Neural consequences of bilingualism for cortical and subcortical function

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We are what we repeatedly do.
Excellence, then, is not an act, but a habit.

(Aristotle)

27.1 Introduction

Experience is a prime catalyst for change in the human brain and this capacity for change enables us to optimally engage with our environment. Just as continued practice swinging a tennis racket can lead to increased muscle strength in the racket-swinging hand (Lucki & Nicolay, 2007), the nervous system dynamically adapts to meet task demands. Underlying this experience-dependent plasticity are structural and functional changes in brain regions engaged by these experiences. For example, learning to play golf results in plasticity of the sensorimotor cortex (Bezzola et al., 2011), learning to juggle induces plasticity in neural centers devoted to complex visual processing (Draganski et al., 2004), and practicing a musical instrument drives plasticity in auditory areas (Kraus & Chandrasekaran, 2010; Schlaug, Norton, Overy, & Winner, 2005). While active engagement in skill-based training reshapes training-related neural circuits, native language acquisition, a fundamental aspect of normal human development, plays a key role in shaping neural circuitry throughout the brain (reviewed in Huttenlocher, 2009). This pervasive wiring of cognitive and sensory circuits for language facilitates expertise in a given language and in doing so language exerts a stronghold on sensory abilities such that...
seeing an object is sufficient to activate its linguistic label (Chabal & Marian, under review).

Acquisition of more than one language offers a distinct way to tune cognitive and sensory circuits to wire the brain with the ability to communicate in a multilingual environment (e.g., Abutalebi et al., 2011; Luk et al., 2011; Mechelli et al., 2004). For example, by learning more than one language, bilinguals necessarily have to make a variety of sound-to-meaning connections that they must subsequently compartmentalize into their two language systems (Shook & Marian, 2013). Moreover, whereas language input leads to activation of the single language system in a monolingual, in a bilingual both languages are automatically activated (Kuipers & Thierry, 2010; Marian & Spivey, 2003a; Shook & Marian, 2012; Spivey & Marian, 1999) and so one language must be inhibited for communication to proceed (Kroll et al., 2008; van Heuven et al., 2008). This process of cross-linguistic co-activation and the need to inhibit the irrelevant language necessitates increased activation of the executive system during communication for a bilingual relative to a monolingual. The heightened need to actively engage inhibitory and attentional processes – functions of the executive system – during communication leads to an enhancement in some executive abilities. For example, bilinguals show cognitive control advantages on tasks requiring attentional focus, conflict resolution, switching, and flexibility (Bialystok, 2005, 2009c, 2011; Bialystok & Craik, 2010; Bialystok & Majumder, 1998; Bialystok & Martin, 2004; Bialystok, Martin, & Viswanathan, 2005; Bialystok & Viswanathan, 2009; Carlson & Meltzoff, 2008; Krizman et al., 2012; Martin-Rhee & Bialystok, 2008). Moreover, because bilinguals may utilize the components of the executive network differently as a result of their experience managing multiple languages (Abutalebi et al., 2011) this may result in differences in how they interact with their auditory environment relative to monolinguals (Blumenfeld & Marian, 2011). Given this unique auditory–executive link resulting from experience with more than one language, in this chapter we explore the neural consequences of multilingualism on cognitive and sensory function through the lens of the auditory and executive systems.

27.2 Anatomy of the auditory and executive systems

27.2.1 Overview of the executive system

The executive system exerts top-down control on cognitive and sensory processing. Brain areas that are implicated in cognitive control include the prefrontal cortex, the anterior cingulate cortex, and the basal ganglia, including the caudate and putamen of the striatum (see Figure 27.1) (MacDonald et al., 2000; Redgrave, Prescott, & Gurney, 1999; Zou et al.,
27.2.2 Overview of the auditory system

