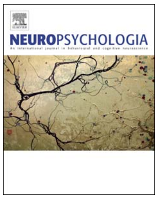
ARTICLE IN PRESS

Neuropsychologia ■ (■■■■) ■■■–■■■

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia



Early bilingualism, language attainment, and brain development

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ARTICLE INFO

Article history:
Received 23 January 2016
Received in revised form
10 June 2016
Accepted 31 August 2016

Keywords:
Bilingualism
Magnetic resonance imaging
Brain development
Language attainment
Brain function
Brain structure
Neural connectivity

ABSTRACT

The brain demonstrates a remarkable capacity to undergo structural and functional change in response to experience throughout the lifespan. Evidence suggests that, in many domains of skill acquisition, the manifestation of this neuroplasticity depends on the age at which learning begins. The fact that most skills are acquired late in childhood or in adulthood has proven to be a limitation in studies aimed at determining the relationship between age of acquisition and brain plasticity. Bilingualism, however, provides an optimal model for discerning differences in how the brain wires when a skill is acquired from birth, when the brain circuitry for language is being constructed, versus later in life, when the pathways subserving the first language are already well developed. This review examines some of the existing knowledge about optimal periods in language development, with particular attention to the attainment of native-like phonology. It focuses on the differences in brain structure and function between simultaneous and sequential bilinguals and the compensatory mechanisms employed when bilingualism is achieved later in life, based on evidence from studies using a variety of neuroimaging modalities, including positron emission tomography (PET), task-based and resting-state functional magnetic resonance imaging (fMRI), and structural MRI. The discussion concludes with the presentation of recent neuroimaging studies that explore the concept of nested optimal periods in language development and the different neural paths to language proficiency taken by simultaneous and sequential bilinguals, with extrapolation to general notions of the relationship between age of acquisition and ultimate skill performance.

1. Introduction

The trophic effect of experience on neural development is reflected in demonstrable changes in brain function and structure. Neural reconfiguration in response to environmental exigencies, whether triggered by the requirement for specific motor behaviors or cognitive skills is referred to as neuroplasticity. Once established, these changes influence the development of subsequent competencies. Such experience-dependent brain modifications, likely the result of alterations in gene expression in neuronal substrates (Flavell and Greenberg, 2008), appear limited by the age at which a given skill is learned and the domain in which that ability is acquired. While most skills appear to be maximally attained during an *optimal* or *sensitive* period of development, recent observations have demonstrated that neuroplastic changes take place throughout the lifespan, even into senescence (Boyke et al., 2008). Identifying the mechanisms of neuroplasticity and the factors that influence its trajectory is essential in order to sort out the complexities of the learning process and the compensatory changes in the brain that promote near peak performance despite suboptimal circumstances for skill acquisition.

Neuroplasticity has been investigated from the biochemical and neuronal perspectives to the level of the intact human brain (For a review see Zatorre et al., 2012). Over the past several decades, neuroimaging has become central to the study of neuroplasticity at the macrostructural and functional levels, with an initial focus on the skills of specialized experts, whose abilities developed late in childhood, adolescence, or adulthood (Münte et al., 2002). Professional musicians were among the earliest groups studied using a variety of applications of magnetic resonance imaging (MRI) to determine the size and gray matter density (GMD) of auditory and motor brain regions (Bermudez et al., 2009; Amunts et al., 1997; Schlaug et al., 1995a, 1995b). However, while a vast majority of published reports have revealed brain alterations in children and mature adults resulting from skill attainment, inferences based on such studies cannot be fully extrapolated to brain models of native acquisition.

