interest in speech (Kuhl et al 2005a) may be essential in this process. The combination of computational and social abilities may be exclusive to humans (Kuhl 2007).

Ultimately, determining the specificity of humans’ language capacity will require functional measures of the infant brain. Brain

measures are ideal for language because infants simply have to listen—there is no need for them to make an overt response—as new brain technologies record the infant brain’s language processing. The promise that neural measures will provide the answer to the initial state query as well as the query regarding the specificity of the learning mechanisms has motivated intense work on the development of brain technologies that are safe and feasible with infants and young children.

The goal of this review is to examine the neuroscience techniques now in use with infants and young children and the data these techniques have produced. Neural substrates uncovered using these techniques now extend from the smallest building blocks of language—phonemes—to children’s encoding of early words and to studies examining children’s processing of the semantic and syntactic information in sentences. We review the neural signatures of learning at each of these levels of language. Using brain measures, we can now link infants’ processing at these various levels of language: Brain measures of perception of the elemental phonetic units in the first year are strongly associated with infants’ processing of words and syntax in the second and third year of life, showing continuity in the development of language. The studies suggest that exposure to language in the first year of life begins to set the neural architecture in a way that vaults the infant forward in the acquisition of language. Our goal is to explore the neural mechanisms that underlie this capacity.

WINDOWS TO THE YOUNG BRAIN

Noninvasive techniques that examine language processing in infants and young children have advanced rapidly (**Figure 1**) and include electroencephalography (EEG)/event-related potentials (ERPs), magnetoencephalography (MEG), functional magnetic resonance imaging (fMRI), and near-infrared spectroscopy (NIRS).

ERPs have been widely used to study speech and language processing in infants and young children (for reviews, see Kuhl 2004, Friederici 2005, Conboy et al. 2008). ERPs, part of the EEG, reflect electrical activity that is time-locked to the presentation of a specific sensory stimulus (for example, syllables, words) or a cognitive process (recognition of a semantic violation within a sentence or phrase). By placing sensors on a child’s scalp, the activity of neural networks firing in a coordinated and synchronous fashion in open field configurations can be measured, and voltage changes occurring as a function of cortical neural activity can be detected. ERPs provide precise time resolution (milliseconds), making them well suited for studying the high-speed and temporally ordered structure of human speech. ERP experiments can also be carried out in populations who, because of age or cognitive impairment, cannot provide overt responses. Spatial resolution of the source of brain activation is limited, however.

MEG is another brain-imaging technique that tracks activity in the brain with exquisite temporal resolution. The SQUID (superconducting quantum interference device) sensors located within the MEG helmet measure the minute magnetic fields associated with electrical currents produced by the brain when it is performing sensory, motor, or cognitive tasks. MEG allows precise spatial localization of the neural currents responsible for the sources of the magnetic fields. Cheour et al. (2004), Kujala et al. (2004), and Imada et al. (2006) have shown phonetic discrimination using MEG in newborns and infants in the first year of life. The newest studies employ sophisticated head-tracking software and hardware that allow correction for infants’ head movements and examine multiple brain areas as infants listen to speech (Imada et al. 2006). MEG (as well as EEG) techniques are completely safe and noiseless.

Magnetic resonance imaging (MRI) can be combined with MEG and/or EEG to provide static structural/anatomical pictures of

Phonemes: the contrasting element in word pairs that signals a difference in meaning for a specific language (e.g., rake-lake; far-fall)

Phonetic units: sets of articulatory gestures that constitute phoneme categories in a language

EEG: electroencephalography

Event-related potentials (ERPs): scalp recordings that measure electrical activity in the brain that can be time-locked to specific sensory stimuli or cognitive processes

Magnetoencephalography (MEG):

measures magnetic fields from electrical currents produced by the brain during sensory, motor, or cognitive tasks

Functional magnetic resonance imaging (fMRI):

measures changes in blood oxygenation levels that occur in response to neural firing, allowing precise localization of brain activity

Near-infrared spectroscopy (NIRS):

uses infrared light to measure changes in blood concentration as an indicator of neural activity throughout the cortex

Neuroscience techniques used with infants

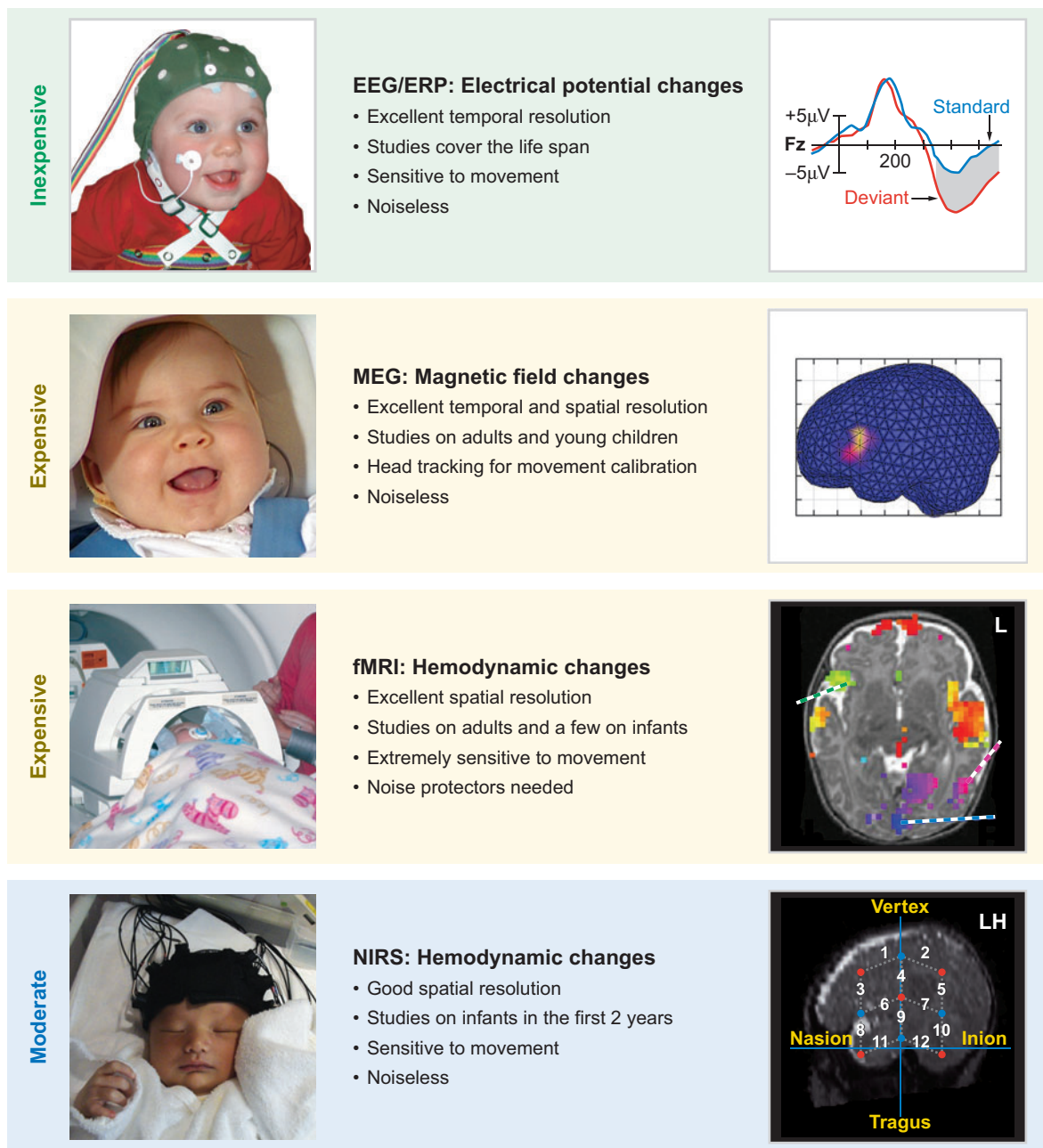


Figure 1

Four neuroscience techniques now used with infants and young children to examine their brain responses to linguistic signals.

