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Neural plasticity in speech acquisition and learning*

YANG ZHANG
University of Minnesota
YUE WANG
Simon Fraser University

Neural plasticity in speech acquisition and learning is concerned with the timeline trajectory and the mechanisms of experience-driven changes in the neural circuits that support or disrupt linguistic function. In this selective review, we discuss the role of phonetic learning in language acquisition, the "critical period" of learning, the agents of neural plasticity, and the distinctiveness of linguistic systems in the brain. In particular, we argue for the necessity to look at brain–behavior connections using modern brain imaging techniques, seek explanations based on measures of neural sensitivity, neural efficiency, neural specificity and neural connectivity at the cortical level, and point out some key factors that may facilitate or limit second language learning. We conclude by highlighting the theoretical and practical issues for future studies and suggest ways to optimize language learning and treatment.

A fundamental goal in language neuroimaging research is to link mind and brain for a better understanding of the neural circuits that support language(s) and the connections between the changes in behavior and the changes in the brain. This paper discusses the empirical and theoretical framework in exploring the brain mechanisms of plasticity and the important measures of language learning that are particularly relevant to a proper characterization of neural plasticity. We focus on how recent data on phonetic learning may shed new light on the nature of cortical representations of language and brain plasticity in first and second language acquisition.[1]

Our phonetic focus is primarily based on developmental data and training data showing the strong associations between the characteristics of language input and the development of speech perception in parallel with the strong associations between phonetic perception and other language skills. Research suggests that the implicit learning mechanisms that operate on the probabilistic transitions and statistical distributions of the language input are fundamental to language acquisition early in life (Kuhl et al., 2001; Saffran, 2003), second language acquisition (Zhang et al., 2000; Kuhl et al., 2001; Mueller et al., 2005) and artificial grammar learning (Lieberman et al., 2004; McNealy, Mazziotta and Dapretto, 2006).

We summarize findings of our recent phonetic training studies and discuss the complex nature of neural plasticity in language learning in terms of the signature markers of sensitivity, efficiency, specificity and connectivity in the neural system and the timeline trajectories. Throughout the paper, we examine three questions of interest: (a) what factors facilitate or limit language learning from a developmental perspective, (b) whether the "critical period" or "sensitive period" of learning becomes so definitive and irreversible that people lose the ability to learn with age, and (c) what brain mechanisms can support and help explain language acquisition; for instance, whether learning two languages requires two distinct neural substrates. Finally, we discuss theoretical implications and suggest possible ways to optimize learning and treatment.

Behavioral approach vs. neurophysiological approach

By all accounts, behavioral approaches have been the most dominant and productive tool in the study of language acquisition. However, behavioral data are often inadequate for answering questions of neural plasticity regarding changes in the temporal dynamics of speech processing and the functional neuroanatomy of language representation in the human brain. For example, behavioral experiments in speech perception are typically designed to elicit overt responses such as identification,

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[1] In this paper, the terms "learning" and "acquisition" are used interchangeably to avoid the explicit vs. implicit distinction suggested by some theorists (Higgs, 1985). The theoretical considerations for differentiating the two terms are acknowledged and beyond the scope of this paper.

Address for correspondence
Yang Zhang, Department of Speech-Language-Hearing Sciences & Center for Neurobehavioral Development, University of Minnesota, Minneapolis, MN 55455, USA
E-mail: *zhang470@umn.edu*

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discrimination, stimulus similarity ratings, goodness ratings, intelligibility ratings, and judgments of other criteria. The measurements of reaction time and accuracy allow researchers to make inferences about various aspects of the information processing system. Although most behavioral paradigms permit an objective assessment, the results typically reflect the output of a prolonged focused decision process. It is certainly true that lesion-deficit studies have made significant contributions to our understanding of the correlations between damage to a certain brain area and the concomitant speech/language deficits. But lesions are either unethically invasive or due to accidents of nature with no experimental control. The findings reflect a static view of the disruptive end products instead of online processing in a functional brain.

Recent years have witnessed a paradigm shift in the studies of human language and cognition (Gazzaniga, 2000; Nelson and Luciana, 2001). An increasing number of studies have started to measure noninvasively the electrophysiology, biomagnetism, metabolism and hemodynamics of brain activities responsible for various aspects of linguistic and cognitive processing. Among the most commonly used techniques are electroencephalography (EEG), magnetoencephalography (MEG), positron emission tomography (PET) and functional magnetic resonance imaging (fMRI). The EEG and MEG systems use electrodes positioned on the scalp or superconductor sensors directly above the scalp, which measure the variations in scalp voltages or magnetic fields generated by the neuronal activities in the brain. EEG and MEG measures are direct and noninvasive. In event-related paradigms, responses time-locked to the presentation of the stimuli are recorded, known as the event-related potential (ERP) for EEG and event-related field (ERF) for MEG. The recordings can be taken from subjects when no overt behavioral response is required. Because the critical acoustic features for different speech sounds are only tens of milliseconds long in time or less, a detailed measurement of neural processing of speech sounds requires excellent time resolution. Compared with PET and fMRI measures that reflect hemodynamic and/or metabolic changes associated with neuronal activities with good localization information but poor temporal resolution in the order of seconds, the ERPs and ERFs have temporal resolution on the order of milliseconds with modest localization accuracy.