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http://dx.doi.org/10.1016/j.neuropsychologia.2016.08.031
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Please cite this article as: Berken, J.A., et al., Early bilingualism, language attainment, and brain development. Neuropsychologia (2016), http://dx.doi.org/10.1016/j.neuropsychologia.2016.08.031

A comparison of how the brain wires both in infancy and later in life provides immeasurable insight into how age of acquisition (AoA) influences brain structure and function and how the brain maximizes the efficiency of information processing (Butz et al., 2014; Achard and Bullmore, 2007; Watts and Strogatz, 1998). It appears that during the first few years of life, when the brain is in an active phase of being built, early sensory experience has the greatest capacity to strengthen neural circuitry. Understanding how the timing of language experience shapes brain structure and function is the objective of this review, and bilingualism will serve as the model to make sense of how this early versus late experience affects brain organization.

2. Development of the language network: optimal periods in language acquisition

Language is a cardinal human ability that lends itself to the study of how age of experience differentially influences brain development. The capacity to distinguish spoken language from other sounds, in fact, appears to begin in utero, with newborns demonstrating a preference for their mother's speech (Decasper and Fifer, 1980). There is debate, however, as to how the neural systems that develop for language are affected by biological maturation and experience (Elman et al., 1997). Penfield and Roberts (1959) proposed that language acquisition is tied to and restricted by age-dependent plasticity, basing their hypothesis on the more successful recovery of language function in children than in adults following surgery, and positing that young children had the facility to learn multiple languages. Lenneberg (1967) popularized Penfield and Roberts' (1959) observation that the acquisition of a fully native-like language capacity was constrained by age, becoming progressively more difficult to attain after a *critical period* that he believed ended at puberty, reflecting a significant degree of brain maturation.

Neuroimaging studies of language development in neonates and young children have provided considerable data about when fetuses and newborns can discriminate sounds and frequency changes. Discriminative ability of the auditory system is a prerequisite for the development of language. Draganova et al. (2007), using magnetoencephalography (MEG), demonstrated that two-thirds of fetuses as young as 28 weeks gestation and 89% of neonates responded to a change in tone-burst frequency. Perani et al. (2011) used fMRI and diffusion tensor imaging (DTI) to study the neuroanatomic basis for the discrimination of different speech sounds and prosodies by newborns, and observed that two-day-old infants activated language regions bilaterally, with dominance in the right auditory cortex. Moreover, three-month-olds were found to process speech in the inferior frontal gyrus (IFG) and temporal regions, similar to adults. Activation in the superior temporal gyrus (STG) and in the primary and secondary auditory cortices was also observed in response to normal speech. In addition, DTI has revealed a dorsal axonal pathway connecting the temporal and premotor cortices, providing a route for sensory-to-motor mapping, thus facilitating the processing of phonological feedback, a necessity during the babbling phase of language development (Goldstein and Schwade, 2008). The early presence of this pathway strengthens the connection between language perception and language production required for the subsequent acquisition of speech (Perani et al., 2011). Although evidence suggests that connectivity between the IFG and the temporal cortex (i.e., the arcuate fasciculus) has not yet formed in the 1–4 month postnatal period, one might speculate that early language input might have an organizing effect on this developing connection (Dubois et al., 2008).

An fMRI study by Dehaene-Lambertz et al. (2002) provided further evidence that the cortical language substrate was significantly developed in infants at 3 months of age, demonstrating that there was increased activity in response to speech, especially in the superior temporal gyrus, with lateralization of activity to the left STG at the level of the planum temporale (Wernicke's area). Of note, similar levels of activity were induced in the temporal lobe with both forward and backward speech, suggesting that, although this structure is functional in 3-month-olds, it has not yet acquired an adult-type preference for native language at this juncture (Dehaene-Lambertz et al., 2002).