the brain. Structural MRIs show maturational anatomical differences in brain regions across the life span. Individual or averaged MRIs can be used to superimpose the physiological activity detected by MEG or EEG to refine the spatial localization of brain activities.

fMRI is a popular method of neuroimaging in adults because it provides high spatial-resolution maps of neural activity across the entire brain (e.g., Gernsbacher & Kaschak 2003). Unlike EEG and MEG, fMRI does not directly detect neural activity, but rather detects the changes in blood oxygenation that occur in response to neural activation/firing. Neural events happen in milliseconds; however, the blood-oxygenation changes that they induce are spread out over several seconds, thereby severely limiting fMRI's temporal resolution. Few studies have attempted fMRI with children because the technique requires infants to be perfectly still and because the MRI device produces loud sounds making it necessary to shield infants' ears while delivering the sound stimuli (Dehaene-Lambertz et al. 2002, 2006).

Near-infrared spectroscopy (NIRS) also measures cerebral hemodynamic responses in relation to neural activity (Aslin & Mehler 2005). NIRS utilizes near-infrared light to measure changes in blood oxy- and deoxy-hemoglobin concentrations in the brain as well as total blood volume changes in various regions of the cerebral cortex. The NIRS system can determine the activity in specific regions of the brain by continuously monitoring blood hemoglobin level. Reports have begun to appear on infants in the first two years of life, testing infants' responses to phonemes as well as to longer stretches of speech such as sentences (Peña et al. 2002, Homae et al. 2006, Bortfeld et al. 2007, Taga & Asakawa 2007). As with other hemodynamic techniques such as fMRI, NIRS does not provide good temporal resolution. One of the strengths of this technique is that coregistration with other testing techniques such as EEG and MEG may be possible.

Each of these techniques is being applied to infants and young children as they listen to speech, from phonemes to words to sentences.

In the following sections, we review the findings at each level of language, noting the advances made using neural measures.

NEURAL SIGNATURES OF PHONETIC LEARNING

Perception of the phonetic units of speech—the vowels and consonants that constitute words—is one of the most widely studied behaviors in infancy and adulthood. Phonetic perception can be studied in children at birth and during development as they are bathed in a particular language, in adults from different cultures, in children with developmental disabilities, and in nonhuman animals. Phonetic perception studies conducted critical tests of theories of language development and its evolution. An extensive literature on developmental speech perception exists, and brain measures are adding substantially to our knowledge of phonetic development and learning (see Kuhl 2004, Werker & Curtin 2005).

Behavioral studies demonstrated that at birth young infants exhibit a universal capacity to detect differences between phonetic contrasts used in the world's languages (Eimas et al. 1971, Streeter 1976). This capacity is dramatically altered by language experience starting as early as 6 months for vowels and by 10 months for consonants. Two important changes occur at the transition in phonetic perception: Native language phonetic abilities significantly increase (Cheour et al. 1998; Kuhl et al. 1992, 2006; Rivera-Gaxiola et al. 2005b, Sundara et al. 2006) while the ability to discriminate phonetic contrasts not relevant to the language of the culture declines (Werker & Tees 1984, Cheour et al. 1998, Best & McRoberts 2003, Rivera-Gaxiola et al. 2005b, Kuhl et al. 2006).

By the end of the first year, the infant brain is no longer universally prepared for all languages, but instead primed to acquire the language(s) to which the infant has been exposed. What was once a universal phonetic capacity—phase 1 of development—narrows as learning proceeds in phase 2. This perceptual narrowing is widespread, affecting the perception of

SQUID:

superconducting quantum interference device, a mechanism used to measure extremely weak signals, such as subtle changes in the human body's electromagnetic energy field

Magnetic resonance imaging (MRI):

provides static structural and anatomical information, such as grey matter and white matter, in various regions of the brain

Critical period: a time in development, hypothesized to be determined by both maturation and learning during which learners are maximally sensitive to experience

Native language neural commitment (NLNC): learning shapes neural networks to detect the phonetic and word patterns that define a particular language, facilitating higher language learning

Mismatch negativity (MMN): reflects the brain's reaction to a change in an auditory stimulus

signs from American Sign Language (Krentz & Corina 2008, Klarman et al. 2007), as well as the perception of visual speech information from talking faces in monolingual (Lewkowicz & Ghazanfar 2006) and bilingual infants (Weikum et al. 2007). In all cases, perception changes from a more universal ability to one that is more restricted and focused on the properties important to the language(s) to which the infant is exposed. How learning produces this narrowing of perceptual abilities has become the focus of intense study because it demonstrates the brain's shaping by experience during a critical period in language development. Scientific understanding of the critical period is advancing (see Bongaerts et al. 1995 and Kuhl et al. 2005b for review). Data now suggest that an adult's difficulty in learning a second language is affected not only by maturation (Johnson & Newport 1989, Newport 1990, Neville et al. 1997, Mayberry & Lock 2003), but also by learning itself (Kuhl et al. 2005b).

Kuhl et al. (2005b, Kuhl et al. 2008) explored the relationship between the transition in phonetic perception and later language. This work examined a critical test stemming from the native language neural commitment (NLNC) hypothesis (Kuhl 2004). According to NLNC, initial native language experience produces changes in the neural architecture and connections that reflect the patterned regularities contained in ambient speech. The brain's "neural commitment" to native-language patterns has bidirectional effects: Neural coding facilitates the detection of more complex language units (words) that build on initial learning, while simultaneously reducing attention to alternate patterns, such as those of a nonnative language. This formulation suggests that infants with excellent native phonetic skills should advance more quickly toward language. In contrast, excellent nonnative phonetic abilities would not promote native-language learning. Nonnative skills reflect the degree to which the brain remains uncommitted to native-language patterns—phase 1 of development—when perception is universally good for all phonetic contrasts. In phase 1, infants are open to all possible

languages, and the brain's language areas are uncommitted. On this reasoning, infants who remain in phase 1 for a longer period of time, showing excellent discrimination of nonnative phonetic units, would be expected to show a slower progression toward language.

The NLNC hypothesis received support from both behavioral (Conboy et al. 2005, Kuhl et al. 2005b) and ERP tests on infants (Rivera-Gaxiola et al. 2005a,b; Silven et al. 2006; Kuhl et al. 2008). ERP studies conducted on infants (**Figure 2a**) used both a nonnative contrast (Mandarin /ʃ-tʃ^h/ or Spanish /t-d/) and a native contrast /p-t/. The results revealed that individual variation in both native and nonnative discrimination, measured neurally at 7.5 months of age, were significantly correlated with later language abilities. As predicted by the NLNC hypothesis, the patterns of prediction were in opposite directions (Kuhl et al. 2008). The measure used was mismatch negativity, which has been shown in adults to be a neural correlate of phonetic discrimination (Näätänen et al. 1997). The MMN-like ERP component was elicited in infants between 250–400 ms for both contrasts, tested in counterbalanced order (**Figure 2b**). Better neural discrimination of the native phonetic contrast at 7.5 months predicted advanced language acquisition at all levels—word production at 24 months, sentence complexity at 24 months, and mean length of utterance at 30 months of age. In contrast, greater neural discrimination of the nonnative contrast at the same age predicted less advanced language development at the same future points in time—lower word production, less complex sentences, and shorter mean utterance length. The behavioral (Kuhl et al. 2005b) and brain (Kuhl et al. 2008) measures, collected on the same infants, were highly correlated.

