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Abstract

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The aim of this research is to better understand why children consistently surpass adults in their ultimate attainment of language—the sensitive period for language acquisition. I propose the Nested Cognitive and Neural Asynchronies theory to explain this phenomenon. This theory first asserts that an expert neural system for language processing is built in a nested manner, with commitments made first to aspects of language that are learned early. Once built, this system—though expert in processing one's native language—is ineffective in processing other languages, particularly those that differ in these early-learned aspects of language (such as sound structure). Second, asynchronies in the development of neural substrates supporting learning are thought to contribute to sensitive period phenomena. One consequence of the vast differences in the maturation of various substrates important for learning is that children end up with an abundance of implicit learning mechanisms relative to explicit. Since much of language learning is likely to occur via these implicit mechanisms, the result is that children might simply be better built to learn language.

The experiments reported here support this theory. The first study shows that languages that differ from one's native language in the most basic properties (i.e., sounds) are 1) more difficult to learn and 2) represented with distinct neural circuits. The second study demonstrates that the neural circuits recruited by children for a necessary component of explicit learning change substantially over the course of development, suggesting that the neural circuits deployed for learning in children differ greatly from those in adults. The third study shows that explicit learning can be detrimental for learning certain aspects of language. Moreover, when the primary substrate associated with this learning—the prefrontal cortex—is taken offline, this detriment of explicit learning is ameliorated, thereby showing that child-adult learning differences are related to neural maturation. Together, this collection of studies aims not to catalogue sensitive period phenomena in humans but rather to explain why the sensitive period for language exists.

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Chapter 1. Introduction

It has long been noted that children surpass adults in their ultimate attainment of language. This phenomenon is commonly referred to as the sensitive or critical period for language acquisition (Birdsong, 1999; Birdsong & Molis, 2001; DeKeyser, 2005; Johnson & Newport, 1989; Kuhl, 2004; Lenneberg, 1967; Newman, Bavelier, Corina, Jezzard, & Neville, 2002; Newport, 1990; Newport, Bavelier, & Neville, 2001; Werker & Tees, 2005). The sensitive period for language acquisition has long posed a conundrum: why do children excel at learning language but not at countless other basic cognitive processes (Cowan et al., 2003; Gathercole, 1999; Thomas & Nelson, 2001)?

This question is the focus of this dissertation. To that end, I will first briefly review some other sensitive periods observed in nature: bird song learning and visual adaptation in barn owls. A review of sensitive period phenomena for different aspects of language will follow. Then I will propose a theory to account for this perceived paradox in learning. Taking into consideration the nested nature of language structure as well as asynchronies in both learning mechanisms and neural substrates that emerge with age, the theory has two parts and will be referred to as the Nested Cognitive and Neural Asynchronies (NCNA) theory. Study 1 will tackle the first component of this theory pertaining to the nested nature of language. Specifically, it will explore whether it is more difficult to learn a language that differs from one's native language in the most basic properties. This notion is informed by how an expert neural circuit for language processing is built and therefore also probes neural recruitment. Studies 2 and 3 jointly address the role that age-related cognitive and neural asynchronies might play in learning mechanisms. In study 2, I explore the neural circuitry that children recruit for working memory, an ability that is crucial for many if not all forms of learning. Informed by this, Study 3 more directly probes the link between learning mechanisms and neural substrates.

1.1 Sensitive Periods for Learning

A sensitive period is simply a period of time during which experience or learning is optimal. The term critical period (more rigid regarding the time window) has also been used to describe these same phenomena. Sensitive periods have been documented across many species (humans included) for phenomena as varied as sensory and perceptual abilities, socialization, attachment, motor skills, bird song, language learning, and even critical reasoning skills (Bornstein, 1989; Michel, 2005). Before moving to language, I will briefly discuss two very well documented sensitive periods: prey localization in barn owls and bird song learning. Given the possibility of analogies for vocal and auditory learning, these two are particularly relevant for sensitive periods observed in language learning. Since this work is conducted in animals, these two models will additionally lend insight into the possible neural mechanisms underlying sensitive periods in humans, of which very little is currently known.

1.1.1 *Sensitive Periods for Prey Localization and Bird Song*

For barn owls, vision plays a critical role in sound localization. When juvenile owls with normal hearing are raised wearing displacing prisms in front of their eyes, they adjust their auditory orienting response according to the optical displacement of the prisms. However, this is not the case for adult owls (Knudsen & Knudsen, 1990). When experience with prism glasses begins at later ages, the change in orienting response is greatly reduced to less than half of the change seen in younger birds, and by adulthood there is almost no change whatsoever. Likewise, these juvenile—but not adult—owls acquire new neurophysiological maps of visual-auditory space in the optic tectum corresponding to the new auditory-visual mappings induced by the prism experience (Brainard & Knudsen, 1998). This has been taken as strong evidence for a sensitive period. More recently, however, evidence suggests that these maps are more malleable in adulthood than previously thought. Specifically, when visual displacement is introduced incrementally, adult owls do acquire new neurophysiological maps of visual-auditory space in the optic tectum (Linkenhoker & Knudsen, 2002). Together, these findings remind us that while there is a sensitive time during which experience has a great impact, it is not necessarily the case that experience-dependent change does not occur at other times as well. As in the case of incremental exposure for the barn owl, change may occur later on, but in a more protracted or nuanced way.

Sensitive periods for vocal learning in songbirds are perhaps more closely related to sensitive periods for language learning in humans. First, sensitive periods for song learning in birds and sensitive periods for language are both instances of auditory learning. Second, both sensitive periods appear to have multiple stages. Song acquisition by various sparrows and zebra finches is generally split into two phases: sensory acquisition and sensorimotor learning (Marler, 1970). During sensory acquisition, birds process conspecific songs and use the information gleaned from these songs to form a template against which they will compare their own vocalizations. This stage is very important, as birds that are isolated or deafened during this period develop abnormal songs. During the sensorimotor learning phase, birds use auditory feedback from their own vocal productions to gradually match their output to the template they had acquired previously. The end of this process results in a crystallized song that is relatively stable for the rest of the bird’s life. However, if birds are deafened anytime before the onset of sensorimotor learning, they produce degraded, non-crystallized songs (Bottjer, 2004; Leonardo & Konishi, 1999). Interestingly, it has been documented that even adult birds need intact auditory perception in order to maintain this song: even after crystallization, deafening will lead to a more degraded song (Nordeen & Nordeen, 1992). This stereotyped process is well understood in birds and has led to numerous discoveries implicating both excitatory (NMDA) and inhibitory (GABAergic) mechanisms for plasticity (Kandler, 2004; Nordeen & Nordeen, 2004). Most relevant for language learning, however, is the fact that there are multiple stages to this learning. That is, without the relevant sensory learning, there is no template for birds to use during sensorimotor learning with which to compare their vocalizations.

Considering the case of auditory localization in barn owls and song learning in birds together, I will highlight three important principles. 1) There is a time during development in which exposure/learning is optimal and after which learning becomes more difficult but (especially in the case of the barn owl) not impossible. 2) Sensitive periods can be nested and can occur in stages where learning in one area informs learning in another. Likewise, continued exposure, or practice, during adulthood is often necessary to maintain knowledge. 3) In addition to behavioral indications of age-related changes in learning, there is a neural correlate for each system where such change can be measured. In fact, this neural plasticity is thought to be the fundamental difference separating younger from older learners and to be the mechanism mediating sensitive periods.

1.1.2 Sensitive Periods for Language

In many areas of language learning, it is now abundantly apparent that children surpass adults in their ultimate attainment of language (Newport et al., 2001). The first detailed proposal of a sensitive period for language acquisition was put forth by Lenneberg in 1967 (Lenneberg, 1967). In his observations of patients recovering from aphasia, he noticed that children were far more likely than adults to recover language function. He proposed that there was a critical period for exposure to language that lasted from birth to puberty: a time during which, he speculated, there is gradual specialization in the left hemisphere of the brain for language. His proposal has spurred researchers to catalogue many age-related learning differences for different aspects of language

In my review of these age-related learning differences, I will touch on the three important principles I raised in my review of sensitive periods in barn owls and songbirds: 1) there is an optimal time during development for learning, 2) this learning may be nested and occur in stages, and 3) there is an associated neural commitment underlying this learning. I will first review the evidence that there is an optimal time for exposure to many different aspects of language, including phonology, morphology, and syntax, which I will review in turn.

Phonology: It has been well documented that very young infants show a similar pattern of phonetic perception regardless of their language environment. Amazingly, they are able to distinguish many if not all phonetic contrasts that exist across many languages (Eimas & Miller, 1992; Eimas, Siqueland, Jusczyk, & Vigorito, 1971). However, with increasing linguistic experience, infants lose this ability and instead maintain only those distinctions that are relevant for their language environment. This is true for both vowel (Kuhl, Williams, Lacerda, Stevens, & Lindblom, 1992) and consonant perception (Werker, Gilbert, Humphrey, & Tees, 1981). This phenomenon (the loss of discrimination ability) has been referred to as tuning for the relevant sound patterns in one's native language (Werker et al., 1981). Although deprivation experiments cannot be done as in songbirds, various observations suggest that the timing of this tuning is malleable. For example, common phonetic categories are reorganized at an earlier age than ones that are not as frequent (Anderson, Morgan, & White, 2003). Likewise, this tuning is more protracted in infants who are learning more than one language and therefore are learning a greater number of relevant distinctions (Bosh, Costa, & Sebastián-Gallés, 2000).

Morphology and Syntax: Morphology refers to rules that govern the composition of words in language, while syntax broadly refers to rules related to the composition of sentences. The age at which an individual is exposed to a second language appears to predict their ultimate command of morphology and syntax. In comparing late and early second language learners of English as a function of their arrival in the United States, researchers have shown that late-learners are more likely than early-learners to endorse ungrammatical sentences as grammatical (DeKeyser, 2000; Johnson & Newport, 1989). This is especially true for errors that have incorrect placement of determiners (e.g., a, the) and incorrect plural morphology (-s, as in cat vs. cats), but not errors of basic word order or vocabulary knowledge violations. These problems with grammatical processing are further reflected in electrophysiological event related potentials (ERPs) to violations of grammaticality; ERPs are more bilateral and distributed over a greater area for late bilinguals as compared to either early bilinguals or to native speakers of the same languages (C. M. Weber-Fox & H. J. Neville, 1996). Mayberry and colleagues have further examined grammaticality judgments in late-first language learners. These are deaf individuals who, by virtue of being deaf, were unable to learn a spoken language and did not learn a signed language until later in life. They also found that late-first language learners were more likely to endorse ungrammatical sentences as grammatical. This is true for many different grammatical errors, including the simple change of an auxiliary from “be” to “have” (as in “The girl have playing in the water”), and placing the incorrect relative clause marker in a sentence (as in “The boy whose is chasing the girl is happy”) (Mayberry & Lock, 2003; Newport, 1990). Newport (1990) has additionally examined the productions of these late-first language learners and shown that they tend to be “frozen” structures, such that whole-word signs are produced with no morphological variation in situations where such variation is required. Moreover, when morphological variants are produced, they are highly variable and inconsistent, with the correct morpheme being used in some circumstances but not others (Newport, 1990).

Sensitive periods for language: There is therefore a large literature demonstrating sensitive period effects across many aspects of language acquisition, including syntax, morphology and phonology. A pressing question is whether these effects are interrelated in the same way that the various stages of plasticity are in songbirds. In my discussion of how these effects might be related, I will talk about the organization of language as though it is hierarchical. Given that the sound structure of language is learned earlier than most aspects of morphological and syntactic structure, I will refer to morphological and syntactic properties as higher-order.

This view of language is consistent with ideas about critical periods that exist in the literature. Werker and colleagues, for instance, have suggested that these sensitive periods are likely to be interrelated. She has proposed that the sensitive period for language acquisition is best viewed as a series of nested sensitive periods (Werker & Tees, 2005). As such, tuning in one area (say to the phonetic categories that are relevant in one’s language) gives rise, in turn, to an ability to learn other aspects of language for phonology and beyond. Some preliminary evidence for this view comes from studies of infants with repeated middle-ear infections. These infants have compromised hearing and therefore also compromised exposure to language. These infants’ phonetic categories tend to be less sharp than their age-matched counterparts (Clarkson, Eimas, & Marean, 1989). Interestingly, when tested later, they also tend to be delayed on measures of reading and spelling, suggesting that this early lack of exposure might influence other areas of linguistic expertise (Gravel, Wallace, Ellis, Lee, & Mody, 1997).

Similarly, Kuhl has proposed the Native Language Neural Commitment (NLNC) hypothesis (Kuhl, 2004). According to NLNC, with language experience and learning come dedicated neural networks that code the patterns of native-language speech. One consequence of this commitment is a deficit in the processing of language patterns that do not conform to those already learned, i.e. those of a different language. Consistent with this hypothesis, mounting evidence suggests that in adults, first languages are processed with distinct neural tissue as compared to brain regions that process linguistic information not present in the native language (e.g., sounds from other unknown languages (Best & Avery, 1999; Golestani & Zatorre, 2004)) as well as linguistic information from another known language learned late in life (Kim, Relkin, Lee, & Hirsch, 1997; Wartenburger et al., 2003). That is, both known but later-learned as well as unknown languages are processed differently from an early-learned first language. There is some hint that such differences are related to proficiency rather than simply age (Abutalebi, Cappa, & Perani, 2001; Perani & Abutalebi, 2005), as extensive training with phonological contrasts can lead to the involvement of more classic (L1 associated) regions (Golestani & Zatorre, 2004).

However, these neural networks dedicated to processing native language sound patterns have an impact beyond like influencing like, in that they should influence and even promote the brain's future ability to learn other aspects of language, such as words and syntax. That is, these early commitments have an impact later in development. Perhaps the most striking evidence comes from looking at individual differences in infants' ability to accurately discriminate contrasts relevant in their native language and their inability to discriminate contrasts not found in their language. Kuhl et al. found that infants who were good at relevant contrasts and poor at irrelevant contrasts learned more words earlier than infants who showed the opposite pattern (Kuhl, Conboy, Padden, Nelson, & Pruitt, 2005). In line with this work, children who are better at segmenting a natural speech signal as infants are also better in many domains of linguistic expertise during early childhood (Newman, Ratner, Jusczyk, Jusczyk, & Dow, 2006). According to the NLNC hypothesis, early neural commitment to the sounds facilitates the next steps in language acquisition. The flip side of this, however, is that commitment could inhibit or interfere with learning in another language, again, for aspects of language beyond just sounds.

In sum, there is now substantial evidence for a sensitive period for language learning in humans. These age-related learning effects have been observed for many aspects of language. Moreover, theorists have highlighted that each sensitive period is likely related, in a nested way, to others. I will now turn more fully to these ideas, expanding upon them by proposing a new model for understanding sensitive periods for language learning.

1.2 Nested Cognitive and Neural Asynchronies (NCNA) Theory

1.2.1 Part One: Nested Commitment

The Nested Cognitive and Neural Asynchronies (NCNA) theory has two interrelated parts. First, this theory extends the ideas discussed by Werker and colleagues (Werker & Tees, 2005) and Kuhl (Kuhl, 2004) that a neural commitment is made for processing every aspect of language. When a commitment is made to earlier learned aspects of language, this leads to another commitment for later aspects until an expert neural system for language is built. Once built, this system—though expert in processing one's native language—is ineffective in processing other languages, especially those that are highly distinct from one's native language. Given the nested nature of these phenomena, languages that differ in the most basic properties (i.e., sound structure) should be more difficult to learn than those that differ in other, higher-order features. (This theoretical description is depicted in Figure 1). Likewise, neural recruitment for these languages should be distinct: classic language regions expert in native language computations should be recruited to a lesser degree, while other, less classic regions, should be recruited to a greater degree. Experiment 1 of this dissertation directly addresses these predictions.

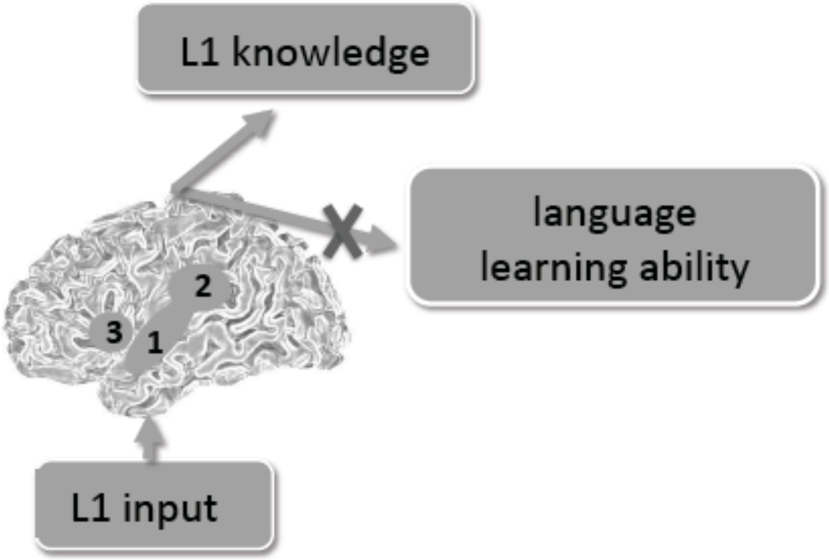

Figure 1. *Nested Neural Commitment to Language*
As a consequence of experience with language (L1 input), there is first a neural commitment to the sound properties of language (1) followed by additional commitments (2 and 3) until an expert neural system is built. This leads to expertise in one's native language (as depicted by the arrow) but leads to difficulty in learning a novel language (arrow with a cross through it).

1.2.2 Part Two: Cognitive and Neural Asynchronies

The second part of this theory tackles asynchronies in the development of neural structures that are relevant for all forms of learning (not just for language) as well as the related learning mechanisms associated with these neural substrates. Given differences in neural anatomy and function, it is likely that children's available learning mechanisms differ from adults', perhaps giving rise to their superior ability to learn language. I will first discuss how these substrates differ anatomically and functionally during childhood and will then discuss related differences in learning mechanisms. Although I will not be directly testing the link between these differences and the sensitive period for language acquisition, I will attempt to relate these differences in learning mechanisms to language learning, and especially, how they may lead to sensitive period effects, at least conceptually.