The auditory system encodes sounds, including language, and consists of a series of neural relays extending from the cochlea to the cortex (see Figure 27.1). At the cochlea, the sound wave is translated into electricity, the currency of the nervous system, and from there is conducted along the ascending auditory pathway. These ascending fibers, or “bottom-up” pathway, carry all auditory-based sensory signals to the brain; there is not a unique ascending pathway for speech relative to non-speech sounds. However, the auditory midbrain and primary auditory cortex do show specialized responses to meaningful vocalizations (De Lucia, Clarke, & Murray, 2010; Woolley et al., 2005; Woolley, Gill, & Theunissen, 2006; Woolley, Hauber, & Theunissen, 2010). What mediates this differential neural response for conspecific vocalizations relative to other auditory stimuli is signaling from the “top-down” or descending auditory system, which extends from the cortex to the cochlea. These descending fibers carry regulatory or feedback information from higher to lower processing centers with the effect of modifying the ascending signal along the auditory pathway. This pathway can function to enhance sensory encoding of relevant signals and inhibit or minimize encoding of irrelevant ones, suggesting an intimate link between auditory and executive systems. Structural support for this link is seen in the projections between executive and auditory centers of the cortex, such as the link between the superior temporal gyrus (i.e., auditory cortex, see Figure 27.1) and the anterior cingulate cortex (Jürgens, 1983), as well as connections between the inferior colliculus...
Figure 27.1 Schematic of the nuclei of the auditory and executive systems. Note: Auditory processing begins at the cochlea, where sound waves are translated into electricity, the currency of the nervous system. This electrical signal is carried from the cochlea to the cochlear nuclei (CN) via the cochlear division of the vestibulocochlear nerve (i.e., 8th nerve) and it subsequently ascends to the superior olivary complex (SOC) of the brainstem. From the brainstem, the signal travels to the inferior colliculus (IC) of the midbrain by way of the lateral lemniscus (LL). The inferior colliculus projects auditory information to the medial geniculate body (MGB) of the thalamus in the midbrain, which subsequently sends auditory information to the primary and secondary auditory cortex (AC) in the left and right superior temporal gyri located on the temporal lobes. At each neural relay, innervation from the ascending system is tonotopically maintained, meaning that the frequency information from the sensory signal is conserved in a spatial arrangement throughout the auditory system. Brain areas that are implicated in cognitive control include the prefrontal cortex, the anterior cingulate cortex, and the basal ganglia, including the caudate and putamen of the striatum. Gray lines indicate top-down (efferent) connections, black lines indicate bottom-up (afferent) projections. Gray ovals are nuclei of the auditory system and black ovals are relays of the executive system.

(i.e., auditory midbrain, see Figure 27.1)\(^1\) and basal ganglia (Casseday et al., 2002; Moriizumi & Hattori, 1991). Additionally, encoding of auditory information in both the midbrain and cortical structures are sensitive to attention (Hairston, Letowski, & McDowell, 2013; Jäncke, Mirzazade, & Joni Shah, 1999; Mesgarani & Chang, 2012; Rinne et al., 2008; Woldorff et al., 1993). These connections between neural regions devoted to auditory processing and executive function likely exist to enhance encoding of acoustic stimuli that carry a learned behavioral significance, such as

\(^1\) The inferior colliculus is located in the midbrain. It is an auditory nucleus that integrates across many ascending auditory fibers and is innervated by efferent fibers from cortical structures. The inferior colliculus plays a key role in sound localization, integration of sensory information across different sensory systems (e.g., audio and visual), and potentially filtering of relevant from irrelevant auditory signals (the inferior colliculus is discussed in great detail in Casseday, Fremouw, & Covey, 2002; Huffman & Henson, 1990).
language, and may underlie the specialized neural responses to speech that are evident in these auditory cortical and midbrain structures.

27.3 Auditory and executive systems develop under the influence of language experience

27.3.1 A monolingual perspective on language development

From infancy, the brain is sculpted by experience and experience provides a strong influence on our subsequent interactions with the world. Through experience, our nervous system becomes capable of dynamically responding to the world in a behaviorally appropriate manner. Within the context of language learning, experience-dependent plasticity in the auditory and executive systems is a natural developmental process that selectively strengthens communication abilities for one’s native language. Indeed, while infants are able to discriminate phonetic contrasts across many languages for a short period after birth (Eimas et al., 1971; Trehub, 1976; Werker & Tees, 1984), with continued exposure to a native language, discrimination abilities are selectively honed for that native language (Kuhl et al., 2006). As this process occurs, the infant transitions from being a universal speech perceiver to a language-specific speech perceiver by 6 to 12 months of age (Cheour et al., 1998; Kuhl et al., 1992, 2006). These enhancements of within-language phoneme discrimination provide the building blocks on which sound-to-meaning mappings for that language can be made. However, expertise in the native language comes at the expense of perception of non-native languages: as fluency in the native language increases from phoneme discrimination to knowledge of words and phrases and the acquisition of syntax, the individual becomes relatively insensitive to non-native contrasts (Krishnan et al., 2005; Miyawaki et al., 1975). Accompanying this change in behavior is a change in the underlying neural architecture.

During normal development of a single language, exposure to native phonemic contrasts sculpts the neural architecture to selectively enhance the recognition of these contrasts while diminishing discrimination of non-native contrasts (Cheour et al., 1998; Kuhl et al., 2006). The neural changes underlying language development appear to rely on the same mechanisms that are known to underlie development generally (Nixdorf-Bergweiler et al., 1995). Normal development is characterized by excessive proliferation of synapses early in life, which can be indexed as changes in gray matter density or gray matter volume (Craik & Bialystok, 2006; Gilmore et al., 2007). Across the brain, this heightened synaptic density

2 Gray matter is the collective of neuronal cell bodies, dendrites, unmyelinated axons, glial cells (i.e., supporting cells), and blood vessels (i.e., capillaries).