The growth of vocabulary clearly shows this relationship: Better discrimination of the native contrast resulted in faster vocabulary growth (**Figure 2c, left column**), whereas better discrimination of the nonnative contrast resulted in slower vocabulary growth (**Figure 2c, right column**). Children's vocabulary growth was measured from 14 to 30 months and was

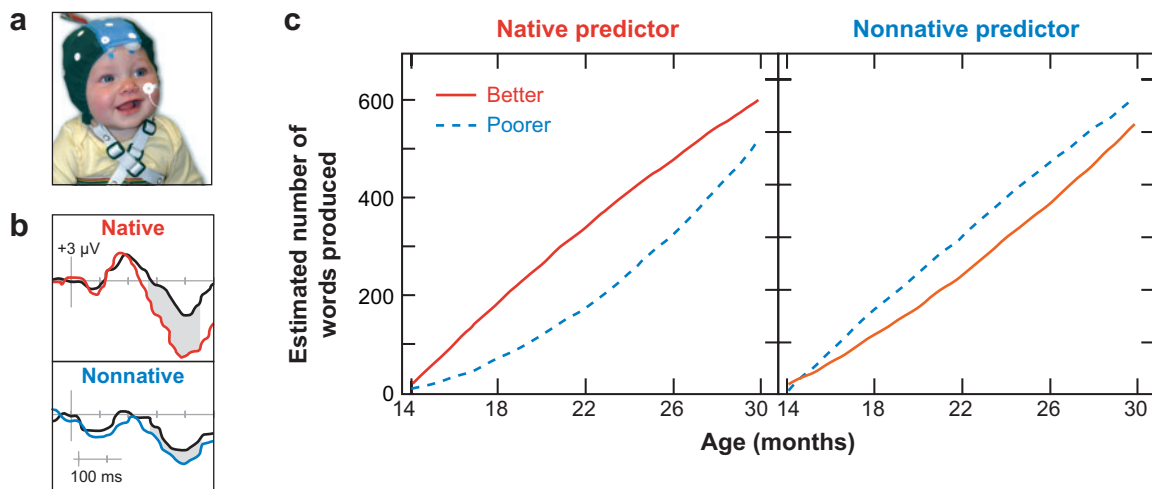


Figure 2

(a) A 7.5-month-old infant wearing an ERP electrocap. (b) Infant ERP waveforms at one sensor location (CZ) for one infant are shown in response to a native (English) and nonnative (Mandarin) phonetic contrast at 7.5 months. The mismatch negativity (MMN) is obtained by subtracting the standard waveform (black) from the deviant waveform (English = red; Mandarin = blue). This infant's response suggests that native-language learning has begun because the MMN negativity in response to the native English contrast is considerably stronger than that to the nonnative contrast. (c) Hierarchical linear growth modeling of vocabulary growth between 14 and 30 months for MMN values of +1SD and -1SD on the native contrast at 7.5 months (*c, left*) and vocabulary growth for MMN values of +1SD and -1SD on the nonnative contrast at 7.5 months (*c, right*). Analyses show that both contrasts predict vocabulary growth but that the effects of better discrimination are reversed for the native and nonnative contrasts. (From Kuhl et al. 2008)

examined using hierarchical linear growth curve modeling (Raudenbush et al. 2005). Analyses show that both native and nonnative discrimination at 7.5 months are significant predictors of vocabulary growth, but also that the effects of good phonetic discrimination are reversed for the native and nonnative predictors. A study of Finnish 11-month-old infants replicated this pattern using Finnish and Russian contrasts (Silven et al. 2006).

Rivera-Gaxiola and colleagues (2005a) demonstrated a similar pattern of prediction using a different nonnative contrast. They recorded auditory ERP complexes in 7- and 11-month-old American infants in response to both Spanish and English voicing contrasts. They found that infants' responses to the nonnative contrast predicted the number of words produced at 18, 22, 25, 27, and 30 months of age (Rivera-Gaxiola et al. 2005a). Infants showing better neural discrimination (larger negativities) to the nonnative contrast at 11 months of age produced significantly fewer words at

all ages when compared with infants showing poorer neural discrimination of the nonnative contrast. Thus in both Kuhl et al. (2005b, 2008) and Rivera-Gaxiola et al. (2005a), better discrimination of a nonnative phonetic contrast was associated with slower vocabulary development. Predictive measures now demonstrate continuity in development from a variety of early measures of pre-language skills to measures of later language abilities. Infants' early phonetic perception abilities (Tsao et al. 2004; Kuhl et al. 2005b, 2008; Rivera-Gaxiola et al. 2005a), their pattern-detection skills for speech (Newman et al. 2006), and their processing efficiency for words (Fernald et al. 2006) have all been linked to advanced later language abilities. These studies form bridges between the early precursors to language in infancy and measures of language competencies in early childhood that are important to theory building as well as to understanding clinical populations with developmental disabilities involving language.

THE ROLE OF SOCIAL FACTORS IN EARLY LANGUAGE LEARNING

Although studies have shown that young infants' computational skills assist language acquisition at the phonological and word level (Saffran et al. 1996, Maye et al. 2002), recent data suggest that another component, social interaction, plays a more significant role in early language learning than previously thought, at least in natural language-learning situations (Kuhl et al. 2003, Kuhl 2007, Conboy et al. 2008). Neuroscience research that reveals the source of this interaction between social and linguistic processing will be of future interest.

The impact of social interaction on speech learning was demonstrated in a study investigating whether infants are capable of phonetic and word learning at nine months of age from natural first-time exposure to a foreign language. Mandarin Chinese was used in the first foreign-language intervention experiment (Kuhl et al. 2003). Infants heard 4 native speakers of Mandarin (male and female) during 12 25-min sessions of book reading and play across a 4–6 week period. A control group of infants also came into the laboratory for the same number and variety of reading and play sessions but heard only English. Two additional groups were exposed to the identical Mandarin material over the same number of sessions via either standard television or audio-only presentation. After exposure, Mandarin syllables that are not phonemic in English were used to test infant learning using both behavioral (Kuhl et al. 2003) and brain (Kuhl et al. 2008) tests.

Infants learned from live exposure to Mandarin tutors, as shown by comparisons with the English control group, indicating that phonetic learning from first-time exposure could occur at nine months of age. However, infants' Mandarin discrimination scores after exposure to television or audio-only tutors were no greater than those of the control infants who had not experienced Mandarin at all (Kuhl et al. 2003) (**Figure 3**). Learning in the live condition was robust and durable. Behavioral tests of infant learning were conducted 2–12 days (me-

dian = 6 days) after the final language-exposure session, and the ERP tests were conducted between 12 and 30 days (median = 15 days) after the final exposure session, with no observable differences in infant performance as a function of the delay.