Anatomical and functional differences: Working Memory (WM) is the ability to hold information in mind that is no longer present in the environment (Curtis & D'Esposito, 2006; Gathercole, 1999). This ability is important for many if not all forms of learning, especially those that require effortful, explicit, processing (Cowan, 2005; Thal, Bates, Zappia, & Oroz, 1996). The Prefrontal cortex (PFC) and the broader fronto-parietal network are the primary neural substrates for these functions (Curtis & D'Esposito, 2006; Goldman, Rosvold, Vest, & Galkin, 1971; Goldman-Rakic, 1987). Recent work has shown that this region in particular is slow to undergo volumetric reductions during development, a measure thought to reflect synaptic pruning (Gogtay et al., 2004; Lenroot & Giedd, 2006; Sowell et al., 2004; Toga, Thompson, & Sowell, 2006). In fact, this region continues to undergo changes well into one's late 20s. The PFC has received a great deal of attention in the developmental literature for this very reason (Bunge, Dudukovic, Thomason, Vaidya, & Gabrieli, 2002; Bunge & Zelazo, 2006; Crone, Wendelken, Donohue, van Leijenhorst, & Bunge, 2006; Crone et al., 2009; Luna et al., 2001; Munakata, 2006; Munakata, Casey, & Diamond, 2004; Paz-Alonso, Ghetti, Donohue, Goodman, & Bunge, 2008; Scherf, Sweeney, & Luna, 2006; Wright, Matlen, Baym, Ferrer, & Bunge, 2007). I will argue that delayed changes in this structure, along with other neural changes we observe, might help explain sensitive period phenomena.

The hippocampus is another important structure for learning; it is regularly implicated especially for explicit or declarative types of learning and memory (Cohen et al., 1999; Davachi, 2006; Kahn, Davachi, & Wagner, 2004; Schacter et al., 1999; Schacter & Wagner, 1999; Squire, Stark, & Clark, 2004). It was previously thought that this structure underwent few structural changes after the age of about 8 or 9 years (Gogtay et al., 2006). However, it has recently been shown that in fact more local changes occur in the hippocampus later than previously thought (Gogtay et al., 2006). While posterior portions of the hippocampus increase in volume, anterior portions decrease, and these changes continue to occur through the mid twenties.

Whereas the hippocampus has been classically considered to be the primary substrate for declarative and explicit processes, the basal ganglia are often discussed as being important for procedural learning and implicit processes (Keele, Ivry, Mayr, Hazeltine, & Heuer, 2003; Knowlton, Mangels, & Squire, 1996; Myers, Shohamy, Gluck, Grossman, Kluger et al., 2003; Myers, Shohamy, Gluck, Grossman, Onlaor et al., 2003; Poldrack & Rodriguez, 2004). Not all the nuclei of the basal ganglia have been investigated in full detail. However, recent studies have shown volumetric changes occurring well into early childhood (Sowell et al., 1999) and even into the early teenage years (Lenroot & Giedd, 2006). Although changes occur in the Basal Ganglia late in development, it is likely that they are mature before both the hippocampus and the prefrontal cortex. Anatomically, this may mean that younger humans have relatively more implicit neural machinery available to them than humans who are fully mature.

Thus far, all the anatomical changes I have discussed are in individual neural regions. However, in addition to changes in grey matter density and volume, functional networks also change, such that younger children have abundant short-range but few long-range connections (Fair et al., 2007). Although largely unexplored, such changes are likely to result from the specialization of functional networks during development. This is an important observation in thinking about how age-related differences in neural anatomy might give rise to sensitive periods. Not only are there important differences in the size of particular regions, but the way these regions interact with one another might also be fundamentally different.

Learning differences: Somewhat counter-intuitively, differences in the functional networks being employed for even very basic aspects of cognition might carry a hidden benefit for child language learners (Elman, 1992; Newport, 1990). I propose that one such benefit could be a relative abundance of implicit versus explicit learning abilities on the part of children as compared to adults. Asynchronies in anatomical development already discussed provide some preliminary support for this notion; specifically, the protracted development of the PFC and hippocampus relative to the Basal Ganglia as well as network level changes. Consistent with this idea, behavioral evidence suggests that, by and large, children and adults do not differ in their implicit learning abilities, whereas there are substantial differences in their explicit abilities. Given that language learning seems to arise especially from more implicit forms of learning, the relative balance (or imbalance) of implicit to explicit learning abilities is a plausible candidate explanation for at least part of the sensitive period for language. In particular, it could be the case that the superior explicit abilities of adults actually impede learning of a new language. I will address these issues in turn.

Implicit learning and language: Language learning can be more implicit than previously thought. In fact, it has been suggested that much of what is learned about linguistic structure could be achieved via distributional or implicit learning. Maratsos was one of the first to propose a distributional mechanism for most, if not all, of language learning (Maratsos, 1980). In brief, he proposed a model of the child language learner as that of an implicit “scanner” who scans incoming speech in order to extract sequential properties. This is done not only for sounds in the language but also for morpheme strings, semantic information, and syntax. Associations or patterns are implicitly extracted until language is learned. Though less specified with regard to the properties of language itself, Reber has likewise stressed the importance of implicit learning for language acquisition (Reber, 1993).

Also stressing the importance of implicit learning for language learning, Ullman and collaborators have proposed that different aspects of language are represented by distinct procedural and declarative memory systems (Ullman et al., 1997). Briefly, procedural memory is often used interchangeably with implicit memory and declarative with explicit. As noted above, the PFC and hippocampus are strongly associated with explicit processes, while the basal ganglia (and the larger basal ganglia-frontal circuit) are more strongly associated with implicit processing. Pointing to patient work and fMRI, Ullman and colleagues suggest that the lexicon (vocabulary knowledge) is part of the declarative/implicit memory system and that grammar is part of the procedural/explicit system (Pinker & Ullman, 2002). As noted in my review of sensitive period effects for different aspects of language, while there are multiple demonstrations of sensitive periods for grammar and morphology, there does not appear to be a sensitive period for vocabulary. If Ullman and colleagues are correct, then adults appear to have a particular impairment in the implicit, but not explicit, system.

In the more applied field of second language learning, DeKeyser (2000) and Bley-Vroman (1988) have put forth very similar ideas (Bley-Vroman, 1988; DeKeyser, 2000). They propose the Fundamental Difference Hypothesis to explain sensitive period effects in language learning, which states that children learn language almost completely through implicit domain–specific mechanisms, while adults cannot as they have lost this implicit ability and therefore must draw on problem-solving capabilities. While problem-solving capabilities are not fully specified by these authors, they contrast them with implicit abilities. Moreover, DeKeyser (2000) has shown that late-learners who scored well on a grammaticality judgment test also scored well on a measure of verbal analytical ability, suggesting that late-learners who achieve a better command of language do so via superior analytical abilities. Importantly, this relationship was not found for early-language learners.

Additional evidence for the importance of implicit learning in language acquisition comes from studies investigating how individuals segment words from running speech. Discovering the units of speech—in this case words—is a significant problem for infant language learners, as speakers rarely pause to mark word boundaries (Liberman, Cooper, Shankweiler, & Studdert-Kennedy, 1967; Woodward & Aslin, 1990). One cue to word boundaries that has received a lot of attention is transitional probabilities (TP), or statistical regularities computed as the frequency of a pair of items (usually a pair of syllables) divided by the frequency of the first item in the pair. Work investigating the use of TP has shown that adults, infants, and even animals can track statistical regularities in running speech and use these regularities to find units akin to words (Hauser, Newport, & Aslin, 2001; Saffran, Aslin, & Newport, 1996; Saffran, Newport, & Aslin, 1996; Toro & Trobalón, 2005). Learners in these studies are presented with a stream of syllables one after another. Some syllables occur together very consistently (for example, 100% of the time that syllable A occurs, syllable B follows it) and others less consistently (for example, syllable D only follows syllable C 33% of the time). Numerous studies have shown that learners are able to extract the words based on this statistical information (i.e., when there is no other information about words or word boundaries except the contingencies) after very little exposure to the stimuli (Aslin, Saffran, & Newport, 1998; Gómez, 2002; Kirkham, Slemmer, & Johnson, 2002). Importantly, studies show that units extracted using TP information are treated as real, potentially meaningful words (Graf Estes, Evans, Alibali, & Saffran, 2007), demonstrating that this learning ability is not simply a laboratory phenomenon. Moreover, studies have also demonstrated grammar learning resulting from the use of TP information (Saffran, 2002; Thompson & Newport, 2007). Taken together, the work on statistical learning suggests that distributional learning is quite useful for acquiring many different aspects of language.

Implicit learning abilities in children and adults: Outside of the domain of language learning, there is ample evidence for robust implicit learning on the part of both children and adults. Adults have been shown to learn implicitly in tasks as varied as artificial grammar learning (Reber, 1967), probability learning (Lewicki, Czyzewska, & Hoffman, 1987; Reber & Millward, 1965), serial reaction time tasks (Keele et al., 2003; Nissen & Bullemer, 1987), and tasks where participants are asked to recall verbally presented sequences (Hebb, 1961), to name a few. On all of these tasks, children have also been shown to learn implicitly. I will review these in turn.

Reber presented 4, 8, and 14 year-old children with various grammatical examples generated from a finite state grammar. As in studies with adults, children were asked to study these grammatical strings before being presented with a surprise well-formedness test. He found that children from all age groups did not differ from college-age participants in their performance on the grammaticality test (unpublished data discussed in Reber, 1993). Likewise, it has been shown (using the head-turn preference procedure) that even 1 year-old infants can discriminate between grammatical and ungrammatical strings after very short auditory exposure to a finite state grammar much like the one employed by Reber (1967) (Gómez & Gerken, 1999).

In studies of probability learning, individuals are generally asked to guess, on a trial by trial basis, if a light will be presented in a particular location (usually one of two). Their guess probabilities can be compared to the underlying probabilities that occur during exposure. When these match, probability learning is said to have occurred. Children as young as 3.5 years have been shown to learn these probabilities (Bever, 1982; Wittig & Weir, 1971).

Studies with repeated presentation of various stimuli have also shown robust implicit learning on the part of children. First, infants can anticipate a repeating pattern of visual stimuli, as measured by anticipatory eye movements (Haith & McCarty, 1990). Likewise, children have been shown to perform well on serial reaction time (SRT) tasks. In these tasks, participants respond as quickly as possible by pressing a button corresponding to the location of a stimulus. Implicit learning is measured by comparing responses to random versus repeating sequences. When a 10-item sequence was presented amidst random trials, 6 and 10 year-olds performed as well as adults (Meulemans, Van der Linden, & Perruchet, 1998). In a slightly different design where random and longer repeating trials were separated into blocks (more like the classic SRT studies in adults), 4, 7 and 10 year-olds learned the sequences implicitly (Thomas & Nelson, 2001). Finally, in the auditory modality, the Hebb repetition task (Hebb, 1967) has been employed. In this task, individuals are asked to repeat a sequence of digits, some of which are novel and some, unbeknownst to the participant, are repeating. Like adults, children as young as 6 years old have been shown to be more accurate in recalling sequences that repeat (Mosse & Jarrold, 2008).

Across many studies in many different modalities, then, it has been shown that implicit learning abilities in children and adults are very robust. This is in keeping with the notion that implicit learning is developmentally invariant (Hasher & Zacks, 1984; Reber, 1993). However, this observation lies in stark contrast to what we know about explicit learning.

Explicit learning abilities in children and adults: While implicit learning has been characterized as a passive process in which one is exposed to information and acquires knowledge of that information simply through exposure, explicit learning is characterized as an active process in which individuals actively seek out the structure of information that is presented to them. Many skills are necessary for this active process. In the literature, these skills are broadly referred to as executive function. Executive function can include many different components, including working memory, long-term memory, inhibitory control and attention. For the purposes of this dissertation, I will focus on two components that I believe are particularly important for explicit learning: working memory and long-term memory.

Working memory is commonly broken into separate maintenance and manipulation components. This first component (maintenance) is characterized by the amount of information an individual can actively hold in mind. Various studies have shown that this ability increases steeply during early childhood; some argue that this changes rapidly through late childhood (Cowan et al., 2003; Gathercole, 1999), while other argue for less change after about 4 or 5 years of life (Davidson, Amso, Anderson, & Diamond, 2006).The second aspect of working memory, the ability to actively manipulate information being held in mind (which also includes this maintenance component), undergoes changes well into the teenage years and perhaps much later (Crone et al., 2006; Davidson et al., 2006; Diamond, 2002; Gathercole, 1999).Thus, although the exact timing is debated, it is clear that both components of working memory are changing (i.e., becoming more adult-like) over childhood.

Developmental studies of long-term-memory present a similar picture. Investigations show that children are less likely than adults to explicitly recall information that was presented to them. This impaired recollection has been shown for a variety of different kinds of information, including words and pictures of places and faces. Again, these abilities tend to improve from early childhood through young adulthood (Billingsley, Smith, & McAndrews, 2002; Cycowicz, Friedman, Snodgrass, & Duff, 2001; Dirks & Neisser, 1977; Ofen et al., 2007). It appears, therefore, to be the case that explicit mechanisms undergo great change during development.

Interaction of explicit and implicit abilities: Until now, I have treated these systems as though they are largely separate. However, there is ample evidence suggesting that in various circumstances, they interact. The notion of asynchronies is important for the NCNA hypothesis; children, compared to adults, have a relative abundance of implicit versus explicit learning abilities. To understand if this is true, we must also understand how these systems interact. I will first outline cases where implicit learning seems to interact with other forms of knowledge in statistical learning and will then discuss how these two systems have been shown to interact in the artificial grammar and SRT literatures.

As discussed previously, there are many demonstrations of robust statistical learning in both adults and children. However, there are some examples showing that older learners might shift from a reliance on implicit learning mechanisms to using already learned information for word segmentation. In comparing younger versus older infants, Thiessen & Saffran (2003) have shown that younger infants prefer to use statistical information to extract words from running speech, while older infants prefer to use stress when forced to choose (Thiessen & Saffran, 2003). It may be the case that the statistical information allows the younger infants to gain entry into the system and learn something about what the units. After gaining entry, infants can learn that stress is a useful segmentation strategy and then use this learned information for later segmentation. Similarly, Carla Hudson Kam and I have shown that when adults are presented with an un-segmented auditory stream that is comprised of statistically regular words having complex onsets, adults segment the items based on statistical information. However, when these words have equally complex onsets that are not allowed in their native language, they do not segment based on statistical information. Instead, they use notions about what words look like in their native language (Finn & Hudson Kam, 2008). Like the older infants, adults rely less upon the statistical information. In both cases, older learners appear to shift from reliance on implicit learning mechanisms to using already learned information for word segmentation.

In addition to a possible shift in strategy with age, there are cases where explicit cues to underlying structure can both help and hinder implicit learning, depending on the circumstance. Gebhardt and colleagues (2009) have presented evidence for an explicit cue helping implicit learning (Gebhart, Aslin, & Newport, 2009). In this statistical learning study, researchers presented learners with two different artificial languages in succession. When languages were presented in succession with no pause in between, only the first language was learned. However, both languages were learned when an explicit cue signaled that there was a change in the language. Likewise, when individuals were explicitly given a cartoon of a Markov-chain grammar and taught about how the grammar works before being exposed to grammatical exemplars and then being asked to judge well-formedness of novel exemplars, there was a facilitation in their judgment ability. Interestingly, the earlier they were shown the cartoon grammar, the better they performed during test (Reber, 1993). Each of these is a case in which explicit cues directed learners to the underlying structure, facilitating learning.

The opposite picture emerges, however, when explicit cues are vague or lead learners to the incorrect structure. Again using Markov grammars, Reber and colleagues have shown that when individuals are told—before exposure to grammatical strings—to simply look for structure, they perform worse than those who were not given any instruction (Reber, 1993). Reber argues that this disadvantage is a consequence of looking for something that is difficult to find. Since individuals did not know to look for Markov chain structure, they tended to make improper inductions about the rules. Additional evidence for a decrement in performance after explicit cuing comes from experiments where the SRT task has been modified to explicitly cue individuals to the onset and offset of a sequence (Willingham, Salidis, & Gabrieli, 2002). This can be done, for example, by telling participants that a sequence starts when the stimulus color changes. With the cue, individuals effortfully attempt to encode the sequence, likely engaging more explicit mechanisms than when the sequence is not cued. This explicit cue does not have an immediate impact on reaction time, the measure of learning. However, it does impact retention of the sequence when measured 8 or 12 hours after initial learning; individuals perform worse after having received the explicit cue.

Moreover, the ability of individuals to explicitly articulate the sequence is negatively correlated with their performance, suggesting that explicit knowledge of the sequence interferes with their implicit representations (Galea, Albert, Ditye, & Miall).

Similar relationships have been reported when individuals complete successive implicit and explicit learning tasks (Brown & Robertson, 2007a; Brown & Robertson, 2007b). One explanation for why explicit knowledge might hurt learners in this scenario has to do with the length of the sequence, which is usually 12 digits long. At best, individuals are known to be able to hold 7 items in working memory (Miller, 1956), and even this estimate has been considered generous (Cowan, 2005). Given that the sequence is longer than what individuals can be expected to keep in mind, explicit attempts at learning are likely to lead them astray.

In summary, explicit and implicit systems seem to interact in nuanced ways. From the statistical learning literature, there is evidence for a developmental shift in reliance on implicit learning mechanisms to a reliance on information that has already been acquired. Additionally, it appears that explicit cueing in implicit learning can facilitate learning when explicit cues correctly direct learners to the underlying structure. The opposite is true when explicit cues are vague or when they direct learners to an underlying structure that is hard to learn. Language, in particular, might be one such case where the underlying structure is difficult to learn via explicit mechanisms. Since children have rather inferior explicit abilities, they may be more likely to employ implicit mechanisms. I will discuss these and other observations under the umbrella of the NCNA theory.

1.2.3 NCNA Theory Synopsis

This brings us back to the NCNA theory, which includes two parts. In the first, nested part, I argue that a commitment is made to earlier learned aspects of language, leading in turn to another commitment for later aspects until an expert neural system for language is built. Once built, this system—though expert in processing one's native language—is ineffective in processing other languages, especially those that are highly distinct from one's native language. Given the nested nature of these phenomena, languages that differ in the most basic properties (i.e., sound structure) should be more difficult to learn than those that differ in other, higher-order features. Study 1 of this dissertation directly addresses these predictions, investigating learning and associated neural recruitment for two languages: one that differs from English in terms of its sound properties and one that does not.

This theory contains a second component in which I propose that the sensitive period for language acquisition has to do with developmental asynchronies in 1) the anatomical substrates that are recruited for learning and 2) the learning mechanisms that are available to learners. Put simply, children might be better built for learning language than adults. This is likely to be the case because children's explicit systems are still changing and inferior to those of adults. This inferiority could be a consequence of ongoing neural development of structures that are crucial for explicit function. As a consequence of the inferiority of the explicit system, it is probable that implicit mechanisms are recruited for learning to a greater degree in children. As argued above, much of language learning is thought to occur implicitly: even in adults, explicit mechanisms will not identify the underlying structure of language, as it is exceedingly complex. Therefore, children's implicit learning may be more effective. This theoretical process is depicted in Figure 2. Study 2 begins to explore this idea by probing the neural substrates that are recruited by children during explicit processing in a WM context.

Since children may be special because they have relatively more implicit as opposed to explicit mechanisms, it is important to probe the extent to which the neural correlates of these explicit processes change with development. Study 3 adds to this picture by more directly exploring the link between anatomical and learning differences. In this study, we ask if adults learn as children when their explicit "machinery" is taken off line. We employ transcranial magnetic stimulation (TMS) to effectively create a reversible lesion in the PFC (as well as control regions). This will be done while they are learning in implicit and explicit contexts. Each of these studies are described in more detail below.