3 Synaptic density refers to the number of synapses per unit area on a given neuron.
persists through early childhood but synapses are subsequently pruned through late childhood into early adulthood to include those that are necessary for function, such as the connections enabling communication in one’s native tongue (Chechik, Meilijson, & Ruppin, 1999; Craik & Bialystok, 2006; Paolicelli et al., 2011). This synaptic pruning is experience dependent (Zuo et al., 2005), is a neural correlate of learning (Craik & Bialystok, 2006) and is competitively driven by Hebbian mechanisms (Hebb, 1949), where neurons activated in response to an experience can strengthen one another and their strengthened activation can lead to the elimination of quiescent synapses (Chechik et al., 1999; Glazewski & Fox, 1996). Ultimately, synaptic pruning increases synaptic efficiency (Balice-Gordon & Lichtman, 1994; Kerschensteiner et al., 2009; Mimura, Kimoto, & Okada, 2003). The outcome of this synaptic pruning is the formation of an expert system that is optimally primed to respond to the environment in a way that has been behaviorally meaningful in prior experiences (e.g., a native English speaker becomes expertly capable of communicating in English).

Additionally, during this period of early language development, changes are occurring in white matter, which is primarily made up of myelinated axons. Although changes in myelination may be largely genetically pre-programmed (Craik & Bialystok, 2006; Tsuneishi & Casaer, 2000) experience does appear to play some role in myelination as it has been shown that increased electrical activity in axons can drive increases in myelination, while a lack of electrical activity can lead to reductions in myelination of those silent axons (Demerens et al., 1996). Given this relationship between myelination and neural activity, it is possible that white matter density may increase with second language experience (e.g., Mohades et al., 2012).

### 27.3.2 A sensitive period for language learning

Optimal native-language learning occurs within a sensitive period (Werker & Tees, 2005). Though the term critical period and sensitive period have sometimes been used interchangeably (e.g., Bruer, 2001; Ruben, 1997), they refer to two distinct ideas. A critical period is defined as a developmental time point in which an experience must occur for a skill (such as language) to be acquired (Lenneberg, 1967). A sensitive (i.e., optimal) period, however, is defined as a time when an experience can have the

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4 These changes in synaptic density are not uniform throughout the brain. Maturation of brain structures occurs in a caudal-to-rostral direction (Rakic, Bourgeois, & Goldman-Rakic, 1994) with synaptic density peaking in the auditory system at 3 months (Ruttenlocher & Dabholkar, 1997), followed by experience-based pruning, a timescale that supports a relationship between changes in synaptic connectivity in auditory structures and language development.

5 Myelination is the accumulation of a fatty layer around a nerve cell, normally around the axon of the nerve cell, to improve transduction of the electrical signal that is carried by the nerve.

6 To avoid confusion, Werker and Tees refer to this period as an "optimal period." This is because until recently 'critical period' and 'sensitive period' were used interchangeably when describing language acquisition.
greatest influence on acquiring a particular skill (Bornstein, 1989; Knudsen, 2004). Early childhood is a developmental period when neural resources are in abundance and the nervous system is highly malleable (Chechik, Meilijson, & Ruppin, 1998), two necessary ingredients of a sensitive period (Greenough, Black, & Wallace, 1987; Jolles & Crone, 2012; Knudsen, 2004) and so early childhood has been suggested as being a sensitive (i.e., optimal) period. It is within a sensitive period that the greatest changes in synaptic density, and subsequently gray matter volume, occur (i.e., experience-dependent pruning of the overabundance of existing synaptic connections; Knudsen, 2004). Native language experience within this sensitive window of development facilitates expertise in the language while failure to be exposed to language within this optimal period results in difficulty acquiring native-like language abilities (as evidenced by children raised in isolation, Curtiss, 1977, 1989). Auditory-based language input during the sensitive period appears to be a major factor in language outcomes as evidenced by the relationship between age of cochlear implantation and eventual language abilities (McConkey Robbins et al., 2004) and the inability of a young bird to learn its song in the absence of a tutor early in life (Doupe & Kuhl, 1999; Mooney, 1999). Moreover, evidence from deaf children implanted with cochlear implants at various ages within this optimal developmental window also suggests that auditory-based language experience provides the scaffolding upon which some executive abilities develop (Cleary, Pisoni, & Geers, 2001; Conway, Pisoni, & Kronenberger, 2009).