In further experiments, 9-month-old English-learning infants were exposed to Spanish, and ERPs were used to test learning of both Spanish phonemes and Spanish words after 12 exposure sessions (Conboy & Kuhl 2007). The results showed learning of both Spanish phonemes and words. Moreover, the study was designed to test the hypothesis that social interaction during the exposure sessions would predict the degree to which individual infants learned, and this hypothesis was confirmed. Social factors, such as overall attention during the exposure sessions, and specific measures of shared visual attention between the infant and tutor predicted the degree to which individual infants learned Spanish phonemes and words (Conboy et al. 2008).

Social interaction may be essential for learning in complex natural language-learning situations—the neurobiological mechanisms underlying the evolution of language likely utilized the kinds of interactional cues available only in a social setting (Kuhl 2007). Humans are not the only species in which social interaction plays a significant role in communicative learning. In other species, such as songbirds, social contact can be essential for communicative learning (see e.g., Immelmann 1969, Baptista & Petrinovich 1986, Brainard & Knudsen 1998, Goldstein et al. 2003).

The importance of social interaction in human language learning is illustrated by its impact on children with autism. A lack of interest in listening to speech signals is correlated with aberrant neural responses to speech and with the severity of autism symptoms, indicating the tight coupling between language and social interaction (Kuhl et al. 2005a). Typically developing infants prefer speech even from birth (Vouloumanos & Werker 2004), and particularly infant-directed (ID) speech (see sidebar on

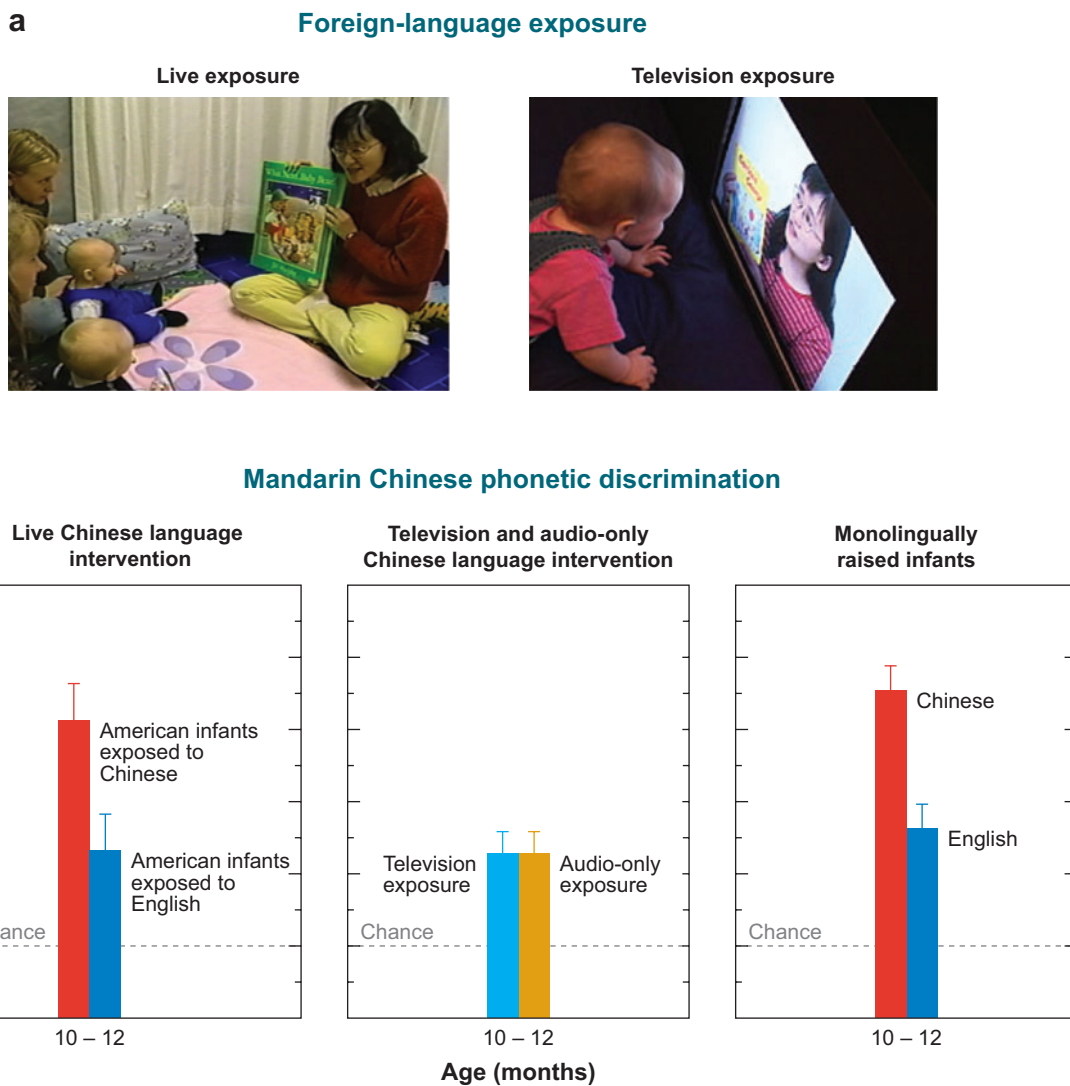


Figure 3

(a) Effects of natural foreign-language intervention using Mandarin Chinese at 9 months of age. Infants experience either live exposure or a television presentation. (b) Live exposure (*left panel*) produced significant learning of a Mandarin Chinese phonetic contrast when compared with a control group exposed only to English, whereas television exposure or audio-alone exposure did not produce learning (*middle panel*). Performance after 12 live exposure sessions beginning at 9 months produced performance in American infants (*left panel*) that equaled that of monolingual Taiwanese infants who had listened to Mandarin for 11 months (*right panel*) (from Kuhl et al. 2003).

Motherese) (Fernald & Kuhl 1987, Grieser & Kuhl 1988).

The data on phonetic and word learning from a foreign language indicate that at the earliest stages of language learning, social factors play a significant role, perhaps by gating the computational mechanisms underlying

language learning (Kuhl 2007). Interaction between the brain mechanisms underlying linguistic and social processing will be of strong interest in the future. Neuroscience research focused on shared neural systems for perception and action has a long tradition in speech, and interest in “mirror systems” for social

MOTHERESE

Adults use a special speech “register,” called “motherese,” when addressing infants and children. Motherese has a unique acoustic signature: It is slower, has a higher average pitch, and contains exaggerated pitch contours (Fernald & Simon 1984). Typically developing infants and children (Fernald & Kuhl 1987), though not children with autism (Kuhl et al. 2005a), prefer Motherese over adult-directed speech or a nonspeech analog signal when given a choice. Motherese exaggerates the phonetic differences in speech, both for vowels (Kuhl et al. 1997, Burnham et al. 2002) and for consonants (Liu et al. 2007), making the words contained in Motherese easier to discriminate for infants. Some evidence indicates that Motherese may aid language learners: Mothers who stretch the acoustic cues in phonemes to a greater extent in infant-directed speech early in life have infants who are better able to hear subtle speech distinctions when tested in the laboratory months later (Liu et al. 2003). Motherese also facilitates word recognition (Thiessen & Saffran 2003). Brain measures of infants’ responses to ID speech are enhanced, as shown by NIRS—more activation was seen in left temporal areas when infants were presented with ID speech as opposed to backward speech or silence (Peña et al. 2002), and also when six- to nine-month-old infants were presented with audio-visual ID speech (Bortfeld et al. 2007).

cognition (Kuhl & Meltzoff 1996, Meltzoff & Decety 2003, Rizzolatti & Craighero 2004, Pulvermüller 2005, Rizzolatti 2005, Kuhl 2007) has reinvigorated this tradition (see sidebar on Mirror Systems and Speech). Neuroscience studies using speech and imaging techniques have the capacity to examine this question in infants from birth (e.g., Imada et al. 2006).