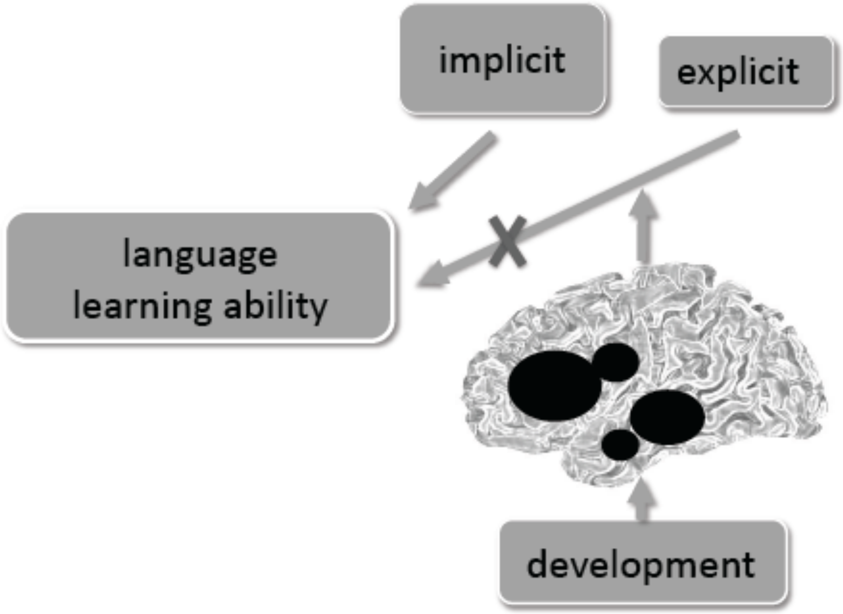

Figure 2. *Neural and Cognitive Asynchronies*
Neural development produces asynchronies in the development of substrates that are important for implicit and explicit learning, with explicit developing later. This produces a situation where a child has an abundance—relative to an adult—of implicit learning abilities, which in turn lead to superior language learning outcomes.

Finally, these different aspects of the theory are presented together in order to provide a full explanation for why we observe sensitive periods for language learning in humans. Although this dissertation does not directly test the relationship between these nested aspects and the asynchronies discussed above, they are likely to interact. Questions regarding this interaction are important for arriving at a complete understanding of sensitive period effects for language and will, no doubt, keep me busy in the years to come.

Chapter 2. Learning Language with the Wrong Neural Scaffolding: The Cost of Neural Commitment to Sounds

2.1 Summary of Research and Findings

The brain's early neural commitment to the phonetic and phonological properties of one's first language could help explain the sensitive period for language acquisition. Here we ask if a commitment to one's native language sounds might carry a cost for adults attempting to learn a new language with a phonology that is distinct from their native language. Twenty adult native English speakers learned one of two miniature artificial languages (MALs) over the course of 4 days, after which they were scanned using fMRI while assessing the grammaticality of MAL and English sentences. Crucially, the phonological inventory of one MAL was English-like (EP), while the other was maximally distinct (NEP). The MALs shared the same grammar, which was different from English and so had to be learned. Participants successfully learned all components of the languages regardless of condition. However, NEP learners were worse overall on measures of vocabulary and on novel tests of verb agreement and noun class. Neural recruitment also differed for the two groups. Neural recruitment for processing the grammar of the EP language, but not the NEP language, overlapped substantially with processing the grammar of English in Broca's region. This difference in noteworthy since recruitment of this region, across learning groups, is predictive of learning scores and accuracy in grammaticality judgments. In addition, NEP learners recruited regions important for auditory and phonological processing to a greater degree than EP learners. Together, these behavioral and neural data suggest that learning of a new grammar is affected by the phonological and auditory scaffolding that support it. Because the NEP phonology is different from English, learners are less able to take advantage of their existing phonological knowledge and its corresponding neural circuitry.

2.2 The Neural Representation of Multiple Languages: Relevant Background

For learning language, one principle is clear: the sooner the better. Individuals who learn language as children consistently outperform those who learn language as adults (Birdsong, 1999; Mayberry & Lock, 2003; Newport et al., 2001). For theories of learning, this sensitive period for language acquisition has long posed a paradox: why do children outperform adults when it comes to learning language but not on countless other basic cognitive measures (Cowan et al., 2003; Gathercole, 1999)?

One classic explanation for these differences is neural plasticity (Lenneberg, 1967). On this idea, once myelination and lateralization are complete, the brain is no longer open to learning language. This theory has led researchers to investigate age of acquisition (AoA) effects in terms of differences in brain representation for languages that are learned early versus late. On the plasticity account, later-learned languages should be represented with distinct cerebral structures as compared to those learned early in life (Pulvermüller & Schumann, 1994; Ullman, 2001). Some evidence for differential representation comes from work with bilinguals and polyglots who acquire aphasia. Cataloging the recovery of these patients has shown that different languages are recovered at differing rates, suggesting that cortex is not entirely shared across the languages (Obler & Albert, 1977; Pitres, 1895; Ribot, 1881; Scoresby-Jackson, 1867). Moreover, work localizing language-sensitive cortex in patients who undergo brain surgery has shown that cortical sensitivity for the second, as compared to the first learned language, is more diffuse (Lucas, McKhann, & Ojemann, 2004; Ojemann & Whitaker, 1978), although these findings have not been replicated in all bilingual patients. Still, the existing data suggest that multiple languages could be represented differently in the brain, possibly as a consequence of age-related changes in plasticity.

Recent neuroimaging work allowing even more detailed exploration of the neural representation of multiple languages has demonstrated striking similarities but also important differences in the neural representation of multiple languages. (for comprehensive reviews see (Abutalebi, 2008; Indefrey, 2006; Kotz, 2009; Perani & Abutalebi, 2005; Sakai, 2005). Many studies have noted, for instance, that the neural representation of two languages in bilinguals is very similar insofar as both languages are associated with the recruitment of classic language regions (Chee et al., 1999; Klein, Milner, Zatorre, Meyer, & Evans, 1995; Rüschemeyer, Fiebach, Kempe, & Friederici, 2005; Rüschemeyer, Zysset, & Friederici, 2006; Yetkin, Zerrin Yetkin, Haughton, & Cox, 1996). However, many studies have reported a greater extent of activation, especially in the left Inferior Frontal Gyrus (IFG; Broca's area) (Chee, Soon, & Lee, 2003; Dehaene et al., 1997; Golestani et al., 2006; Rüschemeyer et al., 2006) and the involvement of additional regions (Klein, Zatorre, Milner, Meyer, & Evans, 1994; Perani et al., 1996) for a second language (L2) as compared to a first. Studies have also shown more overlapping recruitment in the left IFG for early versus late bilinguals (Kim et al., 1997), and more versus less proficient bilinguals (Dodel et al., 2005; Golestani et al., 2006; Perani et al., 1998; Tatsuno & Sakai, 2005). Since late bilinguals tend to be less proficient overall (Flege, Munro, & MacKay, 1995; Johnson & Newport, 1989; C. Weber-Fox & H. Neville, 1996), the effects of proficiency and AoA can be hard to isolate. However, when both were systematically varied, it was found that AoA predicts similarity of neural recruitment during grammatical processing while proficiency predicts similarity for semantic processing (Wartenburger et al., 2003). This fMRI finding is in line with well established behavioral and EEG work showing that grammatical, but not semantic, processing is influenced by AoA (C. Weber-Fox & H. Neville, 1996). Together, these studies show that there are important differences in the neural representation of languages that are learned later versus earlier in life, especially for grammatical processing and in the left IFG.

Studies investigating grammar learning have additionally highlighted the importance of this same region (the left IFG) for language learning. In one study, learners were taught a new language that was either organized by rules that occur in natural language or rules that do not occur in natural language. Only the language with natural rules was associated with increasing activation with learning in the left IFG (Musso et al., 2003). Opitz and Friederici have further shown that this region is associated especially with the learning of abstract and hierarchically organized rules (Opitz & Friederici, 2004, 2007). Importantly, these results are not restricted to artificial languages: learning of both artificial and natural languages is associated with increasing recruitment of this region as the language is learned (Indefrey, Hellwig, Davidson, & Gullberg, 2005; Newman-Norlund, Frey, Petitto, & Grafton, 2006; Sakai, Miura, Narafu, & Muraishi, 2004).

Indefrey (2006) proposed that the additional recruitment of this region on the part of late and less proficient learners has to do with the special role this region plays in language learning and processing. On this idea, the left IFG is optimized for processing one's native language and is therefore less efficient when processing languages that are learned later in life, leading to greater recruitment of this region for other languages. This raises the question of how this region comes to be optimized for processing a native language. An interesting possibility is suggested by some recent theories of language acquisition. Werker and Tees (2005) proposed that language learning is best viewed as a series of nested sensitive periods and that tuning in one area (say to the phonetic categories that are relevant in one's language) gives rise, in turn, to an ability to learn other aspects of language, both within phonology and beyond. Similarly, Kuhl (2004) has proposed that with language experience and learning come dedicated neural networks that code the patterns of native-language speech. One consequence of this commitment is a deficit in the processing of language sound patterns that do not conform to those already learned, i.e. those of a different language. Indeed, additional and canonical neural substrates are recruited to a greater extent when adults process sounds not present in their native language (Best & Avery, 1999; Golestani & Zatorre, 2004). Importantly, Kuhl further suggests that the neural networks dedicated to processing native language sounds has an impact beyond like influencing like, promoting the brain's future ability to learn other aspects of language, such as words and syntax. Therefore, the optimization of the left IFG in processing one's native language—as observed in the aforementioned studies of neural representation in adults—is likely to arise from a series of nested neural commitments to many aspects of language over the course of development.

Some evidence for the nested nature of sensitive periods comes from looking at individual differences in infants' ability to accurately discriminate contrasts relevant in their native language and their inability to discriminate contrasts not found in their language. Kuhl et al. found that infants who were good at relevant contrasts and poor at irrelevant contrasts learned more words earlier than infants who showed the opposite pattern (Kuhl, Conboy, Padden, Nelson, & Pruitt, 2005). In line with this work, children who are better at segmenting a natural speech signal as infants are also better in many domains of linguistic expertise during early childhood (Newman, Ratner, Jusczyk, Jusczyk, & Dow, 2006). (See also (Thal et al., 1996) for a similar relationship between word and grammar learning.). When it comes to learning language, it has therefore been established that learning in one domain facilitates learning in another.

The brain's important role in this nested learning has yet to be shown. With learning in each area, there is likely to be an associated neural commitment. When a commitment is made to earlier learned aspects of language, this should allow the learning of later aspects, which should also be associated with a neural commitment. This cascade should continue until an expert neural system for language is built. Once built, this system—though optimized for processing one's native language—should be less effective in processing other languages, especially those that are highly distinct from one's native language. Given the nested nature of these phenomena, languages that differ in the most basic properties (i.e., sound structure) should be 1) more difficult to learn and 2) processed with different neural substrates.

To test these ideas, we explore the impact of the sound structure of a second language (L2) on both learning and neural recruitment. In particular, we investigate learning and neural recruitment during grammatical processing of two miniature artificial languages (MALs). One MAL is phonologically similar to English (EP)—the native language of learners in this study—and one is distinct (NEP). Both MALs differ from English in their grammatical structure, but not from each other, and so have to be learned. If these ideas are correct, it should be more difficult to learn the NEP versus EP language. Since this learning difficulty is proposed to arise from the inappropriate use of a neural circuit tuned to one's native language, we should also observe distinct neural recruitment for the NEP language. Given previous work on neural representation in bilinguals, this difference should be observed especially in the left IFG, a region that is important for the learning and processing of grammatical structure. NEP learners should also recruit additional regions associated with auditory processing. That is, if difficulty in processing the grammar of the NEP has to do with the brain's inability to process its phonological structure, we would expect to see a greater recruitment of phonological regions in an attempt to process this information more fully. Importantly, this difference in neural recruitment should occur not simply for processing the sound structure of the language, but also higher-order aspects such as grammar.

2.3 Experiment 1

2.3.1 Experiment 1 Methods

Participants

Twenty adult, native-English speakers participated; ten in each condition.

Stimuli

Both EP and NEP languages are comprised of 30 nouns and four transitive verbs. There are two arbitrarily determined noun classes demarcated by two suffixes (Figure 1). They follow subject-object-verb word order and have subject-verb agreement. Importantly, the two languages have the exactly the same grammatical structure, allowing us to investigate the precise impact of phonological differences on grammar learning.

Critically, the languages differ from one another in their phonological inventories. The EP language is comprised of phones that occur regularly in English. Individual token frequencies were matched to English in both syllable position frequencies and syllable structure frequencies. For example, if a syllable occurs at the beginning of a word 5% of the time in English, this is also true for EP. Likewise, if 20% of English words follow a consonant-vowel-consonant pattern, 20% of EP words do as well[1]. On the other hand, the NEP language is comprised of phones that do not occur in English[2]. To construct words in the NEP language, non-native phones were substituted into EP words,

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[1] Following these constraints, 60 possible words were actually generated, of which 30 were chosen based on English-likeness ratings from native English speaking raters blind to the overall goals of the study (n=10).

[2] 150 phones that do not occur in English were chosen. Native English speaking participants blind to the study design rated these phones, presented individually, on their English-likeness (n=10). The lowest ranked phones (13 vowels, 19 consonants) were chosen for constructing the words.

attempting to maintain major manner and place features (See Appendix A for a list of all phones used to construct each language).

The languages were created in conjunction with a small world of objects and actions. Even with the semantic restrictions imposed by the referent world, there are over 3,600 possible sentences. This creates a wide scope for testing participants using novel sentences. The stimuli set comprised 57 video vignettes and the corresponding EP and NEP sentences, which were repeated 3 times per day for a total of 12 times each over the course of the experiment.

$$\text{SubjN}_{\text{NC1}}\text{-ihd}_{\text{NC1suf}}\ \text{ObjN}_{\text{NC2}}\text{-ihn}_{\text{NC2suf}}\ \text{Verb-niy}_{\text{NC1agr}}$$

Figure 1. *Grammatical Structure of MALs*
Each MAL follows Subject, Object, Verb word order. Each Noun (Object and Subject) belongs to one of two categories, demarcated by a suffix (noted here as /ihd/ and /ihn/). The Verb agrees with Subject and therefore ends with one of two corresponding suffixes (i.e. /niy/ corresponds with /ihd/).

Procedure

Participants were randomly assigned to learn one of the two MALs over the course of four days and were then tested on their knowledge of the language and underwent a functional MRI (fMRI) scan on the fifth day. (The scanning procedure is described more fully in Experiment 2 of this paper.) Each day of learning started with a short pre-exposure where individuals viewed pictures of all the nouns in the language and listened (over head phones) to the corresponding label for that object. Learners were told that these were some of the words in the language they were about to learn and to watch, listen and repeat the label. They were explicitly told not to write anything down. After this two-minute presentation, individuals were exposed to the language. Similar to previous studies using MALs (Hudson Kam & Newport, 2009), the languages were learned by watching a series of short scenes on the computer. For example, one scene depicts a toy plastic ring hitting a frog. Participants see the scene and then hear a sentence in the MAL describing the scene. Before exposure, they are told to pretend that they are on a desert island and that they should try and learn as much as possible about the language by watching these vignettes and repeating the sentences as they hear them.

On days 1-3 participants were presented with the exposure set three times, lasting a total of 90 minutes, with the possibility of breaks every 30 minutes. After each day of exposure, participants were given a vocabulary test. At the end of the 3rd day, they were additionally tested on there aspects of grammar. If they did not achieve greater than 75% correct on all of these measures at this test, they received an additional exposure session (again, consisting of the entire set presented three times) on day 4. However, if they were above 75% correct on all measures, the exposure set was only presented once (for 30 minutes) on the fourth day.

Regardless of performance on the tests administered on day 3, all individuals were again tested on all measures at the end of the fourth day. If a learner was still not above 75% correct on all measures, she was not invited to participate in the fMRI portion of the experiment. This precaution was built into the experiment in order to minimize differences in proficiency across the two groups of learners at the time of the fMRI experiment.

Tests: Participants were tested on their knowledge of vocabulary, verb agreement, word order and noun-classes. Data for all tests, unless otherwise specified, were collected using E-prime software (Schneider, Eschman, & Zuccolotto, 2002). Vocabulary was always tested first, followed by verb agreement, noun class and word order.

Vocabulary test: The vocabulary test, administered after each day of exposure, consisted of viewing a picture and hearing three possible labels for that picture. Subjects indicated which of the labels they thought best matched the picture by pressing a “1”, “2”, or “3” on the keyboard, corresponding to the order of presentation. Test items were presented in random order. This test was administered each day after exposure.

Verb agreement test: The test of verb agreement was forced-choice, consisting of a total of 24 items, 12 of which were administered in random order at the end of day 3, and the remaining 12 (also in random order) at the end of day 4. Learners were asked to indicate which of two sentences sounded like a better sentence in the language they just learned. Individuals listened to the sentences over headphones and pressed “1” if they thought the first sentence was better and “2” if they thought the second was better. In all cases, they chose between a correct subject-verb pairing and an incorrect pairing, with every other aspect of the sentences being equivalent (and correct). Half of the test items were sentences they had heard before, and half were novel sentences that followed the grammatical structure of the languages.

Noun class test: The noun class test followed the same forced-choice structure. There were a total of 40 items, half of which were administered on each test day. In all cases, individuals chose between a sentence with a correct noun class suffix and an incorrect noun class suffix, and everything else was equivalent. Half of the errors occurred in the subject position and half in the object position. Like the verb-agreement test, half of the items were familiar and half were novel.

Word order test: The word order test was also forced choice, consisting of 12 items in total with six administered on each day. Individuals were presented with a scene and heard two possible sentences that could correspond to that scene. One sentence followed the correct subject-object-verb word order and one flipped this arrangement, having object-subject-verb word order. Participants indicated their response by circling “1” or “2” on a sheet of paper. Half of these were familiar scenes and half were novel.

2.3.2 Experiment 1 Results

In order to match EP and NEP learners as much as possible prior to the scan, learners of either language received an additional 60 minutes of exposure on the final day if they did not achieve more than 75% correct on all test measures on the previous day:

vocabulary, verb agreement, word order and noun class. Three NEP learners and two EP learners required this additional exposure.

Figure 2 shows EP (black dots) and NEP (white dots) learners' performance on all test items. In this and all other figures, error bars represent standard errors of the mean. For all test types on each test day, both EP and NEP learners were significantly better than chance, indicating successful learning of the languages (Appendix B). Performance on the vocabulary test, however, shows that EP learners were significantly better than NEP learners overall (repeated measures ANOVA: $F(1,18)= 19.352$, $p<0.001$) and on all four days this was tested (test 1: $t = 2.78$, $p = 0.012$; test 2: $t = 3.29$, $p = 0.028$; test 3: $t = 2.33$, $p = 0.031$; test 4: $t = 3.33$, $p = 0.032$; Figure 2a). There was a significant group by test day interaction, showing that this difference in performance differed across the days for the two groups ($F(1,18)= 2.69$, $p=0.05$); this difference was greatest on the first test day ($t = 2.78$, $p = 0.012$) and waned a bit by the final day of exposure ($t = 2.33$, $p = 0.031$).