27.3.3 Neural consequences of second language learning
In regard to second language learning, there is a strong relationship between the age at which a second language is acquired and the subsequent proficiency in that language (e.g., see Hakuta, Bialystok, & Wiley, 2003), where a later age of acquisition often relates to lower proficiency. Given that some level of second language proficiency is seen throughout life, this has been taken as evidence against the ‘critical period hypothesis’ (Birdsong & Molis, 2001; Flege, 1999; Hakuta et al., 2003), which posits that the nervous system is only capable of language acquisition within a finite developmental period extending from infancy to puberty (e.g., see Lenneberg, 1967). In addition to second language learning, evidence of late-in-life learning and subsequent neuroplasticity for other skills has further debunked the hypothesis that acquisition of a skill must occur before the door to the critical period closes (Boyke et al., 2008; Draganski et al., 2004).

Although the greatest neural and behavioral changes tend to occur early in childhood, in contrast to the critical period hypothesis, experience-based neuroplasticity persists throughout life, suggesting that the door for learning never fully closes. That ultimate attainment wans with
increasing age of acquisition would however support the proposed ‘sensitive period’ (Johnson & Newport, 1989; Krashen, Long, & Scarcella, 1979). Indeed, it would be expected that a sensitive period – especially one that slowly declines but never fully closes – would result in a negative relationship between age of acquisition and proficiency, with the trend that earlier acquisition relates to higher proficiency and later acquisition relates to lower proficiency. On the other hand, the relationship between age of acquisition and proficiency also has been interpreted as resulting from greater interference by the more developed native language system with increasing age of second language acquisition (e.g., see Flege, Yeni-Komshian, & Liu, 1999). Whether the relationship between proficiency and age of acquisition results from maturational (i.e., optimal period) changes or interference from prior learning, it is likely that neural encoding of the second language is influenced by proficiency and acquisition age. In support of a relationship between brain structure and behavior, these metrics (i.e., proficiency and age of acquisition) have been shown to track with differences in neural encoding of the second language: poorer neural responses to second language utterances, as indexed by evoked response potentials, are seen with increasing age of second language acquisition (e.g., Peltola et al., 2012; Weber-Fox & Neville, 1996) and decreased proficiency (Peltola et al., 2003).

These changes in the evoked neural response to second-language utterances likely reflect differences in the neural architecture underlying the second-language abilities, with more robust evoked responses relating to enhancements in the neural structures. Support for this link between auditory evoked potentials and neural structure comes from work in congenitally deaf cats fitted with cochlear implants which find that evoked activity increases as gray matter density increases (i.e., with increased synaptic density; Kral & Sharma, 2012; Kral et al., 2005). Therefore, increases in evoked response potential in individuals who acquired their second language early in life suggests that linguistic experience increases gray matter density, potentially through increases in synaptic connectivity, and that differences in age of second language acquisition are linked to differences in the underlying neural architecture (e.g., Grogan et al., 2012). Moreover, if the auditory and executive systems are involved in second language acquisition and language acquisition is heightened during the sensitive period, then areas devoted to auditory and executive processing should show greater gray matter density in multilinguals relative to monolinguals and this change in gray matter density should be dependent on age of acquisition, with larger increases in gray matter density being seen in bilinguals who learned both languages earlier in life (e.g., see Mechelli et al., 2004). Furthermore, if plasticity in the auditory and executive systems are dependent on language experience, then the degree of plasticity observed in these regions should be dependent upon the number of languages the
individual knows (e.g., trilinguals would show greater plasticity than bilinguals).

Indeed, evidence for language-dependent plasticity resulting in enhancements in neural structure for bilinguals relative to monolinguals is seen in both auditory-related and executive systems. Bilinguals who learned both languages within the presumed sensitive period for language (Johnson & Newport, 1989; Ruben, 1997) demonstrate structural differences from monolinguals in Heschl’s gyrus (Ressel et al., 2012), an area of the brain that comprises the primary auditory cortex (Figure 27.2). Ressel and colleagues found that early Spanish–Catalan bilinguals had larger Heschl’s gyrus volume than Spanish monolinguals. This volume difference was driven by greater volume of both white and gray matter in Heschl’s gyrus. Moreover, enhanced gray matter density in the inferior colliculus (i.e., auditory midbrain, Figure 27.2) has been found for simultaneous interpreters (Green, Crinion, & Price, 2006), lending further support to the involvement of auditory areas in multilingual language acquisition and use.