To date, the neurophysiological data have produced a rich set of findings on different levels of linguistic processing and various aspects of language acquisition, which have significant theoretical implications. Take, for example, the mismatch response – mismatch negativity (MMN) and its magnetic counterpart, mismatch field (MMF or MMNm). The MMN is considered an "endogenous" component that peaks at 100–300 ms after the onset of a stimulus change and reflects the automatic detection of the stimulus change in auditory sensory memory (Näätänen, 2001). The MMN magnitude provides an objective measure of perceived acoustic change, demonstrating good correlations with psychophysical discrimination for various parameters of speech and nonspeech stimuli, including stimulus omission, stimulus category change, and discriminable increment/decrement in frequency, intensity, and duration. In other words, the MMN is a signature marker of NEURAL SENSITIVITY that corresponds to behavioral discrimination accuracy. The MMN has been recorded from adults, children, premature infants, newborns and older infants, and clinical populations, irrespective of the listener's attention. Researchers can examine the latency and amplitude measures of the neural responses such as MMN to search for answers to their questions. Source localization techniques, when applicable, allow researchers to describe the neural activities in various brain regions at different points in time during the process of speech perception. Consequently, the neurophysiological approach has opened a new horizon to develop our understanding of speech and language representation in the brain and how the neural representation changes in the course of language learning. For instance, when can the infants automatically differentiate speech contrasts in the native language? When do they start to show less sensitivity to a nonnative language? Would the early changes in MMN for phonetic discrimination predict later language development?

Strong associations between phonetic learning and first language acquisition

Behavioral data

Developmental research has documented a clear perceptual transition from "language-general" to "language-specific" in the first year of life (Kuhl et al., 2001; Werker and Tees, 2005; Kuhl et al., 2006). Before 6–8 months of age, infants are able to discriminate all the phonetic contrasts in behavioral tests; by 12 months, they show an increase in discrimination sensitivity for native phonemes accompanied by a decline in perceptual sensitivity for nonnative phonemes. In this process, infants extract formal regularities from ambient language based on properties of the speech input, and perceptually "map" the critical speech features of their native language. This early perceptual reorganization is considered to reflect a continuous process of neural commitment towards the first language and gradual decrease in neural plasticity to acquire another language.

Theorists are well aware of the gaps between acoustical properties of linguistic input, measures of speech perception, and data on language acquisition beyond the realm of phonetics – Are there close links among them? Some recent studies have provided insightful

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answers to this question. First, maternal speech clarity, as measured by the degree of acoustic expansion of the vowel space, is significantly correlated with infants' phonetic discrimination ability (Liu, Kuhl and Tsao, 2003). Second, phonetic learning as early as 6 months of age is significantly correlated with their later (under the age of 3 years) language comprehension and production skills in terms of vocabulary and syntax (Tsao, Liu and Kuhl, 2004; Kuhl et al., 2005; Kuhl et al., 2006). Strikingly, an early competitive pattern between native and nonnative phonetic perception can be seen even in infants who are raised in monolingual families. At a group level, infants who showed better native phonetic discrimination at the age of 7 months had better performance in their later language skills as assessed by using the MacArthur-Bates Development Communicative Inventory (Fenson et al., 1993). On the other hand, infants who had better nonnative phonetic discrimination at the age of 7 months demonstrated reduced later language abilities in their first language development during the first three years (Figure 1). These results, though at a different level, are highly compatible with Li and colleague's computational modeling of lexical development in the first and second languages (Li, Farkas and MacWhinney, 2004; Li, Zhao and MacWhinney, 2007).

Neural sensitivity data

Infant ERP data confirmed the native vs. nonnative competition in the correlations between the preattentive MMN measures and the behavioral measures of phonetic discrimination (Kuhl et al., 2005; Rivera-Gaxiola, Silva-Pereyra and Kuhl, 2005). The d' is a statistical objective measure of the subject's true sensitivity and response biases based on the number of hits, misses, correct rejections, and false positives – the larger the d' is, the better the listener's ability to detect the signal change (Green and Swets, 1966). When the language factor was controlled, larger MMNs (more negative values) were associated with larger d' values in the infants (Figure 1), suggesting that those who were neurally more sensitive in detecting the phonetic distinction were also behaviorally more accurate in discriminating of the same phonetic contrast regardless of whether it is a native or nonnative distinction. However, when MMNs for native contrast were plotted against nonnative d' data, and when MMNs for nonnative contrast were plotted against native d' data, an opposite trend was seen: infants who were neurally more sensitive to the native phonetic contrast performed worse in discriminating nonnative phonetic contrast, and infants who were neurally more sensitive to the nonnative phonetic contrast performed worse in discriminating native phonetic contrast. Further statistical analyses indicate that the early MMN measures are good predictors of later language skills under the age of 3. This phenomenon extends to older children,