NEURAL SIGNATURES OF WORD LEARNING

A sudden increase in vocabulary typically occurs between 18 and 24 months of age—a “vocabulary explosion” (Ganger & Brent 2004, Fernald et al. 2006)—but word learning begins much earlier. Infants show recognition of their own name at four and a half months (Mandel et al. 1995). At six months, infants recognize their own names or the word Mommy as a word seg-

mentation cue (Bortfeld et al. 2005) and look appropriately to pictures of their mothers or fathers when hearing “Mommy” or “Daddy” (Tincoff & Jusczyk 1999). By 7 months, infants listen longer to passages containing words they previously heard rather than passages containing words they have not heard (Jusczyk & Hohne 1997), and by 11 months infants prefer to listen to words that are highly frequent in language input over infrequent words (Halle & de Boysson-Bardies 1994).

One question has been how infants recognize potential words in running speech given that speech is continuous and has no acoustic breaks between words (unlike the spaces between words in written text). Behavioral studies indicate that by 8 months, infants use various strategies to identify potential words in speech. For example, infants treated adjacent syllables with higher transitional probabilities as word-like units in strings of nonsense syllables (Saffran et al. 1996, Saffran 2003, Newport & Aslin 2004a); real words contain higher transitional probabilities between syllables and this strategy would provide infants with a reliable cue. Infants also use the typical pattern of stress in their language to detect potential words. English, for example, puts emphasis on the first syllable, as in the word *BASEball*, whereas other languages, such as Polish, emphasize the second). English-learning infants treated syllables containing stress as the beginning of a potential word (Cutler & Norris 1988, Johnson & Jusczyk 2001, Nazzi et al. 2006, Hohle et al. 2008). Both transitional probabilities between adjacent syllables and stress cues thus provide infants with clues that allow them to identify potential words in speech.

How is early word recognition evidenced in the brain? ERPs in response to words index word familiarity as early as 9 months of age and word meaning by 13–17 months of age: ERP studies have shown differences in amplitude and scalp distributions for components related to words that are known to the child vs. those that are unknown to the child (Molfese 1990; Molfese et al. 1990, 1993; Mills et al. 1993, 1997, 2005; Thierry et al. 2003).

Toddlers with larger vocabularies showed a larger N200 for known words vs. unknown words at left temporal and parietal electrode sites. In contrast, children with smaller vocabularies showed brain activation that was more broadly distributed (Mills et al. 1993). This distributional difference, with more focalized brain activation linked to greater vocabulary skill, also distinguished typically developing preschool children from preschool children with autism (Coffey-Corina et al. 2007). Increased focalization of brain activation has also been seen in adults for native- as opposed to nonnative phonemes and words in MEG studies (Zhang et al. 2005). This indicates that focal activation has the potential to index language experience and proficiency not just in childhood, but over the life span.

Mills et al. (2005) used ERPs in 20-month-old toddlers to examine new word learning. The children listened to known and unknown words and to nonwords that were phonotactically legal in English. ERPs were recorded as the children were presented with novel objects paired with the nonwords. After the learning period, ERPs to the nonwords that had been paired with novel objects were shown to be similar to those of previously known words, suggesting that new words may be encoded in the same neural regions as previously learned words.

ERP studies on German infants reveal the development of word-segmentation strategies based on the typical stress patterns of German words. When presented with bisyllabic strings with either stress on the first syllable (typical in German) or the second syllable, infants who heard first-syllable stress patterns embedded in a string of syllables showed the N200 ERP component similar to that elicited in response to a known word, whereas infants presented with the nonnative stress pattern showed no response (Weber et al. 2004). The data suggest that German infants at this age are applying learned stress rules about their native language to segment nonsense speech strings into word-like units, in agreement with behavioral data (Hohle et al. In press).

MIRROR SYSTEMS AND SPEECH

The field has a long tradition of theoretical linkage between perception and action in speech. The Motor Theory (Liberman et al. 1967) and Direct Realism (Fowler 1986) posited close interaction between speech perception and production. The discovery of mirror neurons in monkeys that react both to the sight of others' actions and to the same actions they themselves produced (Rizzolatti et al. 1996, 2002; Gallese 2003) has rekindled interest in a potential mirror system for speech, as has work on the origins of infant imitation (Meltzoff & Moore 1997). Liberman & Mattingly (1985) view the perception-action link for speech as potentially innate, whereas Kuhl & Meltzoff (1982, 1996) view it as forged early in development through experience. Two new infant studies shed light on the developmental issue. Imada et al. (2006) used magnetoencephalography (MEG) to study newborns, 6-month-old infants, and 12-month-old infants while they listened to nonspeech, harmonics, and syllables (**Figure 4**). Dehaene-Lambertz et al. (2006) used fMRI to scan three-month-old infants while they listened to sentences. Both studies showed activation in brain areas responsible for speech production (the inferior frontal, Broca's area) in response to auditorily presented speech. Imada et al. reported synchronized activation in response to speech in auditory and motor areas at 6 and 12 months, and Dehaene-Lambertz et al. reported activation in motor speech areas in response to sentences in three-month-olds. Is activation of Broca's area to the pure perception of speech present at birth? Newborns tested by Imada et al. showed no activation in motor speech areas for any signals, whereas auditory areas responded robustly to all signals, suggesting that perception-action linkages for speech develop by three months of age as infants produce vowel-like sounds. Further work must be done to determine whether binding of perception and action requires experience. Using the tools of modern neuroscience, we can now ask how the brain systems responsible for speech perception and production forge links in early development, a necessary step for communication development.

INFANTS' EARLY LEXICONS

Young children's growing lexicons must code words in a way that distinguishes them from one another. Words—produced by different speakers, at different rates, and in different contexts—have variations that are not relevant to word meaning. Infants have to code the

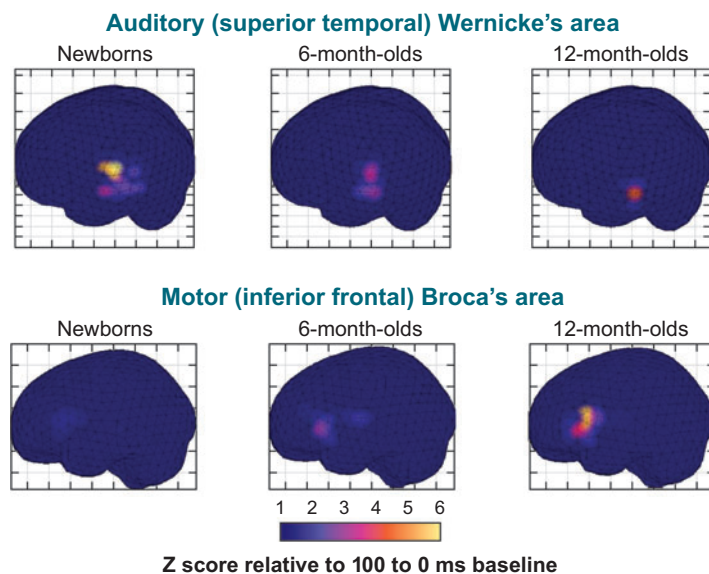


Figure 4

(*top*) Neuromagnetic signals were recorded in newborns, 6-month-old (shown) and 12-month-old infants in the MEG machine while listening to speech (shown) and nonspeech auditory signals. (*bottom*) Brain activation in response to speech recorded in auditory (*top row*) and motor (*bottom row*) brain regions showed no activation in the motor speech areas in the newborn in response to auditory speech, but increasing activity that was temporally synchronized between the auditory and motor brain regions was seen in 6- and 12-month-old infants when listening to speech (from Imada et al. 2006).

critical features of words in sufficient detail to allow them to be distinguished.