These structural enhancements in the auditory system are not limited to those who learned to speak multiple languages earlier in life. Longitudinal studies assessing second language learning in adults have found structural enhancements following second language learning in areas known to subserve language and auditory function, including increases in gray

Figure 27.2  Schematic of the nuclei of the auditory and executive systems. Note: The darker-colored structures are neural relays known to be sensitive to multilingualism. Abbreviations are: CN: cochlear nucleus; SOC: superior olivary complex; IC: inferior colliculus; MGB: medial geniculate body; AC: auditory cortex; BG: basal ganglia; ACC: anterior cingulate cortex; PFC: prefrontal cortex.
matter volume in the left inferior frontal gyrus (Osterhout et al., 2008; Stein et al., 2012), and increased cortical thickness in the superior temporal gyrus (which contains the primary auditory cortex, see Figure 27.2; Mårtensson et al., 2012). Additionally, although unable to disentangle pre-existing differences in neural structure from language training induced plasticity, two recent studies have shown that for monolinguals learning a foreign speech contrast, those who learned the foreign contrasts had a larger Heschl’s gyrus volume than those who struggled to learn the contrast (Golestani et al., 2007; Wong et al., 2008). Taken together, these results show that cortical and subcortical areas involved in auditory processing are sensitive to language experience and that these structures are likely involved in language acquisition and use for both monolinguals and bilinguals. Through their role in language learning, these auditory regions show higher gray matter density with increasing proficiency in the second language, suggesting a heightened involvement of these regions during multilingual communication.

Additionally, observations have been made for structural plasticity in areas that integrate auditory signals with information from other systems involved in language processing; and, these studies have found that the amount of plasticity in these regions is related to age of second language acquisition. For example, Mechelli and colleagues found higher gray matter density in the left inferior parietal cortex for bilinguals relative to monolinguals (Mechelli et al., 2004). The left inferior parietal region includes the angular gyrus and supramarginal gyrus. It lies roughly superior and posterior to the primary auditory cortex and it may provide an important connection between the auditory perception of a speech sound and its motor production (Hickok & Poeppel, 2000) as it is known to project to Broca’s area (Aboitiz & García, 1997). Not only are these auditory-related areas sensitive to age of acquisition of the second language, but they also demonstrate increased plasticity with increased number of languages. For example Grogan and colleagues (2012) examined structural plasticity in bilinguals and multilinguals and found that multilinguals who spoke two or more non-native languages had higher gray matter density in the right posterior supramarginal gyrus compared to bilinguals who only spoke one non-native language. Moreover, in bilinguals, gray matter density in the left pars opercularis (i.e., part of the left inferior frontal gyrus that comprises Broca’s area) was positively related to lexical efficiency in their second language. Other recent work has shown that in L1-German speakers increases in gray matter volume in the supramarginal gyrus and Broca’s area relate to better imitation of words and sentences in their second language (i.e., English) as well as a foreign language (i.e., Hindi) (Reiterer et al., 2011). Though for a long time Broca’s area was thought to be involved exclusively in language production, there is evidence that this area is also involved in language comprehension, including the processing of complex sentences (D’Ausilio, Craighero, & Fadiga, 2012;
Rogalsky & Hickok, 2011) and understanding of auditorily presented instructions (Schäffler et al., 1993). Thus, not only is the neural architecture of the auditory midbrain (i.e., inferior colliculus) and auditory cortex (i.e., superior temporal gyrus) shaped by language experience, but the cortical areas that these structures send auditory information to, such as the angular gyrus and supramarginal gyrus, are also sculpted by experience with multiple languages. This plasticity suggests that brain regions that interact with auditory structures are also highly involved in multilingual communication.

It is not only auditory areas or auditory-associated areas of the brain that show plasticity with the acquisition of a second language. Studies have also shown that following acquisition of novel phonological-to-orthographic mappings, larger evoked responses to the learned orthography are seen in the visual word form area, which has been taken as evidence for experience-dependent plasticity (Song et al., 2010). Moreover, while future research should investigate the structural changes associated with improved production in a second language, behavioral measures of learning a difficult to perceive phonetic contrast in a second language (e.g., /r/-/l/ distinctions for Japanese speakers) appear to support the idea that changes in performance are driven by Hebbian-based plasticity (McCandliss et al., 2002).

Moreover, the brain areas implicated in cognitive control (i.e., the prefrontal cortex, the anterior cingulate cortex, the caudate and putamen of the striatum, the inferior parietal lobe and the supplementary motor area) (Abutalebi et al., 2011; Zou et al., 2012) also show plasticity that is related to language experience (Figure 27.2). For example, it has been shown that bimodal7 bilinguals have greater gray matter density than monolinguals in the head of the left caudate nucleus (Zou et al., 2012). This neural structure is called upon when bilinguals switch between languages (Abutalebi et al., 2008) or when bilinguals encounter response competition (Abutalebi et al., 2008). It is likely, then, that the continued use of the caudate by bilinguals during daily communication leads to experience-based enhancements in the synaptic density of this structure. Furthermore, differences have been found between monolinguals and bilinguals in the anterior cingulate cortex. Though differences were not seen in overall gray matter density in this region, only in bilinguals was there a positive relationship between gray matter density in the anterior cingulate cortex and a measure of conflict resolution (Abutalebi et al., 2011). These results suggest that the neural infrastructure of the bilingual anterior cingulate cortex is optimally wired for resolving conflict and that the executive system is enhanced through experience with more than one language. Additional research should address the roles of age of acquisition and effects of knowing.