The maturation of speech production ability correlates with a remarkable increase in overall brain size as the child transitions from babbling to one- and two- word utterances, to full sentences, reaching adult size before age 6, and 80% of its ultimate volume at the time of sentence production (Sakai, 2005). The greatest increase in cortical surface area occurs during the first and second years of life (1.80 times and 1.20 times respectively; Li et al., 2013), with considerable tertiary folding occurring postnatally, driven by specific patterns of cortical connectivity (Nie et al., 2012; Van Essen, 1997). The variability in the folding observed in the adult brain, however, is thought to be established by the time of birth (Hill et al., 2010). Of note, the most significant growth of the STG occurs during the first year of life, an observation consistent with the functional evidence of the very early development of the infant's ability to discriminate speech sounds. An anatomical sequence study of cortical development in young children demonstrated that the earliest parts of the brain to mature are the motor and sensory brain areas, followed by regions involved in spatial orientation and speech and language, including parts of the temporal lobe and the IFG. Other parts of the temporal lobe, however, have a more protracted course of development into adulthood (Gogtay et al., 2004). This pattern of early maturation of language-related brain areas may account for a potential loss of the brain's capacity for cortical and subcortical reorganization in later childhood, although dynamic changes in the brain continue during development, with significant restructuring possible due to the growth of new synapses, progressive myelination, and the pruning of superfluous connections within networks (Homae et al., 2010; Gogtay et al., 2004).

3. Optimal period in bilingual language development

Since language develops from birth, the acquisition of a second language (L2), studied with the tools of neuroimaging, permits researchers to observe the attainment of a complex skill in a naturalistic environment. The structural and functional brain alterations associated with learning two languages concurrently from birth (simultaneous bilinguals) can be compared with observed changes related to learning a second language after the first language (L1) has already been established (sequential bilinguals). More broadly, understanding the patterns of L2-related neuroplasticity will likely help disentangle what are believed to be the two most important variables influencing the capacity for experience-dependent skill learning and brain development, namely, age of acquisition and proficiency (Perani and Abutalebi, 2005).

Evidence suggests that language acquisition is influenced from the beginning by both endogenous and experiential factors. For example, neonates prefer listening to speech over other sounds (Vouloumanos and Werker, 2004; Moon et al., 1993). In this regard, infants exposed to language from birth demonstrate, at first, a universal capacity to perceive the phonemes of all spoken languages (Kuhl, 2010; Werker and Tees, 1984; Eimas et al., 1971). By the age of 6 months, however, the child's ability to discriminate non-native phonemic contrasts begins to wane, initially for vowels and later for consonants (Kuhl, 2004; Kuhl et al., 1992; Werker and Tees, 1984). By 9–10 months of age, the pre-linguistic vocalizations

Please cite this article as: Berken, J.A., et al., Early bilingualism, language attainment, and brain development. Neuropsychologia (2016), http://dx.doi.org/10.1016/j.neuropsychologia.2016.08.031

of an infant in the conversational stage of babbling closely resemble the phonetics of their native language (Poulin-Dubois and Goodz, 2001). By 12 months, the phonetic capacity of the child has been tuned to acquire the language to which he has been exposed (Kuhl and Rivera-Gaxiola, 2008; Werker and Lalonde, 1988), resulting in the infant's accent becoming indistinguishable from that of a native speaker (Simmonds et al., 2011).

Such observations support the notion of a sensitive or optimal period in the infant's acquisition of language, especially with regard to phonological development, and there is abundant evidence for a correlation between age of acquisition and ultimate language proficiency (Newport et al., 2001; Moyer, 1999; Johnson and Newport, 1989). It appears, however, that there may be different optimal periods corresponding to the various aspects of language acquisition: phonology, syntax, morphology, and semantics. Werker and Tees (2005) described this phenomenon using the term "nested" optimal periods, implying some dissimilarity in the degree of flexibility and vulnerability of each language function to the effects of age.

With regard to phonology, phonetic tuning begins well before one year of age and affects how language sounds are processed (i.e., word segmentation, admissible phonetic combinations). The development of this "phonological awareness" in the first year of life, an appreciation for language sounds and the order in which they occur, appears essential for the acquisition of spoken language and the later development of secondary linguistic behaviors such as reading (Goswami, 2008; Ziegler and Goswami, 2005; Lyytinen et al., 2004). When this development is impeded during infancy (e.g., by chronic otitis media), deficits in phonetic categorization and stimulus timing may result, leading to reading and spelling difficulties later in childhood (Gravel et al., 1997; Clarkson, Eimas, and Marean, 1989). For example, a functional magnetic resonance imaging (fMRI) study of elementary school age children who were late speakers and who performed poorly on a battery of standardized tests of phonological processing skills, literacy, and spelling, demonstrated decreased activation in key language regions, providing further support for the long-lasting and deleterious effect of late speech development on other language processes (Preston et al., 2010).