One approach to this question is to test how children of different ages react to mispronounced words. Reactions to mispronunciations—examining whether children accept “tup” for cup or “bog” for dog—provide information about the level of phonological detail in their mental representations of words.

Studies across languages showed that by one year of age infants do not accept mispronunciations of common words (Jusczyk & Aslin 1995, Fennell & Werker 2003), words in stressed syllables (Vihman et al. 2004), or monosyllabic words (Swingle 2005), indicating that their representations of these words are well-specified by that age. Other studies using visual fixation of two targets (e.g., apple and ball) while one is named (“Where’s the ball?”) indicated that between 14 and 25 months of age children’s tendencies to fixate the target item when it is mispronounced diminishes over time (Swingle & Aslin 2000, 2002; Bailey & Plunkett 2002, Ballem & Plunkett 2005).

Studies also indicate that when learning new words, 14-month-old children’s phonological skills are taxed. Stager & Werker (1997) demonstrated that 14-month-old infants failed to learn new words when similar-sounding phonetic units were used to distinguish those words (“bih” and “dih”) but did learn if the two new words were distinct phonologically (“leef” and “neem”). By 17 months of age, infants learned to associate similar-sounding nonsense words with novel objects (Bailey & Plunkett 2002, Werker et al. 2002). Infants with larger vocabularies succeeded on this task even at the younger age, suggesting that infants with greater phonetic learning skills acquire new words more rapidly. This is consistent with studies showing that children with better native-language phonetic learning skills showed advanced vocabulary development (Tsao et al. 2004; Kuhl et al. 2005b, 2008; Rivera-Gaxiola et al. 2005a).

ERP methods corroborated these results. Mills et al. (2004) compared children’s ERP responses when responding to familiar words that were either correctly pronounced or mispronounced, as well as some nonwords (**Figure 5**). At the earliest age tested, 14 months, a negative ERP component (N200–400) distinguished known vs. dissimilar nonsense words (“bear” vs. “kobe”) but not known vs. phonetically similar nonsense words (“bear” vs. “gare”). By 20 months, this same ERP component distinguished correct pronunciations, mispronunciations, and nonwords, supporting the idea that

between 14 and 20 months, children’s phonological representations of early words become increasingly detailed.

Other evidence of early processing limitations stems from infants’ failure to learn a novel word when its auditory label closely resembles a word they already know (“gall,” which closely resembles “ball”), suggesting lexical competition effects (Swingle & Aslin 2007). How phonetic and word learning interact—and whether the progression is from phonemes to words, words to phonemes, or bi-directional—is a topic of strong interest that will be aided by using neuroscientific methods.

Two recent models/frameworks of early language acquisition, the native language magnet theory, expanded (NLM-e) (Kuhl et al. 2008) and the processing rich information from multidimensional interactive representations (PRIMIR) framework (Werker & Curtin 2005), suggest that phonological and word learning bidirectionally influence one another. According to NLM-e, infants with better phonetic learning skills advance more quickly toward language because phonetic skills assist phonotactic pattern and word learning (Kuhl et al. 2005b, 2008). At the same time, the more words children learn, the more crowded lexical space becomes, pressuring children to attend to the phonetic units that distinguish words from one another (see Swingle & Aslin 2007 for discussion). Further studies examining both phoneme and word learning in the same children will help address this issue.

NEURAL SIGNATURES OF EARLY SENTENCE PROCESSING

To understand sentences, a child must have exquisite phonological abilities that allow segmentation of the speech signal into words, and the ability to extract word meaning. In addition, the relationship among words composing the sentence—between a subject, its verb, and its accompanying object—must be deciphered to arrive at a full understanding of the sentence. Human language is based on the ability

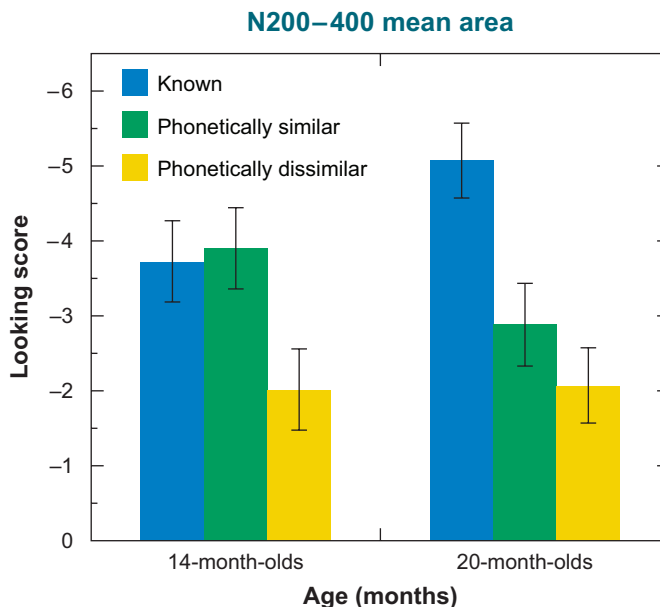


Figure 5

ERP responses to known words, phonetically similar nonsense words, and phonetically distinct nonsense words at 14- and 20-months of age. At 14 months, infants’ brain responses are indistinguishable for known and similar-sounding nonsense words, although they were distinct for dissimilar nonsense words. By 20 months, infants’ brain responses are distinct for all three types of words (from Mills et al. 2005).

to process hierarchically structured sequences (Friederici et al. 2006).

Electrophysiological components of sentence processing have been recorded in children and contribute to our knowledge of when and how the young brain decodes syntactic and semantic information in sentences. In adults, specific neural systems process semantic vs. syntactic information within sentences, and the ERP components elicited in response to syntactic and semantic anomalies are well established (Figure 6). For example, a negative ERP wave occurring between 250 and 500 ms that peaks around 400 ms, referred to as the N400, is elicited to semantically anomalous words in sentences (Kutas 1997). A late positive wave peaking at ~600 ms and that is largest at parietal sites, known as the P600, is elicited in response to syntactically anomalous words in sentences (Friederici 2002). And a negative wave over frontal sites between 300 and 500 ms, known

Native language magnet model, expanded (NLM-e): proposes that early language experience shapes neural architecture, affecting later language learning, and both computational and social abilities affect learning

Processing rich information from multidimensional interactive representations (PRIMIR): a framework for early language that links levels of processing and describes their interaction