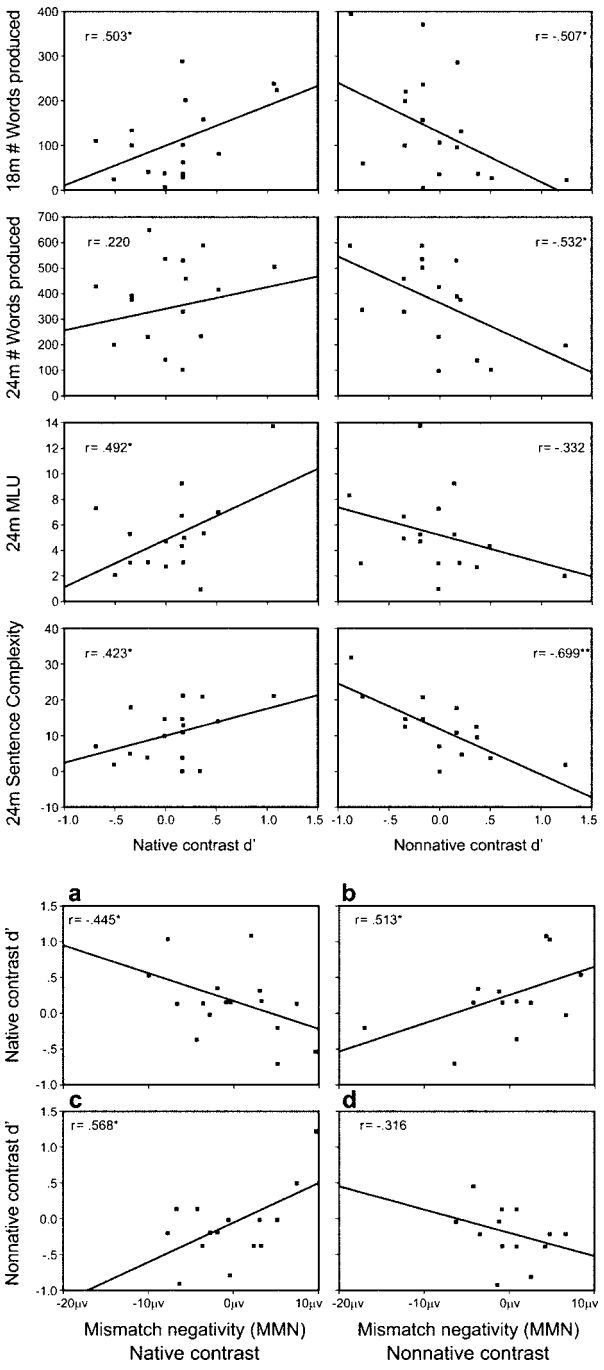


Figure 1. Scatter plots showing associations of early phonetic perception and later language development (ERP study). Top panel shows correlations between behavioral measures (d′) of native and nonnative phonetic discrimination at 7 months old and later language skills in terms of words produced, mean length of utterance (MLU) and sentence complexity. Bottom panel shows correlations between behavioral measures (d′) and MMN measures for phonetic discrimination at 7 months old. (Kuhl et al., 2005; reproduced with the authors' permission.)

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including children with language disabilities (Molfese and Molfese, 1985; Molfese and Molfese, 1997; Molfese, 2000; Kuhl et al., 2004). For example, Molfese and colleagues showed that early ERP measures of phonetic perception can predict with approximately 80% accuracy the classification of high- vs. low-functioning language groups for children between the ages of 3 and 8 years.

The role of phonetic learning: Controversies and consensus

Different underlying mechanisms have been proposed to account for the association between phonetic perception and language learning. Some researchers believe that the association is primarily based on low-level domain-general auditory mechanisms rather than infants' phonetic knowledge (Visto, Cranford and Scudder, 1996; Tallal et al., 1998; Benasich and Tallal, 2002; Ulla et al., 2004; Benasich et al., 2006). Their data show that processing abilities of rapid auditory/visual information for both speech and nonspeech stimuli in early infancy are highly predictive of later language development and literacy including language delay and impairment. More importantly, although individual differences in speech and nonspeech discrimination in infancy are both correlated with later linguistic outcome, nonspeech perceptual ability – the fine acoustic discrimination of rapid tones – appears to have a stronger predictive role than the discrimination of consonant–vowel pairs. Support for the domain-general auditory learning mechanisms has also been found in some adult speech perception studies (Poldrack et al., 2001; Diehl, Lotto and Holt, 2004; McNealy et al., 2006). For example, fMRI activities in the left inferior and middle frontal cortex that index the implicit learning of word boundaries in continuous speech are positively correlated with listeners' rapid auditory processing skills (McNealy et al., 2006).

However, other researchers argue that the early language mapping process is specifically based on statistical, spectro-temporal, phonetic and phonotactic properties of the native language (Saffran, 2003; Kuhl et al., 2005). In particular, the differences in language development associated with early native vs. nonnative speech discrimination abilities could not be explained by the auditory mechanisms – because low-level auditory processing should equally apply to any language. There is also behavioral and neural evidence showing that speech perception can be selectively affected by language experience without a parallel compromise in auditory processing of nonspeech stimuli that simulate the essential spectral properties of speech (Miyawaki et al., 1975; Zhang et al., 2005). Literature review on the rapid auditory processing deficits further suggests that not all people with specific language impairment and dyslexia exhibit auditory deficits. In many cases, there can be little or no relationship between the severity of auditory deficits and language performance (Rosen, 2003). Therefore, the existence of significant statistical correlations between speech and nonspeech deficits as well as those between phonetic perception and language development should not be interpreted as causative or exclusive of cognitive and maturational involvement.

Despite the theoretical debate, both behavioral and neurophysiological data consistently demonstrate the pivotal role of phonetic perception in language learning and the existence of large individual differences. The empirical data provide support for both longitudinal and cross-sectional associations between phonetic perception and language skills. More importantly, speech modifications and acoustic enhancements, which can be found in child-directed speech at the phonetic as well as syntactic and semantic levels, not only facilitate language learning in normal children but also achieve some remarkable success in training second language learners and treating children with language disabilities.

Effects of first language experience on second language learning

Behavioral data

It is well established that our speech perception abilities are indelibly marked by language experience (Oh et al., 2003; Kuhl et al., 2005; Werker and Tees, 2005). Our auditory systems are capable of processing native language with ease despite large acoustic variability in speaker, accent, speech rate, and emotional affect. Yet, as adults, we all encounter great difficulty in processing unfamiliar languages. The universal impression is that foreign speech is fast, confusing, and virtually indistinguishable. This "foreign listening syndrome" (Mehler et al., 994; Pallier, Christophe and Mehler, 1997) has been repeatedly attested in laboratory studies, demonstrating that adult listeners are not as good at identifying and discriminating many nonnative speech sounds when compared to native speech (Strange, 1995).