Phonology appears to be a compelling indicator of how AoA affects language development, since, exposure to the sounds of the native language begins in utero and, appears to be the sensitive period that closes the earliest (Simmonds et al., 2011; Kuhl and Rivera-Gaxiola, 2008). A recent MEG study measuring theta brain rhythms further supports this notion, demonstrating that a learning-based narrowing of infant speech perception occurs between 6 and 12 months of age (Bosseler et al., 2013). Infants exposed to two languages simultaneously from birth, however, can discriminate the phonetic representations of each, even before speaking their first words (Burns et al., 2007). In addition, as noted, while 8- to 10-month old infants in a single language environment demonstrate language-specific boundaries and limitations in phonetic perception, infants exposed to two languages as newborns are able to discriminate and differentiate the phonological confines of both languages (Burns et al., 2007). It also appears that the timeline for the shift from language-general to language-specific processing is extended for the latter group (Werker and Byers-Heinlein, 2008).

It is a long-standing observation that few individuals who acquire a second language later in life are able to speak with a native-like accent (Flege et al., 2006; Asher and Garcia, 1969; Penfield and Roberts, 1959), even after years of practice, and despite high proficiency in all other aspects of language function (Reiterer et al., 2011; Johnson and Newport, 1989; Oyama, 1976). There is considerable literature, however, that demonstrates that simultaneous bilinguals are able to speak with native-like accents in both of their L1s, although some children who learn an L2 early may still speak that language with a detectable foreign accent (Flege et al., 2006; Flynn and Manuel, 1991).

Phonology appears to be the facet of language most associated with ultimate language ability. Moyer (1999), in fact, attempted to challenge the purported role of AoA as central to the development of native-like accent in a cohort study of non-native graduate students living in Germany and immersed in German as an L2. She found that, with the exception of one outlier, all of the late learners demonstrated the maturational defects of late acquisition in their phonology, despite high motivation to learn an L2, and native-like proficiency in all other aspects of the language. Such observations have been attributed to age-related limitations in the neuroplasticity of the motor and auditory systems and the influence of the established L1 phonological system on L2 speech learning (Flege et al., 1995; Flege et al., 1994; Flege, 1987; Baetens Beardsmore, 1986). Flege et al. (2006), in a study of Koreans immigrating to North America, noted that children had less accented speech in their second language, English, than did adults. However, the children, all over the age of 6 years, spoke with detectable foreign accents after 4 years of immersion in English-speaking schools. These authors attributed the milder, but still present accents of the immigrant children in part to greater L2 input than their adult counterparts. However, the children were all sequential bilinguals, ranging from 6 to 14 years of age. None could be considered to have acquired their two languages simultaneously during their earliest years of life, and thus the persistence of accented speech was not unexpected. Significant individual differences in accent quality exist among age- and exposure-matched late bilinguals, a variation posited to relate to intrinsic functional and structural differences in the frontoparietal language areas (Reiterer et al., 2011). Phonology, nevertheless, emerges as the language characteristic most constrained by age of acquisition, whether due to suboptimal recruitment of the neural circuitry subserving speech production, limitations on brain structural maturation, or differences in communication efficiency between speech-language areas. Interestingly, it appears that early childhood memory of language exposure persists despite many years of disuse (Oh et al., 2010) or even discontinuation (Pierce et al., 2014). For example, evidence suggests a superior ability of college-age Korean adoptees, adopted prior to one year of age, to identify Korean phonemes in college-level language classes compared with students without prior Korean language exposure (Oh et al., 2010).