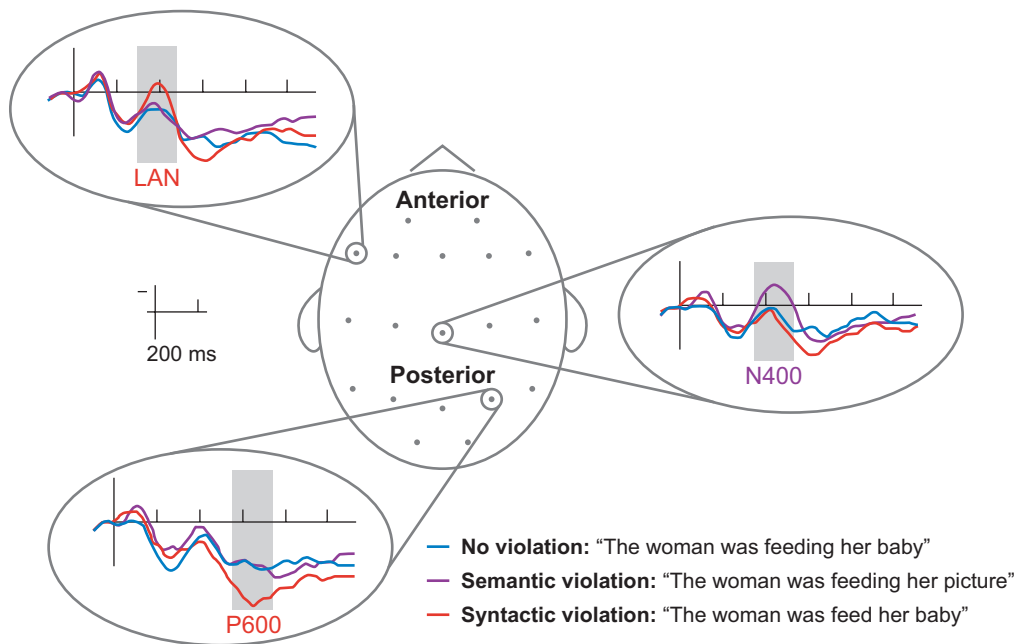


Figure 6

Distribution and polarity of the ERP responses to normal sentences and sentences with either semantic or syntactic anomalies in adults (from Kuhl & Damasio 2008).

as the late anterior negativity (LAN), is elicited in response to syntactic and morphological violations (Friederici 2002).

Beginning in a child's second year of life, ERP data on sentence processing in children suggest that adult-like components can be elicited in response to violations in semantic and syntactic components, but that differences exist in the latencies and scalp distributions of these components in children vs. those in adults (Harris 2001; Oberecker et al. 2005; Friedrich & Friederici 2005, 2006; Silva-Pereyra et al. 2005a,b, 2007; Oberecker & Friederici 2006). Holcomb et al. (1992) reported the N400 in response to semantic anomaly in children from five years of age to adolescence; the latency of the response declined systematically with age (see also Neville et al. 1993, Hahne et al. 2004). Studies also show that syntactically anomalous sentences elicit the P600 in children between 7 and 13 years of age (Hahne et al. 2004).

Recent studies have examined these ERP components in preschool children. Harris

(2001) reported an N400-like effect in 36–38-month-old children; the N400 was largest over posterior regions of both hemispheres. Friedrich & Friederici (2005) observed an N400-like wave to semantic anomalies in 19- and 24-month-old German-speaking children.

Silva-Pereyra et al. (2005b) recorded ERPs in children between 36 and 48 months of age in response to semantic (“My uncle will blow the movie”) and syntactic anomalies (“My uncle will watching the movie”) when compared with control sentences. In both cases, the ERP effects in children were more broadly distributed and elicited at later latencies than in adults. In work with even younger infants (30-month-olds), Silva-Pereyra et al. (2005a) used the same stimuli and observed late positivities distributed broadly posteriorly in response to syntactic anomalies and anterior negativities in response to semantically anomalous sentences. In both cases, children's latencies were longer than those seen in older children and adults (**Figure 7**), a pattern seen repeatedly and

Phonotactic

patterns: sequential constraints governing permissible strings of phonemes in a given language. Each language allows different sequences

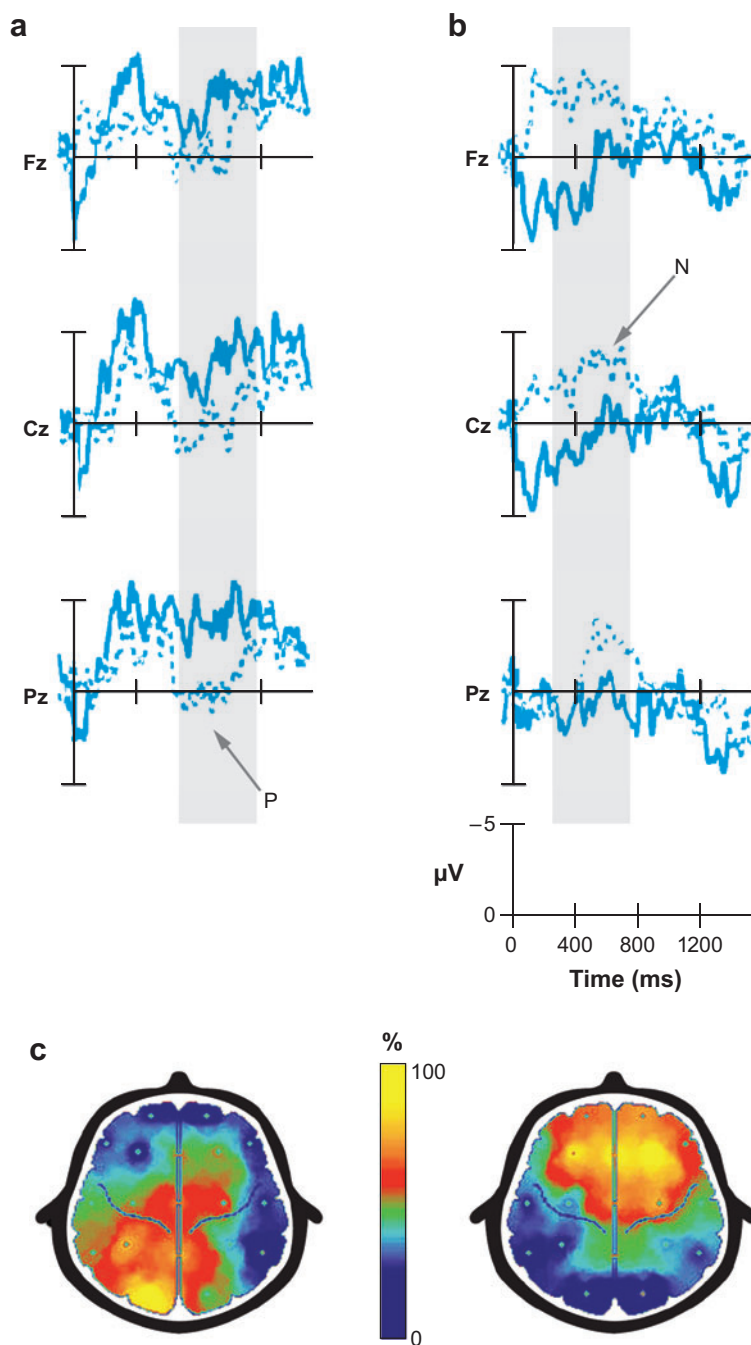


Figure 7

ERP waveforms elicited from 36- and 48-month-old children in response to sentences with syntactic (*a*) or semantic (*b*) violations. Children's ERP responses resemble those of adults (see **Figure 6**) but have longer latencies and are more broadly distributed (*c*) (from Silva-Pereyra et al. 2005b).

attributed to the immaturities of the developing neural mechanisms.