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7 Bimodal bilinguals are individuals who know two languages that differ in modality (e.g., oral and signed language), while a unimodal bilingual is an individual whose two languages are in the same modality (e.g., two spoken languages).
three or more languages on the structural plasticity of networks within this system.

Language is a multifaceted ability that relies on the integration of information across systems and so in addition to greater neural connectivity within the neural structures involved in auditory and executive processing, it is likely that the connections between these structures would be heightened in multilinguals as well. Indeed, in children aged 8–11 years, using fractional anisotropy as an index of white matter organization and structure, white matter along the left inferior occipitofrontal fasciculus was found to be higher in simultaneous bilinguals as compared to monolinguals, while sequential bilinguals had levels that were intermediate relative to the two other language groups (Mohades et al., 2012). This inferior occipitofrontal fasciculus is thought to be involved in semantic processing (Mandonnet et al., 2007) and is a tract that connects the venterolateral and dorsolateral prefrontal cortex with the posterior temporal lobe and the occipital lobe (Maheshwari, Klein, & Ulmer, 2012). Similarly, in older adults, white matter integrity in the corpus callosum is maintained in bilinguals, whereas monolinguals show age-related declines in white matter (Luk et al., 2011). The corpus callosum is the largest white matter structure in the brain and runs along the base of the cortex. It consists of a bundle of myelinated neural fibers that connect the two cerebral hemispheres. The differences in white matter integrity that are observed between older adult bilinguals and monolinguals were evidenced by higher fractional anisotropy values in the bilingual group that extended from the bilateral superior longitudinal fasciculi to the right inferior occipitofrontal fasciculus and uncinate fasciculus (Luk et al., 2011).

Enhancement of these neural tracts in bilinguals suggests that multilingual experience leads to a pervasive rewiring in the neural architecture, likely to meet the need for enhanced and efficient communication between the multitude of systems (e.g., auditory, visual, motor, executive) that are involved in language processing, a need that is presumed to increase with the addition of more than one language. Finally, young adults participating in intensive classroom instruction of Chinese demonstrated pervasive increases in white matter throughout the brain, which the authors interpreted as likely reflecting increased myelination; and, these increases positively correlated with class performance (Schlegel & Rudelson, 2012). The observed changes in white matter during language

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8 Fractional anisotropy is a measure of the directionality of diffusion of water molecules in the brain, whereby molecules located within a tract are restricted to diffuse in a specific (i.e., anisotropic) direction while water molecules outside of a tract have less restrictions on their movement. Fractional anisotropy is often used in diffusion imaging as an index of fiber density, myelination, or axon diameter (discussed in Hasan & Narayana, 2003).

9 The bilateral superior longitudinal fasciculi are a pair of bidirectional bundles of neurons that connect the frontier to the posterior of the cortex. This tract lies superior to the corpus callosum.

10 The uncinate fasciculus is a white matter tract that connects structures of the limbic system located in the temporal lobe with limbic structures in the frontal lobe.
learning provide additional evidence for the role of language in driving neural enhancements.

### 27.3.4 Potential mechanisms underlying differences in neural infrastructure

Two possible mechanisms may underlie differences in neural structure between monolinguals and multilinguals: increased synaptic pruning in monolinguals (de Bot, 2006) and structural plasticity in multilinguals (Mechelli et al., 2004). The close of the sensitive period is marked by stabilization of neural circuitry and a significant reduction in experience-dependent synaptic pruning (Jolles & Crone, 2012; Knudsen, 2004). It is possible that monolingual language abilities are optimal in a system that has fewer synaptic connections than what is needed to facilitate multilingual communication. Experience with a single language within this sensitive window would therefore lead to greater synaptic pruning in the monolingual brain (de Bot, 2006). This honed system would afford the monolingual expertise in the native language but may come at the expense of easily acquiring new languages. A relationship between language experience and amount of synaptic pruning would suggest that acquisition of more than one language inside the sensitive period would result in a greater number of synaptic connections being retained in multilinguals. Moreover, it is possible that the number of connections that are maintained are also dependent on age of acquisition (e.g., Mechelli et al., 2004) in addition to the number of languages acquired within this window (one language vs. two languages, e.g., Mohades et al., 2012).