Performance was also assessed for knowledge of verb agreement, word order, and noun class. Unlike vocabulary, these tests were administered only on the third and fourth days of exposure, in order to keep learning as natural as possible and to minimize any learning that would occur from the testing process itself. In particular, we didn't want to expose learners to ungrammatical sentences during early exposure. Unlike the vocabulary tests, overall performance did not differ for EP and NEP learners on any of these measures: verb agreement ($F(1,18)= 2.53$, $p=0.129$), word order ($F(1,18)= 0.072$, $p=0.791$), or noun class ($F(1,18)= 0.977$, $p=0.336$). In addition, there was no significant learning group by test day interaction for any of these measures (verb agreement: $F(1,18)= 2.53$, $p=0.129$; word order: $F(1,18)= 0.0$, $p=1.0$; noun class: $F(1,18)= 3.24$, $p=0.089$). However, if similarity in sound structure impacts the learning of a second language, it is likely that EP learners could learn more quickly and so performance across groups was compared despite not finding a difference in the omnibus test. An interesting pattern emerged on the morphosyntactic measures such that performance was better for EP as compared to NEP learners on the second, but not the first, test day for verb agreement (test 1: $F(1,18)= 0.071$, $p=.794$; test 2: $F(1,18)= 4.84$, $p=0.041$) and noun class (test 1: $F(1,18)=0.024$, $p=.879$; test 2: $F(1,18)= 5.07$, $p=0.037$). This was not true for word order (test 1: $F(1,18)=0.167$, $p=0.688$; test 2: $F(1,18)= 0.133$, $p=0.719$).

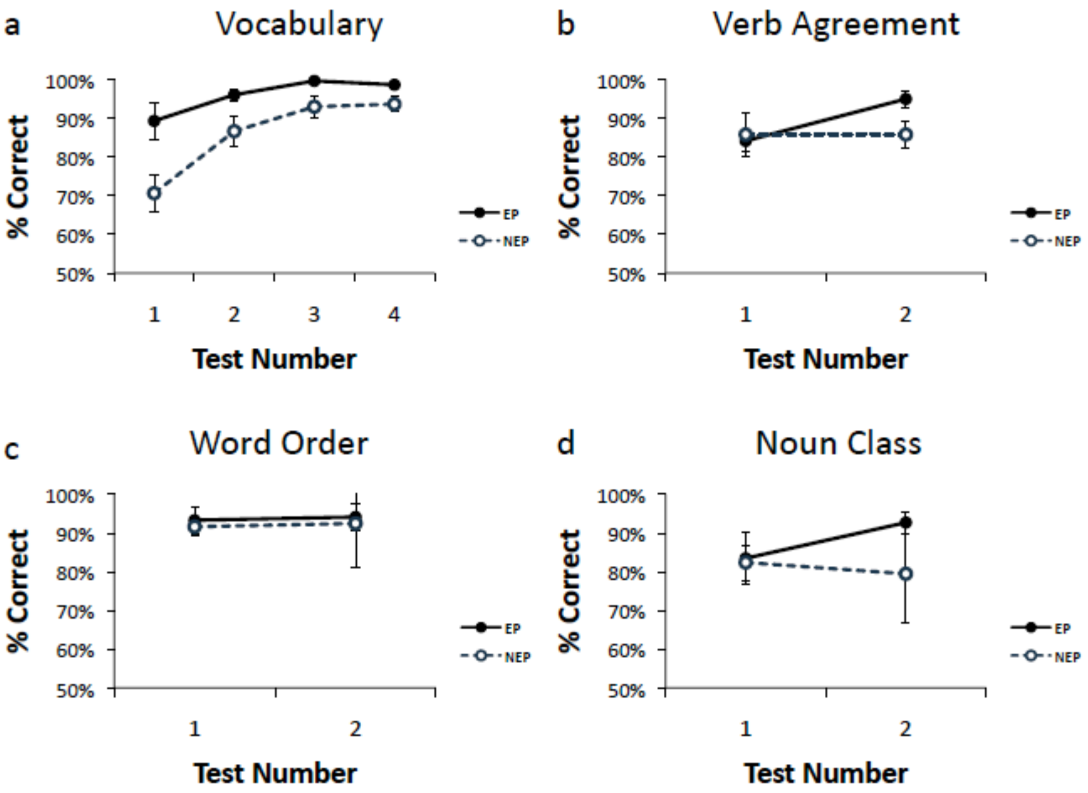


Figure 2. *Behavioral Performance*
Performance is potted separately for each subtest for the day it was tested. Error bars reflect standard errors of the mean.

A careful analysis of these data reveals two important factors. First, EP learners improved from the first to the second test on these morphosyntactic measures. This was significant for verb agreement ($F(1,9)=7.57$, $p=0.022$) and in the predicted direction for noun class ($F(1,9)=3.22$, $p=0.106$). There were no such improvements for NEP learners (verb agreement: $F(1,9)=0$, $p=1.0$; noun class: $F(1,9)=0.414$, $p=0.536$). Second, this improvement was observed especially for novel instances. On the second versus the first test day, EP learners' performance was significantly better for novel, but not familiar tokens on verb agreement ($F(1,9)=6.42$, $p=0.032$). Similarly, while familiar/novel performance on noun class did not differ on the first test day for EP learners ($F(1,9)=1.1$, $p=0.322$), it did on the second ($F(1,9)=11.25$, $p=0.008$). This was not true for NEP learners, whose performance did not differ across test days for either novel or familiar items. Moreover, on the second test day, EP learners were significantly better than NEP learners for novel, but not familiar, items on tests of verb agreement (novel: $F(1,18)=7.03$, $p=0.016$; familiar: $F(1,18)=0.117$, $p=0.736$) and noun class (novel: $F(1,18)=9.06$, $p=0.008$; familiar $F(1,18)=0.991$, $p=0.333$; Figure 3).

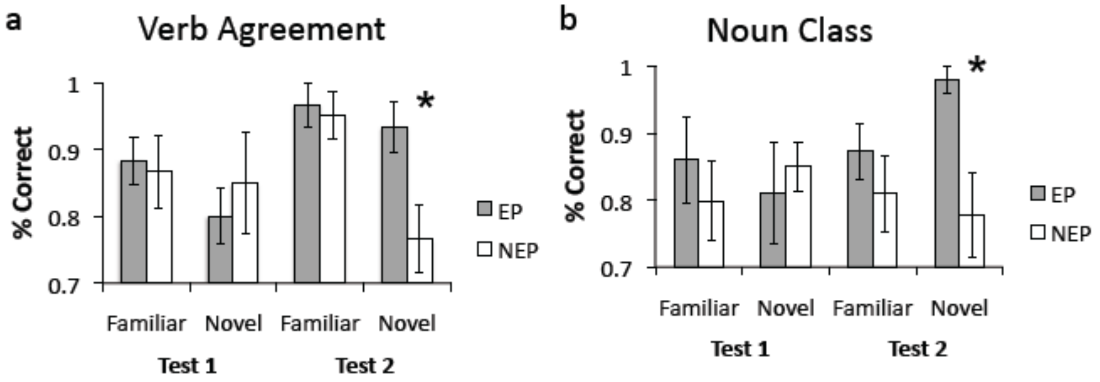


Figure 3*. Morphosyntactic Test Performance on Familiar versus Novel Items* Performance is plotted separately for EP (grey bars) and NEP (white bars) learners. Error bars reflect standard errors of the mean.

Taken together, these learning data indicate that EP and NEP learners were well matched on many grammatical measures, especially as measured by first tests of grammatical knowledge (verb agreement, noun class and word order). However, NEP learners were worse at learning the vocabulary, and EP—but not NEP—learners improved on tests on novel morphosyntactic test items, suggesting an increasing ability to generalize on the part of EP learners. It is worth noting, however, that both EP and NEP learners were significantly better than chance on novel sentences, demonstrating that both groups were able to generalize: however, the EP learners were better at it. These languages were matched exactly in their grammatical structure, which is different from English and so had to be learned. The only difference was the phonological inventories from which the languages were constructed, with EP being composed of phones that occur in English, and NEP being composed of phones that do not. When it comes to vocabulary and generalizing in morphosyntax, therefore, it appears that phonology matters not just for learning the sounds but also other aspects of the language. This learning difference is likely the consequence of using a neural circuit that is optimized based on one's native language. To explore this possibility, we turn to the fMRI portion of the experiment.

2.4 Experiment 2

2.4.1 Experiment 2 Methods

Participants

The same twenty participants described in experiment one were included in this component of the study. Since pervious work has shown that neural recruitment for language might differ by gender (Harrington & Farias, 2008), an equal number of males and females were assigned to each condition.

Procedure

After achieving scores of 75% or higher on either test day on all tests, individuals underwent an fMRI scan. This scan always occurred after the final day of exposure, on the fifth day of participation in the experiment. Before entering the scanner, individuals were exposed to a short, 15 minute version of the exposure set to remind them of the language on that day. The fMRI design was event-related, and individuals were asked to asses the grammaticality of a sentence in blocks of English or the MAL they learned. These blocks were counterbalanced across participants and conditions: half of the scans began with English and half the relevant MAL. These were presented in blocks so that learners were not required to switch between languages when making grammaticality judgments. The task was chosen in order to engage regions associated with grammatical processing. For each language, 15% of the items were not grammatical. This percentage was chosen to maximize the number of grammatical trials that could be used for data analysis, while still having enough ungrammatical items to hold the listener's attention. Ungrammatical items were modeled after Johnson and Newport (1989). Each sentence was presented over noise-cancelling earphones for four seconds, after which participants had two seconds to respond. Finally, there was a rest period prior to the next trial with variable duration (Figure 4).

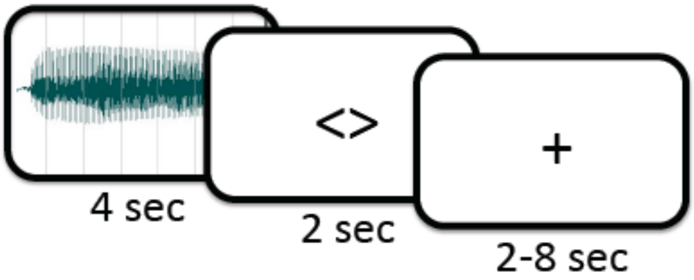


Figure 4. *fMRI Design*
Participants listened to a sentence (either in the MAL or English) for four seconds and then had two seconds to assess its grammaticality. Each trial was followed by a variable-duration rest period before the beginning of the next trial.

fMRI analysis

Functional MRI data were acquired on a Siemens MAGNETOM Trio 3T MR Scanner at the Henry H. Wheeler, Jr. Brain Imaging Center at the University of California, Berkeley. Anatomical images consisted of 160 slices acquired using a T1-weighted MP-RAGE protocol (TR = 2300 ms, TE = 2.98 ms, FOV = 256 mm, matrix size = 256 x 256, voxel size 1 x 1 x 1 mm). Functional images consisted of 27 slices acquired with a gradient echoplanar imaging protocol (TR = 2000 ms, TE = 32 ms, FOV = 138 mm, matrix size = 128 x 128, voxel size 1.8 x 1.8 x 3.5 mm). A projector (Avotec SV-6011, http://www.avotec.org/) was used to display the image on a translucent screen placed within the scanner bore behind the head coil. A mirror was used to allow the subject to see the display. The distance from the subject's eye to the screen was 28 cm.

Image processing and analysis were completed using a Statistical Parametric Mapping program (SPM5 (Friston, Frith, Liddle, & Frackowiak, 1991)). A statistical parametric map was calculated for each participant based on linear combinations of the covariates modelling each task period (Friston, Frith, Turner, & Frackowiak, 1995). Before combining individual results into a group analysis, echo-planar image data were normalized to Montreal Neurological Institute space using a high resolution three-dimensional T1-weighted structural scan. Regions of interest for both brain-behavior and degree of overlap analyses were constructed via the use of probabilistic maps of the left IFG or Superior Temporal Gyrus from previous studies. Contrast values were extracted using MarsBar (Brett, Anton, Valabregue, & Poline, 2002).

2.4.2 Experiment 2 Results

Regardless of learning condition, individuals were more accurate ($F(1,18)=11.05$, $p = 0.004$) and faster ($F(1,18)=5.215$, $p = 0.036$) to respond to sentences presented in English as compared to the MAL they learned. Importantly however, neither accuracy ($F(1,18)=1.14$, $p = 0.301$) nor reaction time ($F(1,18)=.127$, $p = 0.725$) differed across EP and NEP learners (Figure 5).

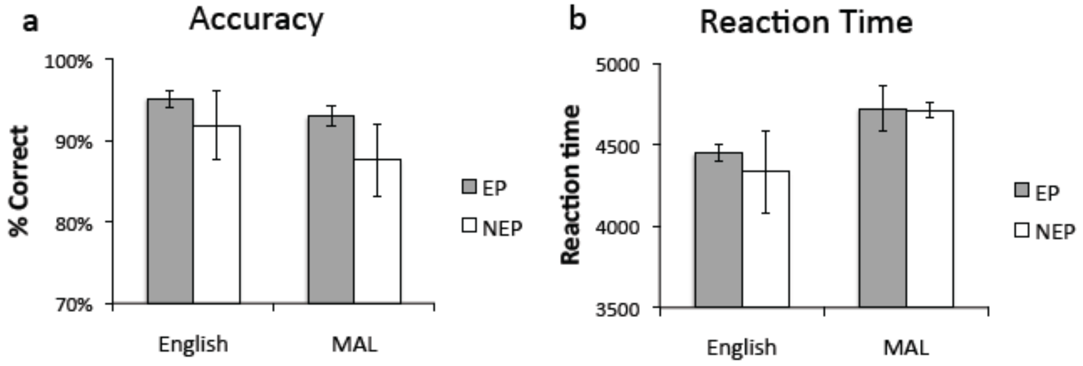


Figure 5. *Performance During fMRI Scanning*
Performance is plotted separately for EP (grey bars) and NEP (white bars) learners. While both groups of learners were more accurate and faster to respond to sentences in English versus the MAL they learned, there were no differences on MAL performance across the groups in accuracy (a) or reaction time (b).

Participants' neural recruitment was assessed while judging the grammaticality of sentences. NEP and EP learners both recruited regions known to be critical for language processing while listening to the MAL as compared to the implicit baseline. These regions include the left IFG (Broca's region), the Insula, the Superior Temporal Gyrus (including posterior language regions—Wernicke's), and the Angular and Supramarginal Gyri (Table 1). This pattern of recruitment overlapped substantially with English for both EP and NEP learners (Figure 6).

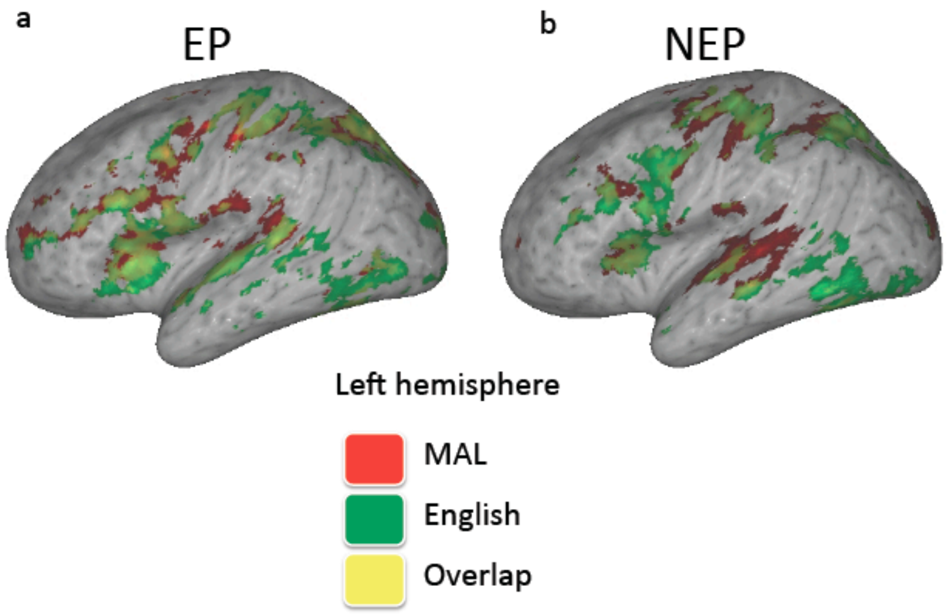


Figure 6. *Overlapping Recruitment for MALs and English*
Conjunction maps were constructed to depict the similarity of neural recruitment for MAL (red) and English (green) processing. These are depicted for EP (a) and NEP (b) learners separately. Data are displayed at a threshold of $t = 3$ or greater.

However, important differences were observed when comparing neural recruitment directly across groups (EP versus NEP learners). EP learners were more likely to recruit the left Middle frontal Gyrus, the Middle Temporal Gyrus, and the Caudate bilaterally (Table 2). NEP learners, on the other hand, were more likely to recruit regions along the Superior Temporal Gyrus bilaterally, including primary auditory cortex (Heschl's Gyrus), the sylvian-parietal temporal junction and the Supramarginal Gyrus. Therefore, comparisons across regions reveal that EP learners were more likely to recruit middle frontal and temporal regions and the Basal Ganglia, and NEP learners were more likely to recruit regions associated with phonological processing of language (Table 2).

Given previous work highlighting the importance of the LIFG for learning grammar and the importance of the STG for phonological processing, we investigated neural recruitment in these regions more carefully. Probabilistic maps of Broca's area (Amunts et al., 1999) and the LSTG (Morosan et al., 2001) were chosen based on independent studies. First, the degree of overlapping recruitment was separately assessed in Broca's region for EP and English and for NEP and English. The number of voxels recruited (t = 1.65 or greater) for both the MAL learned and English were counted. We found that recruitment overlapped more for EP as opposed to NEP learners (Figure 7a). No difference, however, was observed in the LSTG, likely because this region is not recruited to a great extent in either groups of learners when processing English, so the opportunity for overlap is quite restricted (Figure 7b).

The extent and magnitude of recruitment were also assessed in these regions. Extent was measured by counting the number of active voxels (t = 1.65 or greater) within the region of interest. Magnitude was measured by computing the mean recruitment of the region in MarsBar. As observed in the overall group comparisons, neither extent nor magnitude of recruitment differed in Broca's region while processing the MAL for EP or NEP learners. However, both extent and magnitude of recruitment were greater for the NEP as opposed to the EP learners in the LSTG, suggesting that this region was rather crucial for NEP, but not EP learners. Taken together, these data indicate that while there was no difference in the extent or magnitude of recruitment of Broca's region across the groups of learners, recruitment for the EP learners overlapped more with English in this region and neural recruitment was therefore more similar to English for EP learners. Moreover, NEP learners were more likely to recruit the STG bilaterally than EP learners. This was true for both magnitude and extent on the left side. Therefore, NEP learners devoted more resources to processing the sound properties of the language.