The perceptual proclivity for native language originates from linguistic exposure early in life. It is widely accepted that the phonetic categories of the native language acquired early in life, represented in the neural substrate of the brain for speech perception, function like an "assimilator" for perceiving speech sounds in general (see Perfetti et al., 2007 – this volume, for a discussion of L1 writing systems acting as "assimilators" to the learning of an L2 writing system). The degree to which listeners fail to detect a nonnative contrast has been shown to be closely tied to the acoustic, phonetic and phonological similarities between the native and nonnative language

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systems (Best, 1994; Flege, 1995; Escudero and Boersma, 2004). Bilingual studies and perceptual training on adult listeners vividly illustrate the profound effects of first language interference in speech perception. Despite high proficiency in the second language, there is evidence of first language dominance in speech perception (Pallier, Bosch and Sebastian-Gallés, 1997; Bosch, Costa and Sebastián-Gallés, 2000). Phonetic training studies often show limited success in improving listeners' perception and production of difficult nonnative contrasts (Strange and Dittmann, 1984; Bradlow et al., 1999; McCandliss et al., 2002; Takagi, 2002).

Neural sensitivity data

Neurophysiological studies have provided evidence of "memory traces" for language-specific phonemes in the auditory cortex in adult listeners and its emergence in infants before the age of twelve months (Näätänen et al., 1997; Cheour et al., 1998; Rivera-Gaxiola et al., 2005). For instance, Näätänen et al. (1997) used whole-head MEG measures in combination with ERP to examine the cortical representation of language-specific phonemes in adult subjects. Despite the fact that the acoustic difference in the nonnative contrast was larger than that of the native contrast, stronger language-specific MMN and MMNm activity for native vowel discrimination was found in the left auditory cortex. Similar results have been reported in many other MMN/MMF studies (Dehaene-Lambertz, 1997; Winkler et al., 1999; Dehaene-Lambertz, Dupoux and Gout, 2000; Rivera-Gaxiola et al., 2000; Sharma and Dorman, 2000; Zhang et al., 2005). The language samples of these studies covered a wide range, including English, Estonian, Finnish, French, Hindi, Hungarian, Japanese, and Spanish.

Mechanisms in terms of levels of processing

The neurophysiological data provide not only important information of the brain regions specialized in speech perception but also a different perspective regarding the level of processing that is altered by language experience. Behavioral studies suggest that the language-specific pattern of perception results from selective attentional mechanisms and not a change in basic auditory sensitivities (Miyawaki et al., 1975). Given the fact that the neurophysiological data are recorded while the subjects are required to attend to a distraction task, it seems reasonable to argue that language experience alters not only higher-level categorization but also lower-level perceptual processes.

The loss of perceptual sensitivity for nonnative phonetic contrasts may be difficult to reverse in adulthood, because the brain would have become committed to the analysis of native language structure with reduced neural sensitivity for nonnative speech perception at the preattentive level. It is argued that early language learning involves continuous and self-reinforcing neural commitment to the set of statistical and spectral properties characteristic of the native language, which naturally leads to later perceptual interference with second language acquisition (Iverson et al., 2003; Zhang et al., 2005). In this perspective, early learning may be particularly enhanced by exposure to "motherese", a signal that exaggerates the relevant acoustic cues to phonetic categories and facilitates phonetic categorization (Kuhl et al., 1997; Liu et al., 2003).

Mechanisms in terms of hemispheric differences

One distinctive advantage of the brain imaging studies is that brain activation provides direct information of relative hemispheric involvement and cortical localization of cognitive processes. It has been proposed that two parallel processes contribute to the mismatch response of speech discrimination (Näätänen, 2001). One is the process of acoustic change detection with bilateral activation, and the other is phoneme-specific processing, which is lateralized in the left auditory cortex. According to this theory, effects of phonetic learning would be more prominent in the left hemisphere as compared with the right hemisphere. Although there have been many adult studies reporting left-hemisphere dominance for native speech perception, other data tend to show large individual variability and a bilateral activation pattern even for native speech processing (Zhang et al., 2005). Developmental data do not show a clear maturational pattern of left hemispheric involvement for native speech processing as against nonnative or general acoustic processing. Some imaging data suggest that the left dominant areas subserving speech processing are similar in infants and in adults (Dehaene-Lambertz, Dehaene and Hertz-Pannier, 2002; Pena et al., 2003). However, the MMNs in infant often show a bilateral temporal maximum with no laterality effect (Čeponiene, Rinne and Näätänen, 2002).

The fact that different speech sounds are cued by different spectral and temporal parameters further complicates the interpretation of neurophysiological findings. Some PET and fMRI data show that the left auditory cortex is specialized for rapidly changing broad-band stimuli including speech, whereas the right auditory cortex may be good at processing slower narrow-band stimuli such as tonal patterns (Zatorre and Belin, 2001). However, this theory does not provide specific predictions regarding the cortical basis of native vs. nonnative language processing. Its explanatory power for language neuroimaging, especially the changes associated with language learning, remains to be further tested.