4. Early bilingualism and the development of the language network

In early bilingualism, language enrichment during optimal periods of development may promote the development of new synapses, myelination, and the pruning of connections within neural circuits, molding and enhancing the maturation of the brain and furthering the development of neural networks (Hensch, 2005; Sur and Rubenstein, 2005). Because neuronal maturation occurs rapidly during the first few years of life, it is reasonable to postulate that this is the period during which the brain would be most sensitive to the effects of sensory experience. There is evidence that the onset and proper sequencing of events characteristic of an optimal period for neuroplasticity in a given sensory or motor system is triggered, at least in part, by experiential inputs. Experience appears to activate parvalbumin cells in the cortex (Werker and Hensch, 2015) that, under the influence of a variety of triggers and brakes (e.g., neurotransmitters and growth factors), turn the capacity for functional and structural change on and off, at different rates in different brain regions (Takesian and Hensch, 2013; Condé et al., 1996). Such experience-related neuroplasticity

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in the acquisition of language appears, however, to be constrained by the degree of neurobiological brain maturation, as suggested by the different responses of full- and pre-term infants to native language (Peña et al., 2010).

Experience with multiple languages from birth is accompanied by increased complexity of sociolinguistic and sensorimotor processing in order for the infant to learn about and interact with the environment. The consequence is an extension of or delay in the closing of at least one sensitive or critical period of language development (phonology; Flege et al., 1987; 1994; 1999) in order to develop the mapping between the sound structure of the languages. As a result, multi-language exposure may be taking greater advantage of developmental neuroplasticity by delaying the closing of a sensitive period. While the brains of both simultaneous and sequential bilinguals likely undergo reorganization throughout development and into adulthood, the substrate upon which these changes manifest is different for the simultaneous bilingual. Moreover, while the macroscopic differences in brain structure appear to be subtle when examined in adults with comparable levels of proficiency, there are differences in neural network efficiency that may be reflecting these developmental and more microscopic differences (Berken et al., 2016). Exposure to more than one language from birth may provide one important approach to enhance a range of cognitive and language processes and facilitate overall brain development.

5. Age of acquisition and the bilingual brain

After several decades of research, the debate continues regarding how neuroplasticity manifests functionally and structurally in the bilingual brain, specifically whether the same brain regions or supplementary areas are recruited to accommodate two languages and how the age of second language acquisition (i.e., biological maturation) impacts this process.

Bilingualism is an ideal window through which to study how the age of language learning affects the way the brain is built, since learning a second language is a skill that can be acquired both from birth and later in life. It appears that the ability to acquire language is likely governed by one or more constraining developmental periods (Flege et al., 1995). The question is, therefore, whether neuroplasticity manifests differently in bilinguals as a function of simultaneous versus sequential L2 acquisition, and if so, whether such differences relate to the concept of a sensitive period or are rather a function of disparities in proficiency. Most investigations have suggested an optimal interval for language acquisition, especially with regard to phonological attainment. Others, however, have argued instead for a progressive, linear decline with age in the potential for L2 proficiency (Wiley et al., 2005; Hakuta et al., 2003; Flege et al., 1995).

Studies using positron emission tomography (PET) and fMRI have attempted to determine whether age of acquisition results in different functional signatures in the bilingual brain. Although Kim et al. (1997) found evidence for the anatomical separation of the two languages in Broca's area in a heterogeneous group of late bilinguals, available evidence indicates that the acquisition and use of a second and even multiple languages (Briellmann et al., 2004; Vingerhoets et al., 2003) recruits the same neural structures implicated in the acquisition of a first language (Abutalebi et al., 2013; Abutalebi, 2008; Klein et al., 2006; Perani and Abutalebi, 2005; Perani et al., 1998; Dehaene et al., 1997; Klein et al., 1995, 1994). There is general consensus that functional differences in the bilingual brain manifest as alterations in regional brain activation rather than in the localization of involved language areas (Bloch et al., 2009; Abutalebi, 2008; Klein et al., 2006; Frenck-Mestre et al., 2005; Perani et al., 2003; Klein et al., 1995, 1994), although there are, some differences in the degree of hemispheric involvement in early as compared to late bilinguals and monolinguals (Hull and Vaid, 2006, 2007).