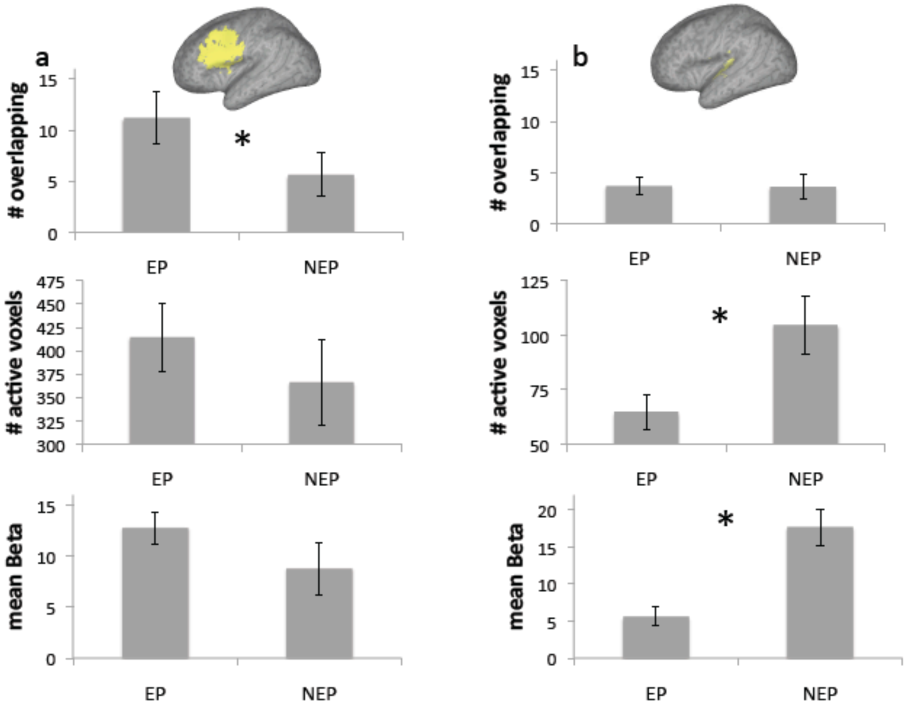


Figure 7. *Overlap, Extent, and Magnitude of Recruitment in Broca's and the LSTG*

Displayed on the top of the figure are the ROIs for which neural recruitment was probed in Broca's and the left STG respectively. Overlap: Recruitment overlapped more for EP as opposed to NEP learners in Broca's region (a) but not the left STG (b). Extent: The extent of recruitment did not differ for EP and NEP learners in Broca's region (c) but did in the left STG (d), with NEP learners recruiting more voxels.

Magnitude: The magnitude of recruitment did not differ for EP and NEP learners in Broca’s region (e) but did in the left STG (f), with NEP learners recruiting this region more. Error bars reflect standard errors of the mean.

What are the consequences of these differences for behavior? To investigate this in more detail, we measured the correlation between recruitment of Broca’s region and the left STG and behavior. For EP and NEP learners together, the magnitude of recruitment within Broca’s region was correlated with accuracy ($r = .516$, $p = .024$), such that individuals who were more accurate in assessing the grammaticality of sentences in the scanner recruited this region to a greater extent. This was also true for an aggregate measure of learning (mean of all tests including vocabulary, verb agreement, word order, and noun class). Additionally, individuals who recruited Broca’s region more while processing the MAL during the scan, performed better on tests prior to entering the scanner ($r = 0.488$, $p = 0.029$) (Figure 8a). These relationships were not observed in the left STG (Figure 8b). Therefore, consistent with previous work, Broca’s region (but not STG) appears to be strongly related to proficiency.

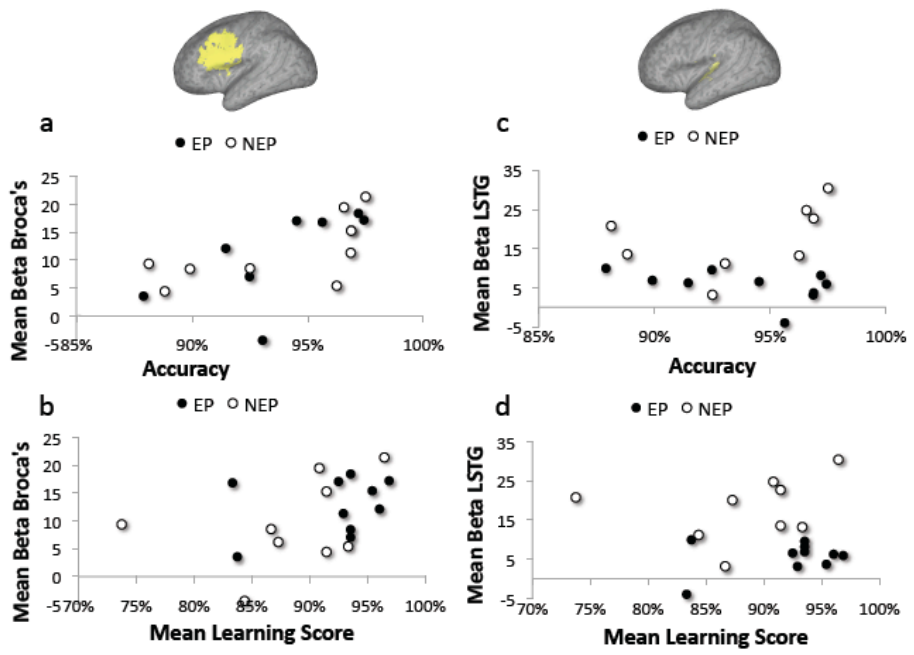


Figure 8. *Brain Behavior Relationships in Broca’s Region and the LSTG*
Displayed on the top of the figure are the ROIs for which neural recruitment was probed in Broca’s and the left STG respectively. There was a strong relationship between the degree of recruitment in Broca’s region and accuracy during scanning (a) as well as learning prior to the scan (b). These relationships were not observed in the LSTG (c and d).

2.5 General Discussion

In this study we asked whether adults' language learning difficulties have to do with the inappropriate use of a neural circuit that was based on one's native language. Since neural circuits are built in a nested way, with commitments being made first to the more basic properties of a stimulus, we further asked whether changing an earlier-learned aspect of language—sound structure—would have an impact on the neural representation of a later learned aspect—grammar. To do this, we created two artificial languages which both differed from English (the native language of our participants) in terms of grammar but had different phonological inventories, one similar to English and the other quite distinct. This allowed us to asses the degree to which an L2 sound structure is similar to the L1 predicts 1) learning of the L2 and 2) the similarity of neural recruitment during grammatical processing.

The data clearly indicate that sound structure impacts both L2 learning and neural recruitment. Although both NEP and EP learners were intentionally matched on proficiency prior to undergoing the scan, subtle group differences remained. NEP learners were worse, overall, on measures of vocabulary and on novel tests of verb agreement and noun class on the second day these were tested. Thus, it appears that phonology is important not just for learning the sounds of a language but also for these later-learned aspects of the language.

In addition to this learning difference, we also observed distinct patterns of neural recruitment. We observed more overlapping recruitment in Broca's area for the EP language and English than for the NEP language and English. EP learners were also more likely to recruit the left Middle frontal Gyrus, the Middle Temporal Gyrus, and the Caudate bilaterally. NEP learners, on the other hand, recruited additional regions associated with auditory and phonological processing, including the bilateral STG, superior-temporal-junction and Supramarginal Gyri. Importantly, these differences were observed even though EP and NEP learners did not differ in reaction time or accuracy when assessing the grammaticality of sentences in the scanner. Thus, we can be fairly confident that the differences in neural recruitment are not simply due to previously documented factors like proficiency. Instead, they emerge from the requirements imposed by phonological processing.

Differences were observed especially in Broca's region, which has been shown to be crucial for learning grammar (Opitz & Friederici, 2004, 2007), a relationship also evident in the current data. In our study, individuals who recruited Broca's region more also performed better on the grammaticality judgments (while in the scanner) and had higher overall learning scores prior to entering the scanner. The fact that there was more overlapping recruitment within this region for English and the EP learners suggests that EP learners were engaging cortex that was more optimized for processing the language, enabling more efficient learning.

EP learners were also likely to recruit the left Middle frontal Gyrus, the Middle Temporal Gyrus, and the Caudate bilaterally. The middle frontal region, the dorsal-lateral Prefrontal Cortex is classically associated with effortfully holding information in mind (Curtis & D'Esposito, 2003). Recruitment of this region could therefore reflect a greater degree of control on the part of EP learners (also see (Abutalebi & Green, 2007). Moreover, the basal ganglia have been shown to be important for processing the statistical properties of speech (McNealy, Mazziotta & Dapretto, 2009) and higher order aspects of language (Ketteler, Kastrau, Vohn, & Huber, 2008), as well as switching between languages in multilinguals (Abutalebi et al., 2008; Crinion et al., 2006) and language control—direct stimulation of the caudate leads to perseveration in monolinguals (Robles, Gatignol, Capelle, Mitchell, & Duffau, 2005). Since this region is recruited in many contexts for natural language, the greater recruitment of this region on the part of EP learners is additional evidence that the EP MAL is being processed more like a natural language. Moreover, the role of the BG in language control is particularly noteworthy. Such control is extremely important for bilinguals who are required to process and switch between more than one language. It appears that EP, but not NEP, learners devote neural resources to this important aspect of linguistic processing.

NEP, learners, on the other hand, recruited regions associated with auditory and phonological processing. This is in line with previous studies on sound processing. In particular, the Superior Temporal Gyrus has been shown to be involved in phonetic processing (Hickok & Poeppel, 2000), including the perception and production of speech sounds (Buchsbaum, Hickok, & Humphries, 2001), and it is engaged to a greater degree bilaterally when individuals process non-native phonological distinctions (Golestani & Zatorre, 2004; Zhang, Kuhl, Imada, Kotani, & Tohkura, 2005). Importantly, training in non-native phonological distinctions has been shown to be associated with decreasing recruitment of these regions over time (Golestani & Zatorre, 2004). The greater recruitment of this region on the part of NEP learners could therefore reflect a similar process, whereby the brain is in the process of tuning to the sounds. With more exposure to the language or perhaps more direct training on the sounds, it is possible that NEP learners would recruit this region less over time and that more native-like recruitment in Broca's region would also be observed. That is, if the brain is not processing the sounds in an effective way, it is likely that the signal being sent to higher-order language regions such as Broca's is impoverished. Ultimately, studies cataloguing the impact of intensive training for non-native contrasts on neural recruitment during *grammatical* processing are required to determine if this is the case.

In sum, NEP learners showed more difficulty in learning and more distinct neural recruitment. Importantly, the NEP language differs from the EP language only in its phonological inventory. The degree to which L2 sound structure is similar to L1 therefore predicts both the ease with which an L2 was learned and the similarity of neural recruitment during grammatical processing. Having an expert neural system for language that is based initially on sound structure therefore appears to be detrimental for learning a new language comprised of different sounds. Taken together, these data suggest that sensitive period phenomena could arise in part from the use of an inappropriate system that is expert in something else (L1).

2.6 Tables

2.6.1 Table 1. MAL versus Implicit Baseline

MAL versus implicit baseline							
			Talairach coordinates (at peak)				
Lobe	**Activation Region**	**Hemisphere/ Brodmann area**	**x**	**y**	**z**	**t-score**	**P value**
EP							
Frontal	Middle Frontal Gyrus	L46	-48	22	28	8.94	.00005
	Middle Frontal Gyrus	L9	-44	4	40	11.2	.00005
	Inferior Frontal Gyrus (pars triangularis)	L44	-50	6	12	9.8	.00005
	Middle Frontal						
	Precentral Gyrus	L4	-46	-8	50	13.03	.00005
	Insula	L	-32	24	12	9.19	.00005
	Medial Frontal Gyrus	L32	-14	22	36	6.73	.0001
	Superior Frontal Gyrus	R10	32	48	28	8.33	.00005
	Anterior Cingulate Gyrus	R32	12	32	28	11.48	.00005
	Insula	R	36	28	4	7.32	.00005
Temporal	Superior Temporal Gyrus	R38	52	16	-8	11.72	.00005
	Superior Temporal Gyrus	R22	62	-20	-2	7.08	.00005
	Superior Temporal Gyrus	L42	-54	-36	14	10.05	.00005
	Transverse Temporal Gyrus	L41	-64	-16	10	6.39	.0001
Parietal	Precuneus	R7	10	-74	42	10.95	.00005
Occipital	Lingual Gyrus	R17	-2	-92	-4	9.24	.00005
	Lingual Gyrus	L17	-8	-60	-4	11.58	.00005
Other	Lentiform Nucleus	L	-24	20	-2	15.59	.00005
	Lentiform Nucleus	R	20	16	-6	10.52	.00005
	Midbrain	R	8	-18	-14	10.21	,00005
NEP							
Frontal	Middle Frontal Gyrus	L46	-46	26	30	7.93	.00005
	Inferior Frontal Gyrus	L45	-26	36	8	7.97	.00005
	Precentral Gyrus	L6	-58	2	30	7.97	.00005
	Precentral Gyrus	L4	-32	-28	58	10.14	.00005
	Insula	L	-32	18	10	7.17	.00005

	Superior Frontal Gyrus	L6	-4	6	60	15.35	.00005
	Middle Frontal Gyrus	R46	42	36	30	8.35	.00005
	Middle Frontal Gyrus	R9	52	26	40	6.46	.0005
	Inferior Frontal Gyrus	R45	38	22	8	7.32	.00005
	Superior Frontal Gyrus	R8	2	16	58	7.75	.00005
	Insula	R	34	22	6	9.16	.00005
Temporal	Superior Temporal Gyrus (Sylvian–parietal–temporal region)	L41	-54	-30	8	12.44	.00005
	Superior Temporal Gyrus (Sylvian–parietal–temporal region)	R41	48	-32	10	8.45	.00005
	Superior Temporal Gyrus	R42	60	-14	12	9.46	.00005
Parietal	Superior Parietal Lobule	L7	-28	-66	48	8.23	.00005
	Postcentral Gyrus	L1	-52	-26	56	8.00	.0001
	Inferior Parietal Lobule (Supramarginal Gyrus)	R40	40	-48	44	8.35	.00005
Occipital	Middle Occipital Gyrus	R19	28	-96	14	12.24	.00005
	Cuneus	L18	6	-76	12	8.07	.00005

2.6.2 Table 2. NEP versus EP

NEP versus EP							
			Talairach coordinates (at peak)				
Lobe	**Activation Region**	**Hemisphere/ Brodmann area**	**x**	**y**	**z**	**t-score**	**P value**
NEP > EP							
Temporal	Superior Temporal Gyrus (Sylvian–parietal–temporal region, including Heschl's Gyrus, Rolandic Operculum & Supramarginal Gyrus)	L41, 13, 22	-50	-24	8	5.18	.001
	Superior Temporal Gyrus (Sylvian–parietal–temporal region, including Heschl's Gyrus, & Rolandic Operculum)	R42, 41, 22	62	-14	12	3.62	.005
EP > NEP							
Frontal	Middle Frontal Gyrus	L10	-32	52	8	3.74	.005
	Inferior Frontal Gyrus	L45,44	-46	18	6	3.23	.005(very small = only 7 voxels)
Temporal	Middle Temporal and Angular Gyrus	L39	-38	-64	24	4.03	.005
Parietal	Precuneus	R7	8	-74	42	3.57	.005
	Precuneus	L7	-16	-78	40	3.63	.005
Other	Caudate (tail)	L	-20	-36	16	3.62	.005
	Caudate	R	23	-33	14	4.01	.005
	Cerebellum (Culmen & Vermis)	L	-6	-60	-2	3.73	.005

2.6.3 Table 3. EP and English

EP and English							
			Talairach coordinates (at peak)				
Lobe	**Activation Region**	**Hemisphere/ Brodmann area**	**x**	**y**	**z**	**t-score**	**P value**
EP>English (non error, correct)							
Frontal	Inferior Frontal Gyrus	L44	-56	4	22	5.87	.001 (super small, this is 13 voxels)
	Superior Frontal Gyrus	R32	16	16	50	7.08	.0005
	Middle Frontal Gyrus	R9	48	8	32	6.77	.0005
Temporal	Superior Temporal Gyrus	R42	64	-22	6	6.00	.0005
Parietal	Superior Parietal Lobule	L7	-28	-64	50	7.33	.0005
	Superior Parietal Lobule	R7	30	-62	58	5.20	.001
Other	Lentiform Nucleus (Putamen)	L	-14	4	4	5.68	.001 (also small only 12 voxels)
English > EP							
Frontal	Inferior Frontal Gyrus	L47	-46	40	-10	6.21	.0005
	Superior Frontal Gyrus	L9	-20	42	44	6.38	.0005
	Superior Frontal Gyurs (Medial)	L9	-8	54	40	6.84	.0005
	Inferior Frontal Gyrus	R47	54	40	-4	4.51	.001
Temporal	Hippocampus	R	30	-6	-20	5.94	.0005
	Parahippocampal Gyrus (& Hippocampus)	L	-20	-2	-20	5.34	.001
	Middle Temporal Gyrus	L21	-56	-18	-22	6.03	.001
Parietal	Angular Gyrus	L39	-54	-66	38	5.45	.001

2.6.4 Table 4. NEP and English

NEP and English							
			Talairach coordinates (at peak)				
Lobe	**Activation Region**	**Hemisphere/ Brodmann area**	**x**	**y**	**z**	**t-score**	**P value**
NEP>English (non error, correct)							
Frontal	Precentral Gyrus	R6	36	-6	46	7.47	.0005
	Middle Frontal Gyrus	R6	30	-12	66	5.81	.001
	Insula	R	28	24	12	5.95	.001
	Precentral Gyrus	L6	-30	-14	58	5.56	.001
	Medial Frontal Gyrus (Supplementary Motor Area)	L6	-6	2	64	4.93	.001
Temporal	Superior Temporal Gyrus (Sylvian–parietal–temporal region, including Heschl’s Gyrus, Rolandic Operculum & Supramarginal Gyrus)	L41, 22, 42	-50	-28	8	7.81	.0005
	Superior Temporal Gyrus (Sylvian–parietal–temporal region, including Heschl’s Gyrus, Rolandic Operculum & Supramarginal Gyrus	L41, 22, 42, 13	68	-20	8	7.38	.0005
Parietal	Inferior Parietal Lobule	L40	-30	-52	56	4.58	.001
Occipital	Cuneus	L18	-2	-84	4	6.05	.001
English > NEP							
Frontal	Inferior Frontal Gyrus	L47, 45	-30	28	-18	8.27	.0005
	Middle Frontal Gyrus	L8	-40	16	54	5.55	.001
	Superior Frontal Gyrus	L8	-6	44	52	5.83	.001
	Middle Frontal Gyurs	R47	34	40	-10	7.31	.001
Temporal	Angular Gyrus	L39	-38	-60	26	7.21	.0005
	Parahippocampal Gyurs	L20	-34	-36	-22	4.51	.001
Parietal	Precuneus	L7	-8	-46	46	5.43	.001