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Neural plasticity in phonetic training

Theoretical motivation

A long-deliberated issue in cognitive neuroscience of language learning is the extent to which human brain has the capacity to change resulting from learning. Theories of language learning have traditionally been dominated by the "Critical Period" Hypothesis, stating that language learning ability is reduced after puberty, as the result of the loss of neurological plasticity of the brain (Lenneberg, 1967). Developmental speech perception reveals how brain plasticity diminishes as a function of language experience. In the ontogeny of development, adults are beyond the critical period early in life during which the brain is most sensitive to language learning. However, current theories posit that language acquisition patterns are influenced by linguistic experience rather than biological or maturational constraints (Best, 1995; Flege, 1995; Kuhl, 2000; Hernandez, Li and MacWhinney, 2005). Indeed, research has consistently shown that language-related cortical responses differ as a function of linguistic experience (Yetkin et al., 1996; Binder, 1999; Gaillard et al., 2000). Bilinguals' second language (L2) may share the same neural system with the first language (L1) or involve specialized neurocircuitry, depending on such factors as age of L2 learning and proficiency levels (Kim et al., 1997; Perani et al., 1998; Xue et al., 2004; Hernandez and Li, 2007).

Phonetic training studies bring up the issue of brain plasticity in adulthood by highlighting the role and exact nature of experience in changing a listener's speech perception. Although performance in nonnative speech perception remains substantially below that shown by native speakers, early language exposure does not produce the complete loss of sensitivity to nonnative distinctions. Success in training is behaviorally shown by significant improvement in accuracy and efficiency of categorization, transfer of learning to untrained stimuli, transfer from enhanced perception to improved production, and long-term retention of the improvements. Assuming that behavioral gains reflect experience-dependent changes in the brain, the successes and failures of various training methods may provide us with a better understanding of the underlying perceptual mechanisms and the nature of neural plasticity in the acquisition of new phonetic categories.

The case of /r–l/ for Japanese speakers

Training Japanese speakers to learn the English /r–l/ contrast has been a classic example in speech research. Using a phonetic discrimination task, Strange and Dittmann (1984) found little generalization to novel stimuli. Pisoni and colleagues improved the training methodology by introducing high variability in an identification task (Pisoni and Lively, 1995). Intensive short-term training produced a small yet statistically significant change, and greater improvement required a more extended training period (Bradlow et al., 1999; Takagi, 2002).

In Kuhl and colleagues' model, Japanese adult trainees had tremendous difficulty and limited success probably because exposure to the natural speech alone was unable to circumvent the strong NATIVE LANGUAGE NEURAL COMMITMENT (NLNC) that hindered full access to, or proper use of, the critical acoustic dimension(s) for accurate phonetic categorization in the second language (Kuhl, 2000; Zhang et al., 2005). NLNC enhances NEURAL SENSITIVITY AND EFFICIENCY for native language processing and meanwhile reduces neural sensitivity and efficiency for nonnative language processing. Enhanced neural sensitivity can be measured by enlarged MMN/MMF, and enhanced neural efficiency can be measured by the reduced amount of activation spread and/or duration for a given task – the less the amount of activation is, the more efficient the system is.

It may require special enriched exposure analogous to "motherese" to circumvent the perceptual interference of NLNC in order for adults to learn nonnative phonetic categories, especially those difficult contrasts that map onto single native categories. The signal enhancement approach was previously found to be effective in treating children with language disabilities in improving their phonetic discrimination and language skills (Tallal et al., 1998). This idea has been tested by developing a training software program that incorporated signal enhancement, visible articulation cues, a large stimulus set with high variability, and self-directed adaptive training (Zhang et al., 2000; Zhang et al., 2001). Approximately 12 hours of training showed over 20% identification improvement with excellent generalization to untrained voices. Training also resulted in a notable enhancement in neural sensitivity to the /r–l/ distinction in the left hemisphere, as measured by preattentive MMF, and increased NEURAL EFFICIENCY in both hemispheres, as measured by a reduction in the amount of activation spread and duration of activation (Figure 2). The training-induced changes in behavioral discrimination were significantly correlated with changes in both neural sensitivity and efficiency measures. The results suggest that both neural sensitivity and neural efficiency appear to be good predictors of phonetic learning. Given enriched linguistic experience, there is substantial neural plasticity for the acquisition of new phonetic categories in adulthood.

The case of Mandarin tones for English speakers

A series of studies have investigated the processing and acquisition of linguistic tone (Wang, Jongman and

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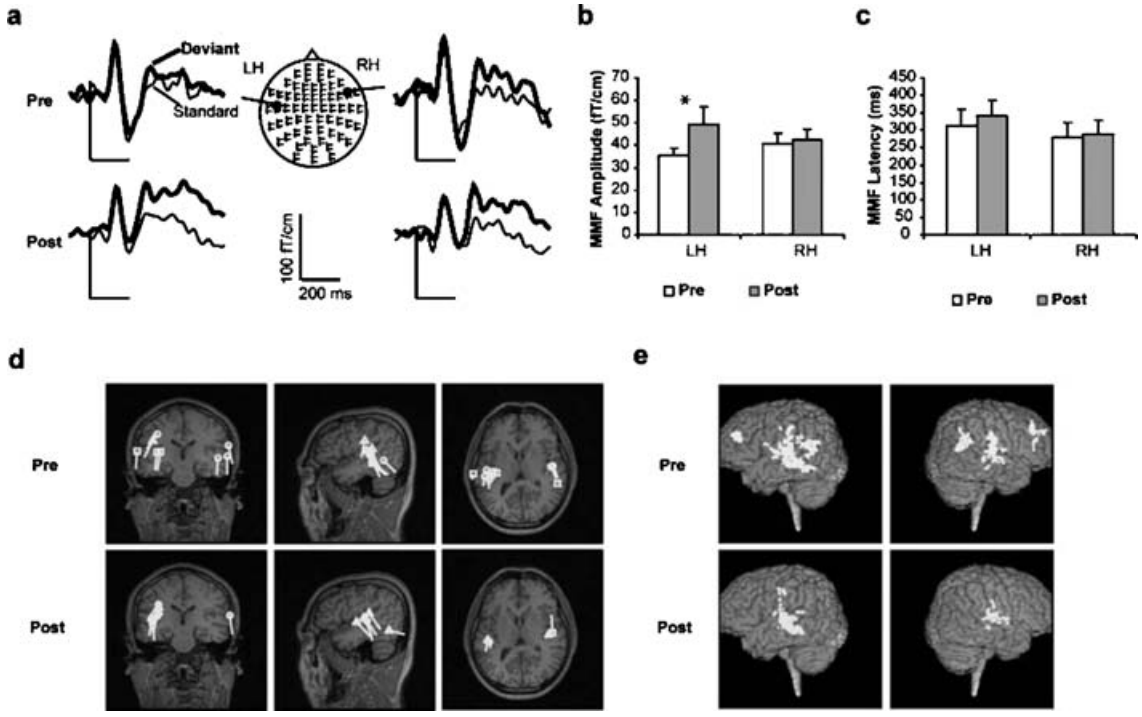