There is evidence supporting the view that these variations in the degree of language area recruitment are related to age of acquisition, in that late but not early bilinguals demonstrate increased activity of many neural substrates when speaking in an L2 compared with an L1 (Abutalebi, 2008). Such differences have been particularly salient in such regions as the IFG (Hernandez and Li, 2007; Golestani et al., 2006; Dodel et al., 2005; Wartenburger et al., 2003), and STG (Rüschemeyer et al., 2005), and several fMRI studies have also demonstrated greater activation of speech-motor areas in late bilinguals than in monolingual controls (Frenck-Mestre et al., 2005). For example, Klein et al. (1994) used PET while late bilinguals repeated words in their first and second languages and found increased recruitment of the left putamen in their L2, a finding that the authors attributed to a greater articulatory effort required to speak a late-learned L2, consistent with subsequent research (Abutalebi et al., 2013; Indefrey, 2006). Perani et al. (2003) found differences in the activation patterns in several brain areas of late versus early bilinguals performing a verbal fluency task. Similar to Klein et al. (1994), these authors posited that a later learned L2 recruits additional neural resources within the language network. The adaptive control hypothesis of Abutalebi and Green (Abutalebi and Green, 2007; Green and Abutalebi, 2013) is a particularly applicable way of looking at such observed differences in brain activation in early versus late bilinguals. The more extensive activation of brain-language regions in sequential bilinguals may reflect a more effortful adaptation of dual language control processes to the demands of a second language learned later in life.

It is likely that concomitant changes in language related brain structures occur that also reflect the second language experience. Mechelli et al. (2004) demonstrated quantitative differences in gray matter density using voxel-based morphometry (VBM) in the inferior parietal region in bilinguals relative to monolinguals, with GMD showing a negative correlation with age of L2 acquisition. Klein et al. (2014) observed significantly increased cortical thickness in the left IFG of late L2 learners compared to early and simultaneous bilinguals. In contrast, these authors found the reverse pattern in the right IFG, namely decreased cortical thickness in late bilinguals. There is evidence, however, that age of L2 acquisition may be a more potent determinant of GMD in the brains of younger versus older bilinguals, with years of language exposure being more important in the latter group (Abutalebi et al., 2015).

Recent studies provide neuroimaging support for different developmental paths for simultaneous and sequential bilinguals to attain high proficiency in two languages. For example, Berken et al. (2015a, 2015b, 2016) demonstrated that while the same structures are recruited in both simultaneous and sequential bilingual groups for speech in an L2 as in an L1, there are differences in the functional activity, connectivity, and structural characteristics of brain language areas. Thus, although neuroplasticity underlies both early and late second language learning, language experience may determine how the same brain substrates are sculpted and interconnected in ways that, while reflecting optimal period limitations, provide compensatory mechanisms to achieve second language proficiency.

In one study, Berken et al. (2015a) used an overt reading paradigm to look at functional brain differences in speech production between simultaneous and sequential bilinguals. Less native accent quality for sequential as compared to simultaneous bilinguals was the only distinguishing characteristic in language performance between the two groups. Both simultaneous and sequential bilinguals activated the motor cortex, the inferior frontal gyrus, the superior temporal gyrus, the thalamus, and the