2.7 Appendices

2.7.1 Appendix A. Phonological Inventories of MALs

EP
English phones
Vowels:
/ɛ/, /ʌ/, /ɪ/, /ai/, /i/, /ɚ/,
/ei/, /æ/, /ɔ/, /a/, /u/,
/ʊ/, /o/
Consonants:
/b/, /ŋ/, /ð/, /p/, /h/, /n/,
/t/, /ɹ/, /m/, /l/, /s/, /d/,
/r/, /k/, /f/, /w/,
/z/, /g/, /v/

NEP
Non-English phones
Vowels:
/i/, /ɔ/, /y/, /oi/, /ɨ/, /œ/,
/ʉ/, /ø/, /e/, /ɪ/, / ʊ /,
/ʏ/, /ɯ/,
Consonants:
/p/, /ŋ/, /ʂ/, /ʙ/, /x/, /ɲ/,
/tʃ/, /ɗ/, /ɳ/, /ɣ/, /ʁ/,
/ɕ/, /ɢ/, /q/, /ɠ/, /ɗ/,
/ʑ/, /ɬ/, /χ/

2.7.2 Appendix B. Differences From Chance by Group on Each Learning Test

Differences from chance by group on each learning test

Tests/ Test Day	Learning Group EP	 NEP
Vocabulary All Days	*t*=40.52, *p*<.001	*t*=18.57, *p*<.001
Vocabulary Day 1	*t*=11.77, *p*<.001	*t*=8.00, *p*<.001
Vocabulary Day 2	*t*=42.71, *p*<.001	*t*=13.15, *p*<.001
Vocabulary Day 3	*t*=200.0, *p*<.001	*t*=21.20, *p*<.001
Vocabulary Day 4	*t*=89.10, *p*<.001	*t*=30.10, *p*<.001
Verb Agreement Both Days	*t*=27.81, *p*<.001	*t*=9.33, *p*<.001
Verb Agreement Day 3	*t*=13.03, *p*<.001	*t*=6.29, *p*<.001
Verb Agreement Day 4	*t*=20.25, *p*<.001	*t*=10.17, *p*<.001
Word Order Both Days	*t*=22.00, *p*<.001	*t*=18.47, *p*<.001
Word Order Day 3	*t*=12.49, *p*<.001	*t*=19.37, *p*<.001
Word Order Day 4	*t*=12.53, *p*<.001	*t*=14.66, *p*<.001
Noun Class Both Days	*t*=10.19, *p*<.001	*t*=6.99, *p*<.001
Noun Class Day 3	*t*=5.06, *p*=.001	*t*=7.12, *p*<.001
Noun Class Day 4	*t*=14.80, *p*<.001	*t*=5.62, *p*<.001

Chapter 3. Longitudinal Evidence for Functional Specialization of the Neural Circuit Supporting Working Memory in the Human Brain

3.1 Summary of Research and Findings

Although children perform more poorly than adults on many cognitive measures, they are better able to learn things such as language and music. These differences could result from the delayed specialization of neural circuits and asynchronies in the maturation of neural substrates required for learning. Working memory—the ability to hold information in mind that is no longer present in the environment—comprises a set of cognitive processes required for many, if not all, forms of learning. A critical neural substrate for working memory (the prefrontal cortex) continues to mature through early adulthood. What are the functional consequences of this late maturation for working memory? Using a longitudinal design, we show that although individuals recruit prefrontal cortex as expected during both early and late adolescence during a working memory task, this recruitment is correlated with behavior only in late adolescence. The hippocampus is also recruited, but only during early, and not late adolescence. Moreover, the hippocampus and prefrontal cortex are coactive in early adolescence irrespective of task demands or performance, in contrast to the pattern seen in late adolescents and adults, when these regions are coactive only under high task demands. Together, these data demonstrate that neural circuitry underlying working memory changes during adolescent development. The diminishing contribution of the hippocampus in working memory function with age is an important observation that informs questions about how children and adults learn differently.

3.2 Development of Working Memory and Neural Anatomy: Relevant Background

Working memory (WM) comprises a set of cognitive processes required for many, if not all, forms of learning (Bayliss, Jarrold, Baddeley, & Gunn, 2005; Cowan, 2005). This ability has been shown to be important for myriad cognitive abilities (Conway, Kane, & Engle, 2003; Unsworth, Redick, Heitz, Broadway, & Engle, 2009), and scholastic achievement (Bayliss et al., 2005). The neural substrates supporting WM undergo changes well into adulthood (Gogtay et al., 2006; Lenroot & Giedd, 2006; Sowell et al., 2004), both within regions that are necessary for WM in adults—the prefrontal cortex (PFC) (Curtis & D'Esposito, 2003; Goldman-Rakic, 1987)—and regions that are recruited only during specific contexts—the hippocampus (Ranganath & Blumenfeld, 2005). Using longitudinal functional magnetic resonance imaging (fMRI) in adolescents, we ask whether these anatomical changes observed in normal development are accompanied by changes in the functional WM circuit.

Adolescence is an important period of time to explore these changes for several reasons. First, adolescence is a critical period for PFC development (Lenroot and Giedd, 2006). Second, neurodevelopmental investigations generally report greater recruitment of brain regions involved in WM in adults compared to children (Casey et al., 1995; Crone et al., 2006; Klingberg, Forssberg, & Westerberg, 2002; O'Hare, Lu, Houston, Bookheimer, & Sowell, 2008; Olesen, Macoveanu, Tegner, & Klingberg, 2007; Scherf et al., 2006; Thomas et al., 1999; Thomason et al., 2009; Tsujimoto, Yamamoto, Kawaguchi, Koizumi, & Sawaguchi, 2004). Comparisons between adolescents and adults however are more varied, with some studies reporting few differences (Crone et al., 2006; O'Hare et al., 2008) and others reporting more diffuse brain activity during adolescence (Olesen et al., 2007; Scherf et al., 2006). We aim to resolve these discrepancies by examining changes in the same adolescents across two time periods. Third, there is growing evidence that adolescence is a time of substantial reorganization on a network level (Fair et al., 2008; Fair et al., 2007). Thus, multivariate analyses of fMRI can illuminate whether the functional circuit supporting WM function also undergoes reorganization, something not addressed in previous developmental investigations. Finally, few behavioral differences are observed between adolescents and adults on simple WM tasks (Cowan et al., 2003; Davidson et al., 2006; Gathercole, 1999; Luciana & Nelson, 1998; Luna, Garver, Urban, Lazar, & Sweeney, 2004) despite the PFC's relative immaturity at this age, suggesting the involvement of additional regions during the engagement of WM processes. Illuminating any such differences could help explain why a behavioral difference is not observed. The hippocampus is a likely candidate. In adults, the hippocampus is recruited during WM tasks only when stimuli are novel or relations between stimuli must be formed (Mitchell et al., 2000; Ranganath and D'Esposito, 2001; Piekema et al., 2006). Likewise, patients and animals with hippocampal damage are impaired on WM tasks involving complex and novel objects (Buffalo, Reber, & Squire, 1998).

The present investigation therefore addresses the following specific questions: (1) Does the WM network change during adolescence? (2) Moreover, is the hippocampus involved in the WM network during early, but not later, adolescence?

3.3 Experiment

3.3.1 Experiment Methods

Participants and Procedure

We used fMRI and followed 10 female adolescents longitudinally, (mean age 15.1 years (*SD:* 1.55) for scan 1 (S1) and 18.3 years (*SD*: 1.45) for scan 2 (S2); all were right-handed, native English speakers). During both scans, we administered a delayed match-to-sample task (Rypma & D'Esposito, 2000; Sternberg, 1969) where participants encoded either 2 (low-load) or 6 (high-load) visually presented upper-case letters for 2 seconds (cue), held the letters in mind for a 13.2 second (delay) period and then responded as to whether a lower-case letter presented at test (probe) matched one of the encoded letters (Figure 1a). There were a total of 80 trials (50% high-load; 50% low-load, 50% where the probe letter matched a letter in the encoding set; randomized across trials).

fMRI data acquisition and analysis

Functional MRI data were acquired using a 4.0 T Varian INOVA MR scanner. Functional data were obtained using a two-shot echo-planar imaging (EPI) sequence sensitive to BOLD contrast (effective TR = 2200 ms, TE = 28 ms, FOV = 22.4 cm^2, matrix size = 64 X 64). Image processing, univariate and multivariate analysis were completed using SPM2 (Friston et al., 1991). Prior to statistical analyses, raw EPI data were normalized to Montreal Neurological Institute (MNI) space, As described previously (Sheridan, Hinshaw, & D'Esposito, 2007), a statistical parametric map was calculated for each participant based on linear combinations of the regressors modelling each task period (Friston et al., 1995). Regressors were convolved with the canonical hemodynamic response function provided by SPM2 and defined for each stage (cue, delay, and probe) of each task condition. Only trials with correct responses were incorporated in the analysis. Individual results were then combined into a group analysis; paired t-tests were used for across-scan comparisons.

To compute functional connectivity, a unique parameter estimate (beta value) for the events in each trial was computed for each participant and then sorted by task period (i.e., cue, delay, probe), yielding a beta series. The extent to which two regions interact is quantified by the extent to which their respective beta series are correlated (Rissman, Gazzaley, & D'Esposito, 2004). Regions of interest (ROIs) for both brain-behavior and connectivity analyses were constructed from these group data by choosing the 10 most active, contiguous voxels within the PFC (all participants at both scan times, $p<.001$) or hippocampus (all participants at S1, $p<.001$). Our definition of the lateral PFC included the Middle and Inferior Frontal Gyri, ventral to the Superior Frontal Sulcus and anterior to the Precentral Sulcus. Contrast values were extracted using MarsBar (Brett et al., 2002).

3.3.2 Experiment Results

Accuracy did not differ across the two scans ($t(9)= .562$, $p = .588$). Consistent with many developmental studies using reaction time (RT) (Kail & Salthouse, 1994; Sheppard & Vernon, 2008; Thomas & Nelson, 2001), participants were faster to respond when they were older (i.e., at S2, $t(9) = 3.658$, $p = .005$). During both scans participants were more accurate ($t(9) = 2.63$, $p = .027$) and faster to respond ($t(9) = -4.678$, $p = .001$) at low load (2 vs. 6 letters).

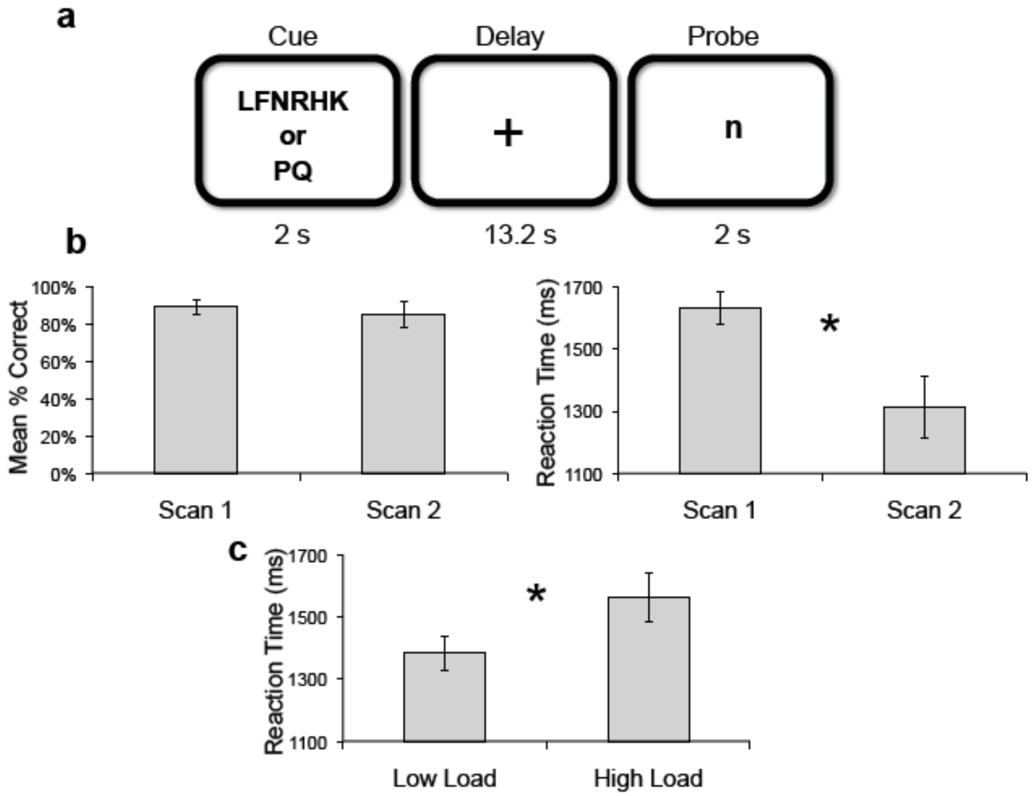


Figure 1. *Experimental Task and Behavioral Data*
(a) Participants encoded either 2 or 6 letters (*cue*) and retained them across a 13.2-second *delay* interval. When a *probe* was presented, they then determined whether or not a single letter was part of the memory set (2 seconds). Accuracy and RTs across scan times (b) and memory loads (c). Error bars represent standard error of the mean.

Neural recruitment was assessed for all task periods (e.g., cue, delay, probe). Consistent with many other investigations of WM, lateral PFC activity was observed during all stages of the task at both scan times (S1 and S2; Tables 1 and 2). Additionally and in accordance with our hypothesis, participants recruited hippocampus during S1, but not S2, for all three task periods (cue, delay and probe; Tables 1 and 2). Accordingly, hippocampal activity was greater during S1 than S2 during all three task periods for each load condition and collapsed across loads (see Figure 2 and Table 3).

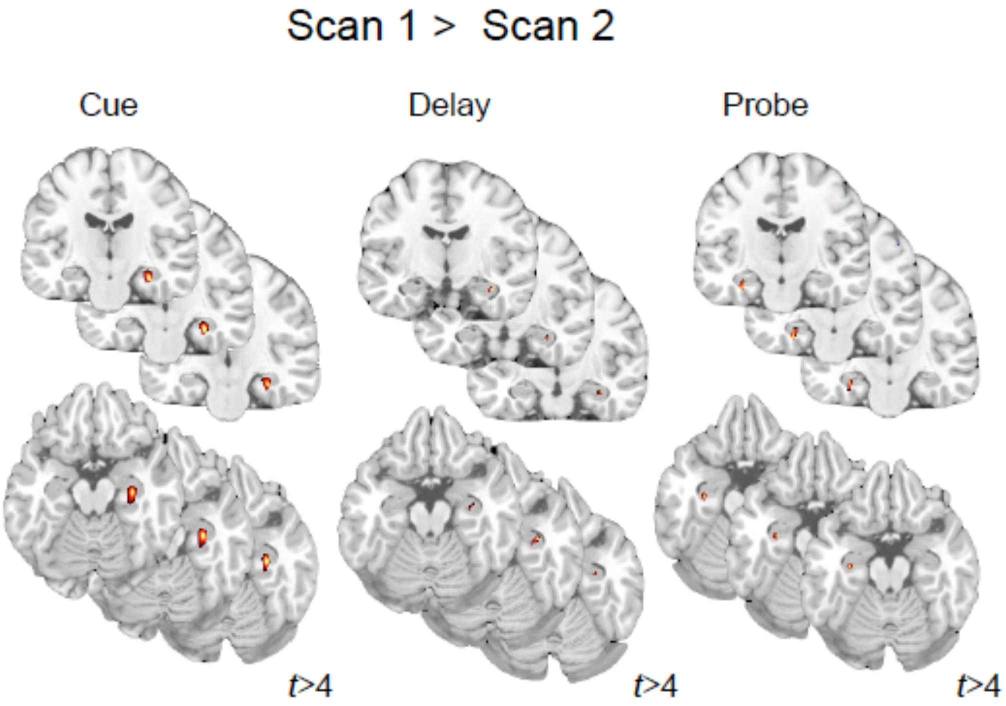


***Figure 2**. Functional MRI Data*
Hippocampal recruitment during scan 1 as compared to scan 2 is shown during all task periods.

These results suggest that while adolescents recruit PFC as expected during a WM task, younger adolescents additionally recruit the hippocampus. This is the first demonstration of hippocampal activity for any age group during a WM task that does not include complex/novel or location-bound objects. Given that neither adults (Rypma & D'Esposito, 2000) nor these same individuals 3 years later recruit the hippocampus for this task, these data show that neural recruitment during WM function is qualitatively different earlier in adolescence. Why do individuals recruit the hippocampus when they are younger but not when they are older? This could be a consequence of several, not entirely separate, factors such as: differences in task difficulty during each of the scan times and differences in developmental trajectories of the hippocampus and PFC. These possibilities are explored in turn.

We explored task difficulty in two ways: first, by examining neural recruitment for high versus low memory loads, and second, by comparing recruitment across scan times on a subset of trials that were matched for RT. Regions that are recruited to a greater extent with increasing load should reflect increased task difficulty. As expected, there was greater recruitment of frontal regions during all task periods for high as compared to low loads during S1 (Table 4) and during the delay and probe periods for S2 (Table 5). However, load-related recruitment was not observed in the hippocampus at S1 or S2, suggesting that frontal, but not hippocampal regions, are sensitive to relative task difficulty.

Thus, it seems that the hippocampus is not recruited simply due the task being more difficult for younger adolescents. However, RTs were slower at S1 than S2. Thus, we compared the subset of trials in which RT was equated across the two time periods to determine if the pattern of hippocmpal activity we observed changed. In this analysis we compared the fastest 75% of trials during S1 (mean RT: 1398.5ms; range: 2273-805ms) and the slowest 75% of trials during S2 (mean RT: 1392.3ms; range: 3674-723ms). This analysis again revealed that hippocampal activity was greater during S1 than S2, as observed separately during the encoding and delay periods (Table 6). Thus, our primary result persists despite comparing trials at S1 with faster RTs, which could be considered easier, with trials at S2 with slower RTs.