Figure 2. Neural sensitivity (MMF) and efficiency measures of pre- and post-tests for the synthetic /ra-la/ stimuli (MEG study). Top panel shows waveform responses (a) from one representative Japanese and the statistical results of MMF amplitudes (b) and latencies (c) in group averages. Bottom panel shows one spatial selection of equivalent current dipoles (ECDs) on the coronal, sagittal, and axial planes (d) from one representative subject and cortical renditions (e) of all the ECDs from the same subject. (Zhang et al., 2001; reproduced with the authors' permission.) Note: * $p < 0.05$; LH = left hemisphere, RH = right hemisphere

Sereno, 2006). Behavioral and neuroimaging research shows that while native tone language speakers (e.g., Mandarin Chinese) process tone as a linguistic property predominantly in the left hemisphere, tone processing by nonnative speakers differs as a function of the linguistic role of tone to these speakers (Hsieh et al., 2001; Klein et al., 2001; Wang, Jongman and Sereno, 2001; Gandour, 2006). Specifically, for non-tone-language speakers (e.g., English), the processing of tone (e.g., Mandarin or Thai) is less left lateralized than that for native tone speakers (Wang et al., 2001; Gandour et al., 2003). Furthermore, native tone language speakers (e.g., Norwegians processing Mandarin tone) do not process tones of another tone language in the left hemisphere, indicating that tones are processed in the left hemisphere only when they are linguistically meaningful (Wang et al., 2004). Further research has shown a native-like lateralization patterns of tone by English listeners who were highly proficient in Mandarin (Wang et al., 2004), indicating a shift from nonnative (L2) to native (L1) patterns as a function of L2 proficiency.

Recent neuroimaging study (Wang, Jongman and Sereno, 2003a) investigated the cortical instantiation of this training-induced learning. Using fMRI (functional magnetic resonance imaging), adult American learners' acquisition of Mandarin Chinese tone was examined by comparing cortical activation during a tone identification task before and after a two-week training procedure. Results show that improvements in performance were associated with an increase in activation in Wernicke's area (left superior temporal gyrus, Brodmann's area 22) and emergence of additional activity within adjacent regions (left superior temporal gyrus, Brodmann's area 42), as well as the right inferior frontal region homologous to the Broca's area (Brodmann's area 44). The results of the expansion of cortical activation after training are consistent with those of the segmental domain with Japanese learners processing English /r/ and /l/ (Callan et al., 2004). These findings indicate that the early cortical effects of learning an L2 involve both the expansion of preexisting language-related areas and the recruitment of additional cortical regions, suggesting the plasticity of the adult human brain in the acquisition of Mandarin tone. Further evidence indicates that for more advanced learners, cortical activity related to lexical tone processing became more focused with learning, with decreased activation after training (Wang et al., 2003a). The possibility of such focused change in cortical activation with relatively higher

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language proficiency has also been noted with visually presented words (Chee et al., 2001). These patterns raise the possibility of progressive cortical changes with increased proficiency, suggesting that cortical representations may be continuously shaped with learning throughout life (van Turennout, Ellmore and Martin, 2000).

The adult learning patterns raise the subsequent question of whether children exhibit the same patterns, or whether differences reflecting developmental changes exist, given children's superiority over adults in speech learning ability. Wang and Kuhl (2003) examined the perceptual learning of Mandarin tone by American children from 6 to 14 years old, covering the age range surrounding the "critical period". The results showed significant improvement after training across age groups. However, comparing the pre-puberty and the post-puberty groups, we did not find an abrupt decrease in the degree of improvement, as would have been predicted by the Critical Period Hypothesis. These results support the view that language learning is not a strictly timed developmental process with rigid cut-off periods (Flege, 1995; Bongaerts et al., 1997; Hakuta, Bialystok and Wiley, 2003).

The nature of neural plasticity in language learning

The term "neural plasticity" applies to processes operative at many levels of our neurocognitive system, an intrinsic property that persists throughout our lives (DeFelipe, 2006; Mahncke et al., 2006). Adaptive changes and reorganizations in structure and function can reflect changes in the neurochemical systems, cell assemblies and connections, brain activation patterns and behavioral performance, which have important implications for psychological development, language intervention, and neurological rehabilitation. Some changes in the brain are known to be genetically determined and "experience-independent" whereas others are either "experience-expectant" or "experience-dependent", which require the reception of certain input from the external environment (Greenough et al., 1999). Given the fact that the brain is an intricate and highly specific neural network with hundreds of billions of excitatory as well as inhibitory interconnections, the complexity of neural plasticity and the end-results can be daunting.