It is also likely that differences in the neural architecture of monolinguals and multilinguals results from experience-induced plasticity and growth of additional neural connections in the multilingual brain. The differences in gray matter density and volume observed between multilinguals and monolinguals could come from experience-induced increases in synaptic connectivity in areas that subserve multilingual language abilities. Experience with more than one language, then, may serve as one form of environmental enrichment in humans that bolsters gray matter changes in the brain. Through animal work on environmental enrichment, it is known that the mechanisms underlying gray matter increases include dendritic arborization (i.e., an increase in the proliferation of dendrites) which leads to greater dendritic density (Ip et al., 2002), sprouting of new axon terminals (Knudsen, 2004) the formation of new blood vessels (i.e., angiogenesis, Black, Sirevaag, & Greenough, 1987), and increased proliferation of both supporting cells (i.e., gliogenesis; Soffié et al., 1999) and nerve cells (i.e., neurogenesis; Kempermann, Kuhn, & Gage, 1997; Nilsson et al., 1999) in the neural region undergoing experience-dependent changes.
Through the enriched environment of multiple languages, multilinguals also demonstrate white matter plasticity. Increased myelination, through myelination of previously unmyelinated axons, or thickening of the myelin sheath of myelinated axons (Juraska & Kopcik, 1988; Markham et al., 2009; Sanchez et al., 1998) underlies the experience-dependent changes in white matter. These changes in myelination may improve conduction velocity, or improve the connection between separate areas of the brain that are simultaneously engaged during the plasticity-inducing experience (e.g., multilingual communication).

### 27.4 Connectivity between auditory and executive systems

Interestingly, the processes that are involved in auditory comprehension of language are presumed to provide the scaffolding for the development of domain-general executive functions (Conway et al., 2009; Pisoni & Cleary, 2004), suggesting that there is a strong link between development of cognitive skills and phonetic discrimination abilities (Kuhl & Rivera-Gaxiola, 2008). Indeed, the auditory and executive systems appear to be highly intertwined, with connections between auditory and executive systems evident both cortically and subcortically (Figure 27.2). These connections have been structurally observed between the anterior cingulate cortex and the auditory cortex (Jürgens, 1983) and between the basal ganglia and the inferior colliculus (Casseday et al., 2002). There have been functional connections observed between the frontal cortex and inferior colliculus (Raizada & Poldrack, 2007) as well as frontal cortex and auditory cortex (Wu et al., 2007). These structural and functional links between the auditory and executive system suggest a privileged role of auditory-based stimuli in facilitating interaction with the environment in a behaviorally relevant manner.

At any given moment, the various sensory systems will receive and subsequently bombard the brain with more information than the brain is capable of processing (e.g., see Marois & Ivanoff, 2005). The ability to perform higher-level actions, such as those involved in communication, requires the cognitive system to not be solely influenced by the incoming stimulus but to also incorporate prior experience (e.g., whether that signal was behaviorally meaningful in the past) in influencing how the stimulus is encoded and responded to. Activation of the executive system influences sensory encoding to focus the brain’s processing capacity on the encoding of sensory stimuli necessary for achieving behaviorally relevant goals as opposed to responding to sensory stimuli in a reflex-like manner (Koechlin & Summerfield, 2007).

The auditory system is sensitive to the effects of the executive system on neural processing. For example, attention to stimuli in another modality decreases neural encoding of auditory stimuli in the inferior colliculus.
(i.e., auditory midbrain) and auditory cortex (Hairston et al., 2013; Oatman, 1976). On the other hand, attentional focus to auditory stimuli selectively enhances important features of the auditory signal in both the auditory midbrain and cortex (Galbraith & Arroyo, 1993; Galbraith et al., 1998; Jäncke et al., 1999). Although the afferent, bottom-up auditory signal begins as a faithful encoding of the incoming stimulus, through descending projections, the executive system configures neural processing in auditory midbrain and cortical structures to meet the current task demands. Physiological studies demonstrate that the top-down (i.e., efferent) pathway can affect many aspects of subcortical processing, including filtering, sharpness of tuning, and response plasticity (Gao & Suga, 1998, 2000; Hairston et al., 2013; Rinne et al., 2008; Sakai & Suga, 2001; Suga, 2008). Top-down feedback will tune the ascending auditory signal at midbrain and cortical nuclei to selectively encode stimulus features deemed behaviorally important based on experience and prior-knowledge (Gao & Suga, 1998, 2000).