The greater involvement of the hippocampus during performance of WM task at S1 could be due to the immaturity of the PFC that leads to compensatory recruitment of the hippocampus. Alternatively, it could simply reflect normal developmental differences in the trajectory of cortical maturation (hippocampal earlier, PFC later). To provide evidence that PFC's functional role in WM function is delayed in time, we explored the relationship between behavior and PFC function across scanning sessions. Across all participants, we therefore correlated left PFC activity during each task period with RT. We found that early in adolescence (S1), there was no significant association between PFC activity and RT for any of the task periods (encoding: r= .222, R^2= .049, p= .538; delay r= -.269, R^2= .073, p= .452; probe r= -.523 R^2= .274 p= .121 collapsed across load). In contrast, at S2 the correlation was robust during encoding (r = -.705, R^2= .497, p = .023; Figure 3a), and in the predicted direction (though not significant) during other task periods. Moreover, there was a significant relationship between the change in the degree to which the PFC (S2-S1) was recruited and change in reaction time (S1-S2) across scan times for encoding and delay periods (cue: r= -.804, R^2= .646 p= .005; delay r= -.653, R^2= .462 , p= .041), showing that adolescents who recruited the PFC more during the second as compared to the first scan, were the ones whose RTs improved the most across scan times (Figure 3b). Thus, data show a tight link between PFC function and behavior at S2 but not S1, suggesting that the functional role of the PFC is developmentally delayed.

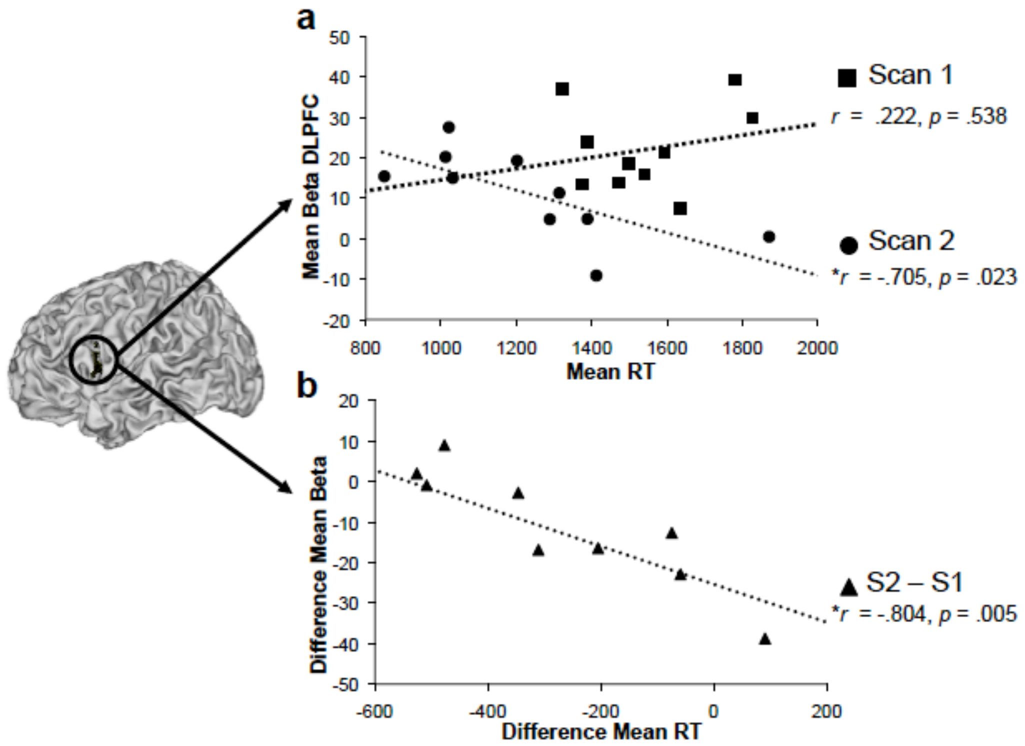


Figure 3. *Brain-Behavior Correlations*
(a) Mean beta values for each individual in left PFC during encoding
(a) and are plotted against the mean RT for individuals separately for
each scan time. (b) The difference across scan times in PFC beta values
during encoding and RTs is plotted.

To investigate the role of the hippocampus in the WM network directly, we measured functional connectivity between the hippocampus and PFC at both scan times. We chose to focus this analysis on the encoding period because S1 hippocampal recruitment is most robust during encoding; and this is also the task phase during which reliable brain-behavior associations were observed at S2. First, we examined functional connectivity (Rissman et al., 2004) between the right hippocampus and the rest of the brain at S1. To directly compare connectivity at S1 and S2, we also measured functional connectivity of the left PFC region used above and the rest of the brain. At S1, activity in the right hippocampus was functionally correlated with bilateral regions in the lateral PFC (Left t=4.40, p<.0001 & Right t=8.39, p<.0001) and the contralateral hippocampus (Left t=4.12, p<.0001; Figure 4; table 9). Also at S1, activity in the left PFC was correlated with bilateral hippocampus (Left: t=4.67, p<.0001; Right: t=4.13, p<.0001; Figure 4; table 7). Despite the strong association between hippocampal and PFC activity during S1, no such association was observed in the same individuals, performing the same task 3 years later. At S2, no significant correlations between PFC and hippocampus were observed (Figure 4). Rather, the left PFC is correlated primarily with the contralateral right PFC (Table 8). Thus, the hippocampus appears to be part of the WM network during earlier stages of adolescence, but not later.

Previous work in adults, however, has shown that hippocampal connectivity with PFC and stimulus-selective posterior association cortex increased with high, but not low loads (Rissman, Gazzaley, & D'Esposito, 2008), or with difficult but not easy tasks. If individuals are more adult-like at S2, hippocampal-PFC connectivity might likewise be present for high, but not low mnemonic loads. To test this hypothesis, we examined hippocampal-PFC connectivity for each scan time separately for high (6 letters) and low (2 letters) loads. As predicted given our reported findings, functional correlations between the left hippocampus and left PFC were significant regardless of load condition at S1 (low load: t=4.53, p< .0001; high load: t=5.02, p<.0001). However, at S2, the left PFC and left hippocampus were correlated only during high load (t=4.85, p< .0001).

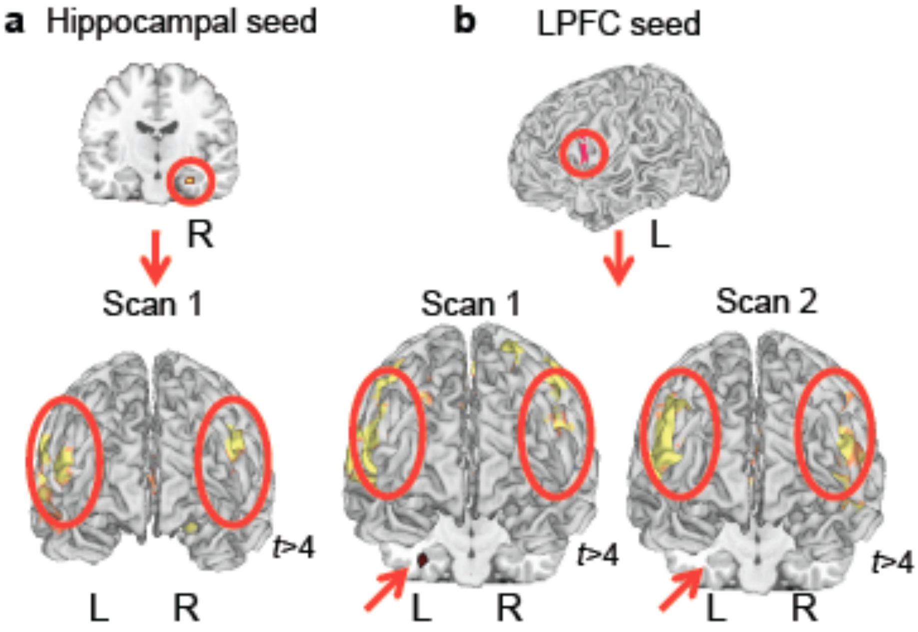


***Figure 4**. Hippocampal-PFC Connectivity*
(a) Hippocampal seed used in the connectivity analyses obtained during the encoding period in scan 1. This seed was functionally correlated with bilateral lateral PFC, and contralateral hippocampus (not depicted) during scan 1. (b) Left PFC seed used in the connectivity analyses obtained during the encoding period across both scan times. This seed was functionally correlated with bilateral lateral PFC during both scan 1 and 2 but only the left hippocampus during Scan 1.

To further explore the factor of task difficulty, we investigated whether RT would show a similar result. We split observations based on median reaction time (for both S1 and S2) and probed PFC-hippocampus connectivity for each load. The most difficult trials are those for which adolescents were slow to respond during a high mnemonic load. As in the previous analysis, functional correlations between the left hippocampus and left PFC were significant regardless of load or RT at S1 (fast/low: t=2.77, p<.005.; fast/high: t=3.43, p<.001; slow/low: t=3.17, p<.001; slow/high: t=2.72, p<.005). At S2, however, functional correlations were significant only during slow trials (low: t=2.90, p<.005; high t=4.42, p<.00005), an effect that was most salient during high load.

3.4 Discussion

In summary, this is the first longitudinal fMRI study demonstrating that functional network specificity changes across adolescence. Data show that the WM circuit becomes increasingly specialized with age. Earlier in adolescence, participants recruited both the lateral PFC and hippocampus during a WM task, but did not recruit the hippocampus three years later during performance of the same task. Moreover, whereas PFC and hippocampal activity are correlated regardless of WM load and behavior during early adolescence, these associations are observed only during high mnemonic loads three years later, a time during which the PFC is also predictive of behavior.

Our data aids in the understanding of the mismatch in the literature on the development of WM during adolescence. Behaviorally, basic WM maintenance processes show minimal changes during this time period (Cowan et al., 2003; Davidson et al., 2006; Gathercole, 1999; Luciana & Nelson, 1998; Luna et al., 2004), but a large body of evidence shows that the primary neural substrate for WM—the PFC—undergoes great structural and functional change during this same time (Lenroot & Giedd, 2006; Sowell et al., 2004; Thomason et al., 2009). By examining functional recruitment and network connectivity, we have shown that younger adolescents recruit an additional region, the hippocampus, during WM function. This recruitment could buttress WM function such that no behavioral differences are observed. Additional studies will be necessary to determine if earlier hippocampal recruitment is compensatory, or due to normal developmental differences in the trajectory of cortical maturation.

Interestingly, previous researchers have suggested that protracted PFC development might actually be a benefit, rather than a hindrance, to children; advanced PFC abilities are hypothesized to interfere with probability, convention, and imitative learning, forms of learning where children have been shown to outperform adults (Ramscar & Gitcho, 2007; Thompson-Schill, Ramscar, & Chrysikou, 2009). Here, we extend these previous theoretical formulations by demonstrating that the hippocampus is engaged in younger individuals during the performance of a WM task that does not engage the hippocampus in older individuals (see also Chatham et al., 2009). Because younger individuals appear to recruit the hippocampus in circumstances that adults do not, they might also bind, consolidate, store, and retrieve information in more situations than adults. Thus, we suggest that this hippocampal involvement in the broader WM network—and not just delayed PFC maturation—might actually be a crucial part of children's learning differences. Qualitative differences in the networks younger individuals employ to achieve basic aspects of cognition such as WM therefore hold the promise of helping us understand age-related learning differences we observe in nature.

3.5 Tables

3.5.1 Table 1. Activity During S1 Time Period

Task period > baseline							
			Talairach coordinates (at peak)				
Lobe	**Activation Region**	**Hemisphere/ Brodmann area**	**x**	**y**	**z**	**t-score**	**P value**
Encoding							
Frontal	Inferior Frontal Gyrus**	L44	-54	16	16	10.04	.0001
	Middle Frontal Gyrus**	L47	-54	18	36	6.48	.0001
	Superior Frontal Gyrus*	L9	-44	36	32	4.86	.001
	Precentral Gyrus**	R6	60	-2	18	5.19	.0001
	Middle Frontal Gyrus*	R6	28	8	54	4.42	.001
	Middle Frontal Gyrus	R46	40	40	22	3.70	.002
	Inferior Frontal Gyrus	R44	54	12	16	3.84	.002
Temporal	Hippocampus*	R	32	-26	-14	4.58	.001
	Fusiform Gyrus*	R37	38	-58	-18	4.29	.001
Occipital	Middle Occipital Gyrus	L37	-40	-64	-16	4.42	.001
Other	Cerebellum**	R	34	-56	-22	8.36	.0001
Delay							
Frontal	Precentral Gyrus*	L6	-34	-24	62	5.29	.001
	Middle Frontal Gyrus*	R9	38	14	48	5.00	.001
	Precentral Gyrus	R6	28	-30	56	3.78	.002
Parietal	Postcentral Gyrus	L4	-60	-20	22	3.49	.003
	Inferior Parietal Lobule	R40	40	-50	56	3.46	.004
Temporal	Hippocampus/Parahippocampal Gyrus	R	36	-10	-22	3.23	.005
Probe							
Frontal	Middle Frontal Gyrus**	R46	38	22	22	9.03	.0001
	Middle Frontal Gyrus	L46	-38	48	10	3.61	.003
	Inferior Frontal Gyrus*	L45	-36	30	-6	4.82	.001
	Anterior Cingulate Gyrus*	L32	-12	30	22	5.07	.001
Parietal	Postcentral Gyrus*	R43	60	-8	22	4.94	.001
	Postcentral Gyrus	R4	58	-20	26	3.19	.005
	Inferior Parietal Lobule*	R40	34	-46	42	4.19	.001
	Posterior Cingulate Gyrus	L23	-8	-54	20	3.43	.004
Temporal	Hippocampus*	L	-30	-16	-18	4.63	.001

	Inferior Temporal Gyrus*	R37	54	-50	-10	5.03	.001

In this and all other supplementary tables reporting univariate data, regions are listed where period-specific parameter estimates were significantly greater than baseline (with a t of 3 or greater that is at least 10 voxels) across scan times. A single asterisk indicates differences where significance was set to p <.001, with a minimum contiguous cluster size to 10 voxels. Double asterisks indicate areas which remain significant after correcting for multiple comparisons, p < .0001 with a cluster size of 3.

3.5.2 Table 2. Activity During S2 Time Period

Task period > baseline							
			Talairach coordinates (at peak)				
Lobe	**Activation Region**	**Hemisphere/ Brodmann area**	**x**	**y**	**x**	**t-score**	**p value**
Encoding							
Frontal	Middle Frontal Gyrus**	R46	26	34	26	6.81	.0001
	Middle Frontal Gyrus	L10	-32	46	24	3.38	.004
	Inferior Frontal Gyrus	L44	-54	10	6	3.0	.007
	Anterior Cingulate Gyrus**	R24	2	24	30	7.85	.0001
	Precentral Gyrus**	R4	40	-20	42	5.76	.0001
Parietal	Postcentral Gyrus*	L2	-42	-26	48	6.36	.0005
	Postcentral Gyrus *	R3	28	-48	28	5.02	.001
Other	Putamen*	L	-30	0	-6	6.56	.0005
	Lentiform Nucleus *	R	16	-14	-2	6.44	.0005
	Cerebellum*	L	-2	-52	-18	5.32	.001
Delay							
Frontal	Superior Frontal Gyrus*	L10	-16	48	24	5.35	.001
	Inferior Frontal Gyrus*	L47	-30	16	-2	6.27	.001
	Inferior Frontal Gyrus*	R47	40	18	-2	6.11	.0005
	Middle Frontal Gyrus*	R46	36	32	28	4.10	.001
	Precentral Gyrus *	R3	52	-16	46	4.34	.001
Parietal	Postcentral Gyrus	L4	-56	-20	42	3.85	.002
	Supramarginal Gyrus	L40	-40	-44	34	3.99	.002
	Inferior Parietal Lobule	R40	50	-54	42	3.56	.003
	Precuneus	L7	0	-58	38	3.84	.002
Probe							
Frontal	Superior Frontal Gyrus*	L10	-26	58	0	5.92	.001
	Inferior Frontal Gyrus*	L45	-50	20	10	5.08	.001
	Precentral Gyrus*	L6	-54	-4	16	4.82	.001
	Insula*	L48	-40	-14	8	5.87	.001
	Middle Frontal Gyrus*	R46	32	14	36	4.74	.001
	Cingulate Gyrus	R24	8	-10	32	3.62	.003
	Cingulate Gyrus	L24	-6	-8	28	3.69	.002
Occipital	Middle Occipital Gyrus	L18	-26	-86	10	3.44	.004

3.5.3 *Table 3. Differences Across Scan Times*

Scan 1 > Scan 2							
			Talairach coordinates (at peak)				
Lobe	**Activation Region**	**Hemisphere/ Brodmann area**	**x**	**y**	**z**	**t-score**	**P value**
Encoding							
Frontal	Inferior Frontal Gyrus*	L45,44	-60	18	8	5.44	.001
	Inferior Frontal Gyrus*	R44	60	14	16	4.46	.001
Temporal	Hippocampus**	R	32	-18	-18	7.46	.0001
	Parahippocampal Gyrus*	L37	-36	-38	-10	5.60	.0005
	Superior Temporal Gyrus*	R22	56	-10	0	4.41	.001
Occipital	Lingual Gyrus	L18	-10	-84	-16	3.67	.003
Other	Cerebellum*	L	-8	-70	-20	4.24	.001
Delay							
Temporal	Hippocampus/Parahippocampal Gyrus*	R	36	-10	-20	4.85	.001
Probe							
Frontal	Middle Frontal Gyrus*	R46	40	20	20	5.07	.001
	Inferior Frontal Gyrus*	R47	48	24	-18	4.92	.001
	Medial Frontal Gyrus*	L8	-12	32	48	4.97	.001
Temporal	Hippocampus*	L	-30	-16	-20	4.99	.0005
	Superior Temporal Gyrus*	L38	-44	18	-16	4.95	.001
Scan 2 > Scan 1							
Encoding							
Frontal	Middle Frontal Gyrus*	R9	14	46	26	4.24	.001
	Superior Frontal Gyrus	R9	24	50	16	3.74	.002
Parietal	Posterior Cingulate Gyrus	R31	22	-28	44	3.37	.004
Occipital	Lingual Gyrus*	R18	24	-62	2	4.08	.001
Delay							
Frontal	Cingulate Gyrus**	L32	-16	10	30	5.90	.0001
	Inferior Frontal Gyrus*	L44	-50	2	30	4.55	.001
	Inferior Frontal Gyrus	R47	34	12	-12	3.60	.003

	Medial Frontal Gyrus*	L9	-18	46	24	4.25	.001
	Superior Frontal Gyrus	L10	-28	46	32	3.52	.003
	Insula	R	48	8	0	3.86	.002
Parietal	Inferior Parietal Lobule*	R40	38	-40	40	4.18	.001
	Inferior Parietal Lobule	L40	-62	-36	42	3.24	.004
	Posterior Cingulate Gyrus*	R30	20	-68	4	4.29	.001
Occipital	Cuneus & Precuneus*	L18	-16	-76	18	4.58	.001
Other	Globus Pallidus	L	-16	-10	-6	3.23	.005
Probe							
Frontal	Inferior Frontal Gyrus	L45	-52	16	2	3.12	.006
	Precentral Gyrus	L6	-48	-4	18	3.38	.004
Parietal	Postcentral Gyrus*	R3	52	-14	48	4.35	.001