In language research, developmental data in normal and injured brains suggest that the neural organization for language is neither predetermined or strictly domain-specific (Bates, 1999). Training studies indicate that language learning is not an irreversible age-bound event. For both supporters and opponents of these ideas, it is important to answer two fundamental questions: (a) What are some of the signature markers of neural plasticity at the system neuroscience level? (b) What is the proper interpretation of these measurements?

Brain activation patterns: Neural sensitivity, neural efficiency, neural specificity and neural connectivity

In theory, learning-induced plasticity can be reflected in (a) increased neural sensitivity, (b) enhanced NEURAL SPECIFICITY, (c) strengthened NEURAL CONNECTIVITY, and (d) improved NEURAL EFFICIENCY. Specificity is shown by the specialization of brain region(s) or neural pathway dedicated to the type of information being processed (Patel et al., 1998; Johnsrude, Penhune and Zatorre, 2000). Connectivity is reflected in white-matter density in regions of interest as well as in the degree of activation coherence between different brain regions (He et al., 2003; Horwitz and Braun, 2004). A change in neural efficiency can be considered a derivative of changes in sensitivity, specificity and connectivity, which presumably lead to faster and shorter activation (Zhang et al., 2005). This assumption becomes empirically testable only when we know what measures of brain activity correspond to the greater efficiency and what variables, including stimulus properties, subject characteristics, the nature of tasks, and time course of learning, may cause changes in the measures. For example, voxel-based morphometry analysis of MRI data shows that faster phonetic learners have more white matter in parietal regions, especially in the left hemisphere (Golestani et al., 2002). Furthermore, the degree of success in training can be reflected in activation levels in specific areas of the temporal, parietal and inferior frontal cortex in the left hemisphere (Golestani and Zatorre, 2004; Wong, Perrachione and Parrish, 2007)

Although learning-induced enhancement in neural sensitivity has been consistently supported (Tremblay et al., 1997; Winkler et al., 1999; Menning et al., 2002), the construct of neural efficiency as a neural signature of learning has been controversial. Intuitively, higher ability should translate into more efficient use of brain resources. A variety of adult fMRI studies on learning effects have reported more focal brain activation (See Zhang et al., 2005 for discussion). However, more focal activation does not necessarily mean smaller, faster and shorter activation. An equally plausible model was proposed based on the principle of Hebbian learning (McCandliss et al., 2002) – "Neurons fire together, wire together". While the Hebbian learning model and the NLNC model endorse similar theoretical constructs of accuracy, speed and sensitivity, they differ in specific predictions about whether improvement in neural efficiency would be shown as an increase or decrease in the strength, spatial extent and duration of neural activation. In the Hebbian model, behavioral improvement would likely be supported by stronger, longer, and expanded activation in a specific brain region.

The complexity of neural plasticity can be exacerbated by the fact that the effects of perceptual learning are

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not limited to the perceptual domain. For instance, adult studies showed great benefits from audiovisual training (Zhang et al., 2001) and long-lasting effects of transfer from perception to production (Callan et al., 2003). Infant MEG data from newborns, 6-month-olds, and 12-month-olds suggested an early basis for the perceptual-motor link for native speech in the left hemisphere (Imada et al., 2006). Given the fact that speech perception involves brain regions for acoustic–phonetic as well as auditory–articulatory mappings, learning-induced plasticity can be associated with DECREASES, INCREASES and SHIFTS in brain activation to facilitate the behavioral improvement. REALLOCATION in hemispheric resources (relative dominance of left and right hemispheres, for instance), RECRUITMENT of additional brain regions, STRENGTHENED ANATOMICAL (increased white-matter density) and FUNCTIONAL CONNECTIONS (increased coherence among regions) in neural pathways, and INCREASES or DECREASES in brain activation can all take place in the course of phonetic learning (Zhang et al., 2001; Golestani, Paus and Zatorre, 2002; Callan et al., 2003; Wang et al., 2003b; Golestani and Zatorre, 2004).

Another confounding factor is that early language learning may not be a unidirectional path towards native language dominance. Here the questions are twofold. If language acquisition neurally commits the brain to bind perception and action in the service of the first language, how flexible can the system be in accommodating and assimilating a second language early in life? Conversely, would second language acquisition have an impact on the neural representation of the first language? Recent studies on adopted children and adults surprisingly showed the dominance of the second language over the first in both behavioral and fMRI measurements; in particular, the responses to the first language were no different from those to an unfamiliar language (Pallier et al., 2003; Ventureyra, Pallier and Yoo, 2004). These data call for further investigations on how the brain adaptively reallocates its resources. More rigorous neurophysiological models and mathematical definitions are also needed to describe neural efficiency, neural specificity, and neural connectivity adequately.

Timeline trajectories

Needless to say, it takes time and effort to learn. The learning process can be conceived as an increased differentiation of the activation pattern, so that when performance is more specialized and highly efficient, only mechanisms absolutely necessary for the occurrence of performance are activated (Zhang et al., 2005). However, changes in brain activation may reflect not only interference from prior learning but also continuously updated cognitive and attentional strategies. Therefore, the learning trajectory does not necessarily entail a monotonic increase in neural efficiency (Wang et al., 2003b; Werker, Hall and Fais, 2004; Werker and Tees, 2005; Zhang et al., 2005).