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cerebellum bilaterally when reading aloud. However, while simultaneous bilinguals activated these areas to the same degree, whether reading aloud in either language, the sequential bilinguals demonstrated increased activation during L2 production in the left premotor cortex, the left inferior frontal gyrus, and cerebellum, areas involved in articulatory-motor planning and verbal fluency (Mariën and Beaton, 2014; Brown et al., 2005; Caramazza and Zurif, 1976), the left fusiform gyrus, a neural region important in decoding print-to-sound, and the inferior occipital cortex and anterior cingulate, regions that play important roles in visual attention and the control and monitoring of speech output (Dehaene et al., 2010; McCandliss et al., 2003; Cohen et al., 2002). Of significance, there was a positive correlation between AoA and activity in many of these regions, suggesting that when L2 experience occurs late, and the second language is learned to a high degree of proficiency, there will be greater activation of speech-motor and reading specific areas. Conversely, sequential bilinguals who acquire an L2 relatively early, but after the optimal period has ended, appear to rely less on brain areas involved in articulatory-motor and phonological processing, as evidenced by a less significant increase in activity in these cortical regions when speaking in the later-learned language. It seems, therefore, that the later in life that the second language experience begins, the greater the activity required to manage the demands of overt reading and articulation. Conversely, the earlier in life a second language is acquired, the less intense the hemodynamic response necessary for proficient speech.

Functional differences associated with age of acquisition are not only evidenced by levels of activation in brain regions involved in language processing and production, but also by functional connectivity within the language network. In particular, resting-state fMRI determines the functional connections between anatomically separated brain areas at rest, in the absence of task-driven behavior, providing information about the organizational patterns in the brain related to a cumulative bilingual experience. Berken et al. (2016) investigated the resting-state connectivity profile of the IFG, a region that previously emerged from several neurofunctional (Berken et al., 2015a; Klein et al., 2006, 1995) and neurostructural (Berken et al., 2015b; Klein et al., 2014) studies in bilinguals, and found greater connectivity between the left and right IFG in simultaneous bilinguals than sequential bilinguals, as well as between the IFG and brain areas involved in language control, including the dorsolateral prefrontal cortex, inferior parietal lobule, and cerebellum. Increased connectivity between the IFG and these brain regions correlated significantly and negatively with age of L2 acquisition in sequential bilinguals, as shown by regression analysis, indicating that the earlier a language is acquired, the more distributed is the network between brain-language areas. Greater functional connectivity between the left and right IFG was also associated with reduced neural activation in the left IFG during speech production. The authors posited, therefore, that increased connectivity at rest and reduced task-driven brain activation in the left IFG during speech performance reflects greater neural efficiency in this important cognitive area. Taken together, these findings highlight how the brain's intrinsic functional patterns are influenced by the developmental timeline in which second language acquisition occurs, and point to a more optimized mechanism to achieve L2 proficiency, when language is learned during the period of significant brain growth and neuroplastic potential.

In addition, since the right IFG plays an important role in response inhibition and attentional control (Hampshire et al., 2010; Hampshire and Owen, 2006; Dove et al., 2000), increased connectivity between speech-motor areas in the left hemisphere and this right hemispheric structure might facilitate more efficient inhibition of the competing language system by simultaneous bilinguals. However, in the case of sequential bilinguals, in whom connectivity networks have already matured prior to the onset of second language experience, the establishment of such interhemispheric connections may be limited by optimal period constraints. Notably, Berken et al. (2016) found that functional connectivity between the left IFG and several other frontal and parietal regions, including the inferior parietal lobule within the frontoparietal network, also varied negatively with L2 AoA, suggesting less interaction between brain language areas in late L2 learners.

As well as observing decreased connectivity between the IFG and distributed language areas in the brains of sequential as compared with simultaneous bilinguals, Berken et al. (2016) demonstrated a negative correlation between resting-state functional connectivity and neural activation during speech production. This observation, coupled with previous findings of greater activity in the left IFG of sequential bilinguals (Berken et al., 2015a) and of age-dependent differences in cortical thickness within the IFG (Klein et al., 2014), suggests that bilinguals who acquire a second language beyond the optimal period enlist compensatory mechanisms to approximate native-like speech, when the brain has already developed efficient activity patterns for a single L1, while simultaneous bilinguals draw upon efficient, neural connections to minimize neural effort during speech production.