The top-down feedback signal will preferentially reinforce patterns of neural firing that represent the behaviorally relevant features of incoming signals. Preferentially selecting the same behaviorally relevant features of a signal can lead to greater synchrony in the stimulus-evoked response across a population of neurons thereby increasing the consistency of the neural response to that signal (i.e., better neural synchrony) and decreasing the neural encoding of irrelevant cues (e.g., noise, Faisal et al., 2008). This heightened neural synchrony across a population of neurons can enhance the saliency of neural responses (Engel & Singer, 2001). Exerting this experience-dependent influence (i.e., enhancing synchrony of response to behaviorally relevant features) earlier in the signaling pathway (e.g., auditory midbrain relative to cortex) is preferable for optimal sound transmission and decoding (Faisal et al., 2008). This is because the synchronous neural response is projected to additional structures along the ascending pathway and at these subsequent structures the synchronous firing can exert a greater influence than neural firings that are temporally disorganized (Engel & Singer, 2001).

This auditory–executive link functions to encode a consistent and precise representation of sound for everyone (e.g., Hornickel & Kraus, 2013). The relationship between executive function and auditory processing likely aids both monolinguals and multilinguals in managing the within-language competition that occurs during communication. However, because multilinguals also must manage cross-linguistic co-activation when communicating, their auditory–executive link may be strengthened (i.e., greater top-down influence, resulting in greater consistency in the representation of the incoming auditory signal) and plasticity of these systems may result from experience with multiple languages (e.g., Krizman et al., 2014).
27.4.1 Heightened integration of auditory and executive systems in multilinguals: a proposal

While the auditory–executive link necessarily must develop in everyone to allow us to navigate complex sensory environments and is a normal process that occurs throughout maturation, we propose that this connection may be particularly strong for speakers of more than one language due to the additional demands of cross-linguistic co-activation during communication, resulting in synergistic activation of both the auditory and executive systems. As described above, it has been shown that both the auditory and executive systems are structurally enhanced in multilinguals relative to monolinguals (Ressel et al., 2012; Stein et al., 2012; Zou et al., 2012). Furthermore, it has been shown that this executive-auditory network functions more efficiently during auditory comprehension for multilinguals relative to monolinguals (Blumenfeld & Marian, 2011). Moreover, we have seen relationships between attentional control and auditory processing that are unique to speakers of more than one language (Figure 27.3; Blumenfeld & Marian, 2011; Krizman et al., 2012, 2014); and, importantly, we have seen these relationships at subcortical levels of auditory processing, which may boost signal transmission and
processing at a greater number of ascending auditory nuclei in a multilingual (Faisal et al., 2008).

From this relationship between attentional control and subcortical auditory function, we propose that, in multilinguals, the executive system biases the neural response of auditory cues important to early and accurate selection of the appropriate language. One potential cue\textsuperscript{11} may be the fundamental frequency ($F_0$), a speech feature that may be subtly manipulated by a bilingual speaker (see Figure 27.3; Altenberg & Ferrand, 2006; Krizman et al., 2012). Through the experience of juggling two languages, the neural pathway encoding these cues (e.g., $F_0$) is continuously selected via top-down feedback from higher order processing centers (Miller & Cohen, 2001), resulting in these pathways being strengthened through Hebbian plasticity mechanisms (Hebb, 1949). We suggest that the bilingual’s unique experience of cross-linguistic co-activation (Marian & Spivey, 2003b; Spivey & Marian, 1999) leads to a rewiring of neural circuitry so that over time the neural architecture of the bilingual brain reflects the experience of using two languages and the heightened need for executive and auditory circuits to interact to manage language co-activation during communication.

This strengthened interaction between auditory and executive systems may facilitate enhancements in bilingual foreign language learning (Bartolotti & Marian, 2012; Marian & Kaushanskaya, 2009) in that bilinguals are able to focus their encoding on the relevant acoustic features (Bartolotti et al., 2011). These enhancements in novel language learning suggest that bilinguals have learned how to actively engage the executive system when the sensory signal is ascending the bottom-up pathway so that the behaviorally relevant features of the signal are emphasized.

\textbf{27.5 Conclusions}

In conclusion, both auditory and executive systems are sculpted by language experience. Learning and using more than one language leads to structural enhancements in auditory and executive systems at both cortical and subcortical processing centers. The degree of plasticity observed in these systems appears to be dependent on both age of acquisition and the number of languages acquired. Through normal development, the relationship between executive and auditory relays is established to facilitate efficient and meaningful interactions with the auditory world. Given the unique relationships seen in multilinguals between auditory and executive functions, we propose that the connection between these two systems is strengthened by experience with more than one language. The strengthened network leads to fundamental differences in how multilinguals and monolinguals process sounds.

\textsuperscript{11} Future work should determine whether there are additional cues that are important for bilingual communication.
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