One plausible trajectory in learning would be an inverted U-shaped activation pattern. While native adult speakers have acquired expertise by automatically focusing at a more abstract (linguistic) level of processing and thus freeing attentional resources, second language learners may have to rely more on bottom-up processing with varying demands on attention in the course of learning depending on age and proficiency. Thus greater attention is required to attend to the task, leading to an overall increase in the activation level initially. As the learning process moves toward expertise, processing may become more and more automatic and specialized in certain brain regions, yielding faster and shorter activation at a reduced level. Such a hypothetical timeline of learning can help explain some of the contradictory findings. Certainly, this over-simplified learning trajectory hypothesis needs to be tested against a number of variables, including not only attentional demands but also motivational factors, age, handedness, and relative language proficiency levels for the first and second languages. Individual differences will also have to be taken into account.

Agents of neural plasticity

Phonetic training studies have all demonstrated a number of physical agents conducive to brain plasticity, which is not strictly bound by time-related biological constraints. These agents include SIGNAL ENHANCEMENT, VISIBLE ARTICULATION CUES, HIGH VARIABILITY STIMULUS SET, IDENTIFICATION TASK, and ADAPTIVE TRAINING (Zhang et al., 2000). The signal processing/progressive fading approach in the form of acoustic amplification, truncation or elongation have been applied widely with commendable success, to training normal adults in second language acquisition as well as children with language impairments in first language acquisition (Tallal et al., 1998). The audiovisual approach is justifiable by the multimodal nature of speech perception (Kuhl, 2000). Laboratory training studies for adults, nevertheless, typically lack the face-to-face social interaction in a natural language learning environment.

Is social interaction an important agent of neural plasticity in language learning? To answer this question, Kuhl's research team conducted an interesting intervention study to teach 9-month-old American infants a Mandarin Chinese speech contrast that does not exist in English (Kuhl, Tsao and Liu, 2003). This particular age was chosen because it reflected the important time window of incremental neural commitment to the phonology of the first language and declining neural plasticity for second

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language phonetic learning. The results of the study demonstrated that American infants who were exposed to live social interaction with speakers of Chinese reading books and playing with toys performed significantly better on discrimination of a Chinese phonetic contrast than infants in the control group who did not have the Chinese exposure. More importantly, exposure to recorded video or audio tapes of the same Chinese speakers via a television set or speaker showed no signs of phonetic learning. The results suggest a close bond between language development, cognitive development and social interaction. The proper design of an optimal learning environment, therefore, would also need to consider the proper delivery mechanism that seeks to enhance learning and treatment.

Distinctiveness of language systems in the brain

Another fundamental question is whether learning different languages involves distinct brain circuits. The existing literature does not provide an unequivocal answer. Clearly, some languages are similar to each other in phonological forms and syntactical structures whereas others can be drastically different. Many studies report overlapping brain regions in processing two languages (Klein et al., 1995; Illes et al., 1999; Chee et al., 2000; Hernandez, Martinez and Kohnert, 2000) whereas others suggest distinct brain mechanisms supporting different languages as a function of age of acquisition or level of proficiency (Kim et al., 1997; Perani et al., 1998). For speakers of highly dissimilar languages such as English and Chinese, both MEG and fMRI data appear to suggest distinct neural substrate or mechanisms in terms of hemispheric laterality, regions of activation, duration of activity, or intensity of activity (Klein et al., 2001; Scott and Johnsrude, 2003; Tan et al., 2003; Valaki et al., 2004). This is partly due to the linguistic peculiarities of Mandarin lexical tones and the unique logographic representation of Chinese characters.

Both intra- and inter-subject variability can pose serious problems on the proper data interpretation, assuming that the observed differences in activation profiles truly reflect differences in the degree and extent cortical/subcortical engagement for supporting different languages. The great discrepancies among studies require robust experimental controls, sufficient data samples with small within-subject variability, and statistical power in future studies in order to reach in-depth understanding of possibly distinct mechanisms mediating different languages.

Conclusions and implications

In summary, we discussed neural plasticity based on recent phonetic studies using neuroimaging techniques. By highlighting the role of phonetic learning in language acquisition, we examined issues concerning the "critical period" or "sensitive period" of learning, the agents of neural plasticity, and the distinctiveness of linguistic systems in the brain. Given the complexity of neural plasticity in activation patterns and timeline trajectories, we discussed four measures that can be employed to characterize the properties of neural plasticity, namely, neural sensitivity, neural efficiency, neural specificity and neural connectivity. We proposed a testable framework of learning trajectory for brain activation in the process of language learning for future studies and discussed the factors that may facilitate or limit the learning process in the Native Language Neural Commitment model.

There are at least three important reasons for investigating neural plasticity and the developmental mechanisms at the phonetic level using both behavioral and neural measures. First, infants' abilities in phonetic categorization at 6–8 months of age have been found to be significantly correlated with their language and literacy skills in the first three years of life and beyond. Second, research on basic auditory vs. linguistic processing mechanisms has led to insightful and effective treatment programs for children and adults with language and memory impairments as well as training programs for normal second language learners. Finally, neurophysiological studies have started to produce a wealth of data on the multimodal speech representations in the developing and mature brains.

The new data have important implications for developing novel teaching and treatment strategies. For example, manipulations to the input and delivery mechanisms will be able to enhance early information processing and thus influence the efficiency of the developing brain in social, cognitive and linguistic domains. Such procedures have been proven to be effective and helpful in acquiring novel phonetic categories from brief exposures and improving literacy skills in children with reading problems. Further research on brain plasticity holds the promise of providing a refined neurobiological framework for interpreting behavioral changes in accuracy, efficiency, attention and preference, which will be instrumental in future studies of language learning in normal and language-impaired populations

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