In addition to these recent functional studies, Berken et al. (2015b) explored AoA effects on brain structure using whole brain VBM to examine highly proficient simultaneous and sequential bilinguals. Simultaneous bilinguals had greater GMD in the left putamen, prefrontal, insular and occipital cortices compared with sequential bilinguals. Only the bilateral premotor cortex had greater GMD in sequential bilinguals. These results suggest that increased GMD in the left putamen is an effect of acquiring two languages from birth that facilitates native-sounding speech. Interestingly, the authors also found a correlation between gray matter density in the left putamen and accent skill in the highly proficient sequential bilinguals, indicating that this structure is important for native-like articulation whether the second language is acquired early or later in development. In addition, sequential bilinguals with more native-like accents demonstrated greater GMD in the left premotor cortex, left IFG, right primary motor cortex, right Heschl's gyrus, right lateral occipital cortex, right cerebellar vermis, and bilateral inferior parietal lobule, suggesting that sequential bilinguals attain articulatory proficiency differently than do simultaneous bilinguals.

6. Conclusions

Language acquisition is likely determined by a series of nested optimal periods of variable onset, offset, and duration that are influenced by both pre-programmed molecular signals and sensory experience (Werker and Hensch, 2015). With regard to the acquisition of two languages from birth, it appears that enriched language exposure results in equivalent proficiency in both learned languages. This occurs because the window for language development is open and because the brain has the capacity to rather easily streamline the wiring of neural circuitry serving the two languages. At the microscopic level, an enriched bilingual environment during the neonatal period may result in a cascade of biochemical events that increase production of the cellular substrates that regulate neuroplasticity, as well as the duration of their synthesis. This in turn, might result in macrostructural changes that manifest as efficient activation during speech, increased size of certain brain-language areas, and stronger connections between distributed brain regions within the language network. Such neuroplasticity takes place in order to manage and

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monitor each language and to prevent interference between the two. The degree to which these changes can occur depends on the age of second language exposure. When exposure occurs after the optimal periods for language acquisition are closing or have closed, neuroplasticity still occurs, allowing for L2 acquisition throughout the lifespan. However, the mechanisms for such neuroplasticity later in life are likely to be qualitatively and quantitatively different from those biologically programmed to begin and end in early childhood.

Second language acquisition shares similarities with the development of behaviors in other sensory domains, such as vision, which appear limited by optimal periods. Deprivation of visual stimulation to an eye from birth, but not later in life, results in amblyopia, irreversibly diminished visual acuity in that eye (Holmes and Clarke, 2006; Wiesel and Hubel, 1963). In addition, for congenitally deaf children, cochlear implantation must be done early in order to maximize the development of the auditory system (Giraud and Lee, 2007). In contrast to reports of sensory deprivation, evidence in the animal literature indicates that stimulatory environments in juvenile, but not in mature mice, increase neurogenesis, and brain connectivity (Hosseiny et al., 2015). In view of these observations, it appears that optimal brain development is facilitated by an enriched sensory environment early in life.

The patterns of language development revealed by recent neuroimaging studies similarly reflect differences in early versus late experience. When two languages are acquired simultaneously from birth, brain function and structure appear to be most effectively organized. When second language expertise develops later in life, however, the ability for neuroplastic change appears to be more limited, and thus the proficient acquisition of a second language takes a different path.

Acknowledgments

Supported by grants from the Natural Sciences and Engineering Research Council of Canada (NSERC) (RGPIN-201405371) to D. Klein and V. Gracco, a Vanier Canada Doctoral Scholarship (NSERC) to J. Berken VCGS3 - 428288 - 2012, the Blema and Arnold Steinberg Family Foundation, and the National Institute on Deafness and Other Communication Disorders (DC012502). We thank Kate Watkins and our colleagues from the Montreal Bilingual Brain Initiative (Shari Baum, Debra Titone, Natalie Phillips) for conversations and thoughts about bilingualism and the brain.

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Please cite this article as: Berken, J.A., et al., Early bilingualism, language attainment, and brain development. Neuropsychologia (2016), http://dx.doi.org/10.1016/j.neuropsychologia.2016.08.031