Syntactic processing of sentences with semantic content information removed—“jabberwocky sentences”—has also been tested using ERP measures with children. Silva-Pereyra and colleagues (2007) recorded ERPs to phrase structure violations in 36-month-old children using sentences in which the content words were replaced with pseudowords while grammatical function words were left intact. The pseudowords differed from real words by only a few phonemes: “My uncle watched a movie about my family” (control sentence) became “My macle platched a flovie about my garily” (jabberwocky sentence without violation) and “My macle platched about a flovie my garily” (jabberwocky sentence with phrase structure violation). The ERP components elicited to the jabberwocky phrase structure violations differed as compared with the same violations in real sentences. Two negative components were observed: one from 750–900 ms and the other from 950–1050 ms, rather than the positivities seen in response to phrase structure violations in real sentences in the same children. Jabberwocky studies with adults (Munte et al. 1997, Canseco-Gonzalez 2000, Hahne & Jescheniak 2001) have also reported negative-going waves for jabberwocky sentences, though at much shorter latencies.

Recent studies on language and pre-reading skills in 5-year old children prior to their entry into school (Raizada et al. 2008), as well as in first- through third-grade children (Noble et al. 2006, 2007), indicate that in healthy, socio-economically diverse populations assessed with various linguistic, cognitive, and environmental measures, significant correlations exist between low socio-economic status and behavioral and brain (fMRI) measures of language skills. Future work on the complex socio-economic factors that potentially mediate language and reading skills in children could potentially lead to interventions that would improve the skills needed for reading prior to the time children enter school.

BILINGUAL INFANTS: TWO LANGUAGES, ONE BRAIN

One of the most interesting questions is how infants map two distinct languages in the brain. From phonemes to words, and then to sentences, how do infants simultaneously bathed in two languages develop the neural networks necessary to respond in a native-like manner to two different codes?

Word development in bilingual children has just begun to be studied using ERP techniques. Conboy & Mills (2006) recorded ERPs to known and unknown English and Spanish words in bilingual children at 19–22 months. Expressive vocabulary sizes were obtained in both English and Spanish and used to determine language dominance for each child. A conceptual vocabulary score was calculated by summing the total number of words in both languages and then subtracting the number of times a pair of conceptually equivalent words (e.g., “water” and “agua”) occurred in the two languages.

ERP differences to known and unknown words in the dominant language occurred as early as 200–400 and 400–600 ms in these 19- to 22-month-old infants and were broadly distributed over the left and right hemispheres, resembling patterns observed in younger (13- to 17-month-old) monolingual children (Mills et al. 1997). In the nondominant language of the same children, these differences were not apparent until late in the waveform, from 600 to 900 ms. Moreover, children with high vs. low conceptual vocabulary scores produced a greater number of responses to known words in the left hemisphere, particularly for the dominant language (Conboy & Mills 2006).

Using ERPs, Neville and colleagues have shown that longer latencies and/or durations of semantic ERP effects are noted for later- vs. early-acquired second languages across individuals (Neville et al. 1992, Weber-Fox & Neville 1996, Neville et al. 1997). In the syntactic domain, ERP effects typically elicited by syntactically anomalous sentences and closed- vs. open-class words have been absent or

attenuated for second languages acquired after infancy (Neville et al. 1992, 1997; Weber-Fox & Neville 1996).

A second question about bilingual language development is whether it takes longer to acquire two languages as compared with acquiring one. Bilingual language experience could impact the rate of language development, not because the learning process is different but because learning might require more time for sufficient data from both languages to be experienced. Infants learning two languages simultaneously might therefore reach the transition from universal phonetic listening (phase 1 of development) to language-specific listening (phase 2 in development) at a later point in development than do infants learning either language monolingually. This delay could depend on factors such as the number of people in the infants' environment producing the two languages in speech directed toward the child and the amount of input these people provide. Such factors could change the development rate in bilingual infants.

Very little data address this question thus far, and what data do exist are mixed. Some studies suggest that infants exposed to two languages show a different pattern of phonetic perception development when compared with monolingual infants (Bosch & Sebastián-Gallés 2003a,b). Other studies report that phonetic perception in bilingual infants is identical to that occurring in monolingual infants (Burns et al. 2007). The data are at present not sufficient to allow us to answer how bilingual vs. monolingual language exposure affects phonetic perception development and the timing of the transition in phonetic perception from one of universal phonetic perception to one reflecting the language(s) to which infants have been exposed.

CONCLUSIONS

Knowledge of infant language acquisition is now beginning to reap benefits from information obtained by experiments that directly examine the human brain's response to linguis-

tic material as a function of experience. EEG, MEG, fMRI, and NIRS technologies—all safe, noninvasive, and proven feasible—are now being used in studies with very young infants, including newborns, as they listen to the phonetic units, words, and sentences of a specific language. Brain measures now document the neural signatures of learning as early as 7 months for native-language phonemes, 9 months for familiar words, and 30 months for semantic and syntactic anomalies in sentences.

Studies now show continuity from the earliest phases of language learning in infancy to the complex processing evidenced at the age of three when all typically developing children show the ability to carry on a sophisticated conversation. Individual variation in language-specific processing at the phonetic level—at the cusp of the transition from phase 1, in which all phonetic contrasts are discriminated, to phase 2, in which infants focus on the distinctions relevant to their native language—is strongly linked to infants' abilities to process words and sentences. This is important theoretically but is also vital to the eventual use of these early precursors to speech to diagnose children with developmental disabilities that involve language. Furthermore, the fact that the earliest stages of learning affect brain processing of both the signals being learned (native patterns) and the signals to which the infant is not exposed (non-native patterns) may play a role in our understanding of the mechanisms underlying the critical period, at least at the phonetic level, showing that learning itself, not merely time, affects one's future ability to learn.

Whole-brain imaging now allows us to examine multiple brain areas that are responsive to speech, including those responsible for perception as well as production, revealing the possible existence of a mirror system for speech. Research has begun to use these measures to understand how the bilingual brain maps two distinct languages. Brain studies are beginning to show, in children with developmental disabilities, how particular disabilities affect the brain structures underlying language learning. Answers to the classic questions about the unique

human capacity to acquire language will continue to be enriched by studies that utilize modern neuroscience tools to examine the infant brain.

FUTURE DIRECTIONS

1. Are the brain structures activated in infants in response to language the same as those activated in adults, and in both cases, are these brain systems speech specific?
2. Why do infants fail to learn language from television presentations—how does social interaction during language exposure affect the brain's ability to learn?
3. Is the neural network connecting speech perception and speech production innate, and if so, is this network activated exclusively in response to language?
4. How is language mapped in the bilingual brain? Does experience with two or more languages early in development affect the brain systems underlying social and/or cognitive processing?
5. How do developmental disabilities such as autism, dyslexia, and specific language impairment affect the brain's processing of speech?
6. Which causal mechanisms underlie the critical period for second language acquisition—why are adults, with their superior cognitive skills, unable to learn as well as young infants? Can techniques be developed to help adults learn a second language?

DISCLOSURE STATEMENT

The authors are not aware of any biases that might be perceived as affecting the objectivity of this review.

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Errata

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