3.5.9 Table 4. Areas Significantly More Active for High vs. Low Load, S1

High load > Low load							
			Talairach coordinates (at peak)				
Lobe	**Activation Region**	**Hemisphere/ Brodmann area**	**x**	**y**	**z**	**t-score**	**p value**
Encoding							
Frontal	Inferior Frontal Gyrus*	L45	-44	36	8	5.23	.001
	Inferior Frontal Gyrus	R9	42	8	32	4.79	.001
	Superior Frontal Gyrus*	R9	28	44	38	4.73	.001
	Anterior Cingulate Gyrus	L24	-8	28	24	3.87	.002
	Medial Frontal Gyrus	R9	14	26	36	3.63	.003
Parietal	Superior Parietal Lobule*	R7	22	-68	36	5.95	.0005
	Precuneus **	L7	-16	-62	50	8.19	.0001
Occipital	Middle Occipital Gyrus*	L19	-40	-76	-12	5.17	.001
	Middle Occipital Gyrus*	R19	36	-82	-8	5.13	.001
Other	Caudate	R	8	10	6	3.62	.003
	Lentiform Nucleus**	L	-22	2	6	6.29	.0001
	Brainstem	L34	-16	-6	-20	4.64	.001
Delay							

Frontal	Inferior Frontal Gyrus*	L45	-54	24	10	5.51	.001
	Middle Frontal Gyrus*	R46	46	34	18	4.94	.001
Probe							
Frontal	Inferior Frontal Gyrus**	L47	-40	18	-12	7.16	.0001
	Anterior Cingulate Gyrus*	L32	-18	36	20	4.80	.001
	Precentral Gyrus*	L43	-60	-8	20	6.69	.0005
Parietal	Postcentral Gyrus*	L2	-42	-32	58	4.22	.001
	Inferior Parietal Lobule*	R40	54	-24	28	4.09	.001
	Inferior Temporal Gyrus	L37	-52	-66	-2	3.74	.002

3.5.5 *Table 5. Areas Significantly More Active for High vs. Low Load, S2*

High load > Low load							
			Talairach coordinates (at peak)				
Lobe	**Activation Region**	**Hemisphere/ Brodmann area**	**x**	**y**	**x**	**t-score**	**Voxel number**
Encoding							
Frontal	Anterior Cingulate Gyrus*	R32	8	24	32	5.34	.001
	Anterior Cingulate Gyrus	L32	-10	18	26	3.61	.003
Parietal	Postcentral Gyrus	R2	32	-32	34	3.29	.005
Delay							
Frontal	Precentral Gyrus	L4	-32	-22	40	6.66	.0005
Probe							
Frontal	Middle Frontal Gyrus*	L10	-28	54	0	4.20	.001

3.5.6 *Table 6. Areas Significantly More Active During S1 as Compared to S2 When Matched on Mean Reaction Time*

Scan 1 > Scan 2							
			Talairach coordinates (at peak)				
Lobe	**Activation Region**	**Hemisphere/ Brodmann area**	**x**	**y**	**x**	**t-score**	**Voxel number**
Encoding							
Temporal	Hippocampus*	R	32	-18	-22	4.6	.001
	Parahippocampal Gyrus	L	-22	-10	-14	3.99	.005
Occipital	Middle Occipital Gyrus*	L18	-42	-66	-6	9.31	.001
Other	Insula*	L	-38	-30	18	6.13	.001
	Cerebellum*	R	26	-66	-22	4.95	.001
Delay							
Frontal	Inferior Frontal Gyrus*	L45	-54	26	20	7.22	.001
	Middle Frontal Gyrus*	R46	40	44	14	6.41	.001
	Middle Frontal Gyrus*	L6	-30	4	56	5.08	.001

Temporal	Hippocampus	R	30	-18	-22	4.21	.002
Occipital	Lingual Gyrus	R18	22	-80	-16	5.02	.001
Other	Cerebellum	R	22	-50	-38	5.10	.001
Probe							
Frontal	Middle Frontal Gyrus*	R9	60	18	36	4.99	.001
Temporal	Parahippocampal Gyrus*	R	14	-38	0	5.76	.001
	Superior Temporal Gyrus*	R	44	20	-26	4.77	.001
Other	Insula*	R	38	-42	18	5.24	.001

3.5.7 Table 7. All Beta Series Correlations, LPFC Seed During S1

LPFC correlations							
			Talairach coordinates (at peak)				
Lobe	**Activation Region**	**Hemisphere/ Brodmann area**	**x**	**y**	**Z**	**t-score**	**Voxel number**
Frontal	Inferior Frontal Gyrus*	L45	-54	18	6	23.41	.0001
	Middle Frontal Gyrus*	L46	-42	41	20	23.41	.0001
	Precentral Gyrus*	L9	-54	6	14	23.41	.0001
	Inferior Frontal Gyrus*	R47	54	18	-5	6.62	.0001
	Middle Frontal Gyrus*	R46	46	11	43	7.10	.0001
	Precentral Gyrus*	R6	46	-14	31	7.10	.0001
Parietal	Postcentral Gyrus*	R4	46	-23	48	7.10	.0001
	Inferior Parietal Lobule*	R40	46	-28	24	6.89	.0001
Temporal	Superior Temporal Gyrus*	L42	-54	-56	13	23.41	.0001
	Middle Temporal Gyrus*	L21	-61	-8	-7	23.41	.0001
	Superior Temporal Gyrus*	R22	54	14	-9	6.62	.0001
	Hippocampus*	L	-30	-14	-21	4.67	.0001
	Hippocampus/Parahippocampal Gyrus	R	28	-22	-16	4.13	.0001
Occipital	Middle Occipital Gyrus*	L,19	-46	-68	14	9.72	.0001
	Middle Occipital Gyrus*	R19	28	-82	14	4.31	.0001
Other	Cerebellum*	L	-34	-66	-16	8.96	.0001
	Cerebellum*	R	37	-66	-25	5.25	.0001

In this and all other supplementary tables reporting beta series correlations, regions are listed where period-specific parameter estimates were significantly greater than baseline where significance was set to $p < .001$, with a minimum contiguous cluster size to 10 voxels. Asterisks indicate areas which remain significant after correcting for multiple comparisons, $p < .0001$ with a cluster size of 3.

3.5.8 Table 8. All Beta Series Correlations, LPFC Seed During S2

LPFC correlations							
			Talairach coordinates (at peak)				
Lobe	**Activation Region**	**Hemisphere/ Brodmann area**	**x**	**y**	**z**	**t-score**	**p value**
Frontal	Inferior Frontal Gyrus*	L45	-56	18	4	22.14	.0001
	Middle Frontal Gyrus*	L46	-45	18	31	22.14	.0001
	Precentral Gyrus*	L6	-52	3	13	22.14	.0001
	Inferior Frontal Gyrus*	R45	48	22	10	10.27	.0001
	Middle Frontal Gyrus*	R46	42	15	30	10.27	.0001
	Precentral Gyrus*	R6	52	8	37	10.27	.0001
	Anterior Cingulate Gyrus*	R24	12	24	14	6.82	.0001
Parietal	Inferior Parietal Lobule*	L40	-50	-28	30	6.44	.0001
	Postcentral Gyrus*	L4	-50	-25	34	6.44	.0001
	Precuneus*	R19	22	-56	32	5.37	.0001
Occipital	Cuneus*	L18	-12	-85	8	6.07	.0001
	Lingual Gyrus*	L18	-12	-78	-2	6.07	.0001
Other	Midbrain & Thalamus*	R	10	-24	-4	7.45	.0001

3.5.9 Table 9. All Beta Series Correlations, Hippocampus Seed During S1

Hippocampus correlations							
			Talairach coordinates (at peak)				
Lobe	**Activation Region**	**Hemisphere/ Brodmann area**	**x**	**y**	**z**	**t-score**	**p value**
Frontal	Inferior Frontal Gyrus*	L45	-48	38	10	4.40	.0001
	Inferior Frontal Gyrus*	R45	46	30	12	8.39	.0001
	Middle Frontal Gyrus*	R46	46	21	28	8.39	.0001
	Precentral Gyrus*	L6	-59	-2	18	7.88	.0001
Parietal	Postcentral Gyrus*	L4	-62	-15	18	7.88	.0001
Temporal	Hippocampus*	R	30	-20	-20	31.19	.0001

	Hippocampus/Parahippocampal Gyrus*	L	-34	-8	-32	4.12	.0001
	Superior Temporal Gyrus*	L22	-62	-22	10	7.88	.0001
Occipital	Lingual Gyrus*	R18	10	-73	-9	7.43	.0001
	Precuneus & Cuneus*	L18	-16	-72	26	5.87	.0001
Cerebellum	Cerebellum*	R	30	-41	-30	31.19	.0001

Chapter 4. The role of effort and the prefrontal cortex in adult learners' use of novel statistics for word segmentation and category learning

4.1 Summary of Research and Findings

Compared to children, adults are notoriously poor at learning language. Children's learning advantage could be the result of their ongoing neural development; the delayed maturation of the prefrontal cortex (PFC)—a structure known to be crucial for effortful processing—could be beneficial for learning language. In a series of studies, we explored this possibility. First we explored the relationship between effortful processing and the ability to extract structure from an artificial language in adults. Second, we used transcranial theta-burst stimulation (TBS) to determine whether this effort-learning relationship is directly related to mature neural function. We exposed learners to an artificial language comprised of words that belong to phonologically defined categories. When learners were instructed to passively listen to the language, they learned both the words and the categories. However, when learners were told to explicitly try to learn the words or the categories, they failed to learn the categories. Administering TBS to the left PFC prior to exposure, however, ameliorated the cost of this effort. These findings contribute to our understanding of the sensitive period for language learning by showing that adults' learning difficulties are due, at least in part, to mature prefrontal function and effortful processing abilities.

4.2 Effort, the Prefrontal Cortex & Language Learning: Relevant Background

Individuals who learn language as children consistently outperform those who learn language as adults (Birdsong, 1999; Flege et al., 1995; Mayberry & Lock, 2003; Newport et al., 2001). This sensitive period for language acquisition has long posed a puzzle: why do children outperform adults when it comes to learning language but not when it comes to learning in other domains such as physics and algebra? One explanation for this mismatch is that children's learning advantage could actually be the consequence of their cognitive immaturity, resulting from ongoing neural development. In particular, the delayed maturation of the prefrontal cortex (PFC) could be beneficial for learning language. Somewhat counter intuitively, the role of this region in effortful processing could be detrimental for language-learning. In a series of studies we explore this possibility. First, we explore the relationship between effortful processing and the ability to extract structure from an artificial language in adults. Second, using transcranial theta-burst stimulation (TBS), we then explore whether this effort-learning relationship is directly related to mature neural function.

The PFC has been shown to be important for many aspects of effortful processing, including working memory (WM) (Curtis & D'Esposito, 2003), cognitive control (Bunge et al., 2002), and goal-directed behavior (Bunge & Zelazo, 2006; Fuster, 2002; Miller, Freedman, & Wallis, 2002), abilities that are broadly considered executive function (Stuss & Knight, 2002). Many separate measures have pointed to this region as particularly slow to mature: grey matter volume (Gogtay et al., 2004; Lenroot & Giedd, 2006; Sowell et al., 2004; Toga et al., 2006), regional metabolism (Chugani & Phelps, 1986), white matter (Yakovlev & Lecours, 1967), and synaptic density and dendritic arborization (Huttenlocher, 1990). Likely as a consequence of this delayed maturation, there have been multiple demonstrations that WM ability increases steeply during childhood (Cowan, Towse, Hamilton, Saults, Elliott, Lacey, Moreno, & Hitch, 2003; Davidson, Amso, Anderson, & Diamond, 2006; Gathercole, 1999). Similarly, the slow development of cognitive control and goal-directed behavior have been well established and even linked to the protracted development of the PFC (Bunge & Zelazo, 2006; Fuster, 2002; Munakata, 2006). Here we address the hypothesis that these developmental "delays" carry a hidden benefit for child language learners.

This notion has been raised in various forms by previous researchers. However, each formulation has a distinct angle, and we review these in turn. Newport (1990) was the first to suggest that children's superior language learning outcomes might be enhanced by virtue of their limited processing, or WM, capacities (Newport, 1990). She argued that since less information can be held in mind at any given time, an analysis of linguistic input is easier to perform. In support of this idea, Elman (1993) has shown that training a connectionist network to process complex sentences succeeds only when the networks begin with limited resources akin to WM and gradually "mature" (Elman, 1993). Likewise, Goldowsky and Newport (1993) have shown that introducing a filtering mechanism—meant to emulate limited WM abilities—in a connectionist network can facilitate the learning of form-meaning associations (Goldowsky & Newport, 1993).This modeling work therefore suggests that diminished WM abilities might actually be beneficial for language learning. However, other modeling work has more recently shown that when the languages to be learned are larger and have more naturalistic structure (including semantic and syntactic constraints), these limited resources do not facilitate and actually interfere with learning (Rohde & Plaut, 1999; 2003). Therefore, the benefit that children have in learning language might not be due to limited working memory abilities per se.

Still, it is possible that there is a more indirect benefit of these limited abilities. Along these lines, is has been suggested that advanced prefrontal abilities interfere with unsupervised, and therefore language, learning (Ramscar & Gitcho, 2007; Thompson-Schill et al., 2009). That is, while the ability to maintain task-relevant (and filter out irrelevant) information facilitates goal-directed behavior and WM (Kane & Engle, 2003; Vogel, McCollough, & Machizawa, 2005), it carries a cost insofar as it minimizes competition between various possible forms present in the input, which has been shown to be advantages for learning (Ramscar & Yarlett, 2007). In support of this idea, research has shown that adults are more likely to learn veridically from the input they are given, while children maximize more frequent forms (Hudson Kam & Newport, 2005; Singleton & Newport, 2004). Interestingly, adults too appear to maximize more frequent forms in situations of extreme unpredictability (Hudson Kam & Newport, 2009); in such situations even the advanced cognitive abilities of adults might fail to learn veridical structure. In maximizing the most frequent form then, it appears that children utilize a form of unsupervised learning whereby the strongest competitor (the most frequent element) wins. Adults on the other hand, have advanced cognitive control mechanisms, which interfere with this unsupervised process. For learning language, this could be especially detrimental.

This idea therefore highlights the balance between advanced prefrontal abilities and unsupervised learning. Unlike the less-is-more hypothesis, advanced prefrontal ability itself does not interfere with learning, but its impact on another, unsupervised, learning process does. While interesting, there is very little direct evidence that these kinds of learning interfere, or even interact, with each other in a language-learning context. However, this question has been tackled in research exploring the role of effort (explicit learning) in implicit learning, an otherwise passive process similar to what Ramscar and collogues call unsupervised learning, where one is exposed to information and acquires knowledge of that information simply through exposure (Reber, 1993). Work by Willingham and colleagues (1999) has shown that implicit and explicit learning can occur in parallel and so effort might not interfere with learning in some situations. In this study, learners were either told that a pattern would be present in a serial reaction time task (SRT) or told nothing at all (Willingham & Goedert-Eschmann, 1999). In these tasks, participants respond as quickly as possible by pressing a button corresponding to the location of a stimulus. Implicit learning is measured by comparing responses to random versus repeating sequences. While learners who were not cued to the pattern were initially faster to respond to patterned items than individuals who were explicitly cued, this difference diminished with more training and both groups showed learning of the sequence during a transfer task, suggesting that implicit and explicit knowledge can be acquired in parallel.

There have been demonstrations, however, of explicit instructions interfering with implicit learning. In a series of studies, Reber has shown that explicit instruction can both interfere with and facilitate implicit learning. Individuals who study grammatical strings generated from a Markov grammar accurately classify strings presented later as either grammatical or not when they are told nothing about the learning situation (Reber, 1967). However, when individuals are told—before exposure to grammatical strings—to simply look for structure, they perform worse than those who were not given any instruction. Interestingly, when individuals were explicitly given a cartoon of a Markov-chain grammar and taught about how the grammar works before being exposed to grammatical exemplars and then being asked to judge well-formedness of novel exemplars, there was a facilitation in their judgment ability. The earlier they were shown the cartoon grammar, the better they performed during test (Reber, 1993). Reber argued that when instructions were vague, learners could have spent time exploring inaccurate hypotheses and therefore failed to learn. However, when explicit instruction was directed to the correct structure, learning improved.

It has also been shown that explicit instruction can interfere with implicit learning when the items to be learned are complex, but not when they are simple. When elderly but not young adult learners were asked to explicitly learn an alternating SRT sequence in which sequence items alternated with non-sequence items, implicit learning was disrupted (Howard & Howard, 2001). One reason why learning was disrupted in the elderly could have to do with the reduced cognitive capacity in that population; the complex sequence could be beyond the cognitive capacity of the elderly but not the young adult population. To test more directly the question of how cognitive capacity might mediate the interaction between implicit and explicit learning systems, Fletcher and colleagues (2004) presented young adults with either complex (alternating) or simple (standard) sequences using either explicit or incidental instructions (Fletcher et al., 2005).

They found that explicit instruction interfered with implicit learning of the complex, but not the simple sequence. Together, these data suggest that under certain conditions, implicit and explicit systems can proceed in parallel relatively unmolested unless the information to be learned is complex (and therefore beyond the limitations of the explicit system) or, as Reber (1993) has shown, the explicit instructions are vague and lead learners to explore incorrect hypotheses.

Language is both complex and difficult to formulate hypotheses about. It could therefore be the case that the effortful processing of language interferes with implicit learning of language. This is noteworthy given that language learning is thought to occur largely via implicit mechanisms (DeKeyser, 2005; Maratsos, 1980; Ramscar & Gitcho, 2007; Seidenberg, MacDonald, & Saffran, 2002; Ullman, 2001). The importance of implicit learning in language acquisition has been shown especially in studies investigating how individuals segment words from running speech. Discovering the units of speech—in this case words—is a significant problem for infant language learner, as speakers rarely pause to mark word boundaries (Liberman et al., 1967; Woodward & Aslin, 1990). One cue to word boundaries that has received a lot of attention is transitional probabilities (TP), or statistical regularities computed as the frequency of a pair of items (usually a pair of syllables) divided by the frequency of the first item in the pair. Work investigating the use of TP has shown that adults, infants, and even animals can track statistical regularities in running speech and use these regularities to find units akin to words (Hauser et al., 2001; Jenny R. Saffran et al., 1996; J. R. Saffran et al., 1996; Toro & Trobalón, 2005).

When both children and adults are engaged in a coloring task and not even told to listen to the stimuli playing in the background, they nonetheless appear to extract the statistical regularities (Saffran, Newport, Aslin, Tunick, & Barrueco, 1997). Despite this, there is some evidence suggesting that effort or attention is required for statistical learning. When performing a concurrent task, the extraction of these statistical regularities has been shown to be impaired (Toro, Sinnett, & Soto-Faraco, 2005). One reason why learning could be impaired in these situations could have to do with capacity limitations. As discussed above, when effort is directed to learning complex structure, implicit learning can be impaired. However, since effort was directed away from the stimulus of interest toward a concurrent task in this study, it is not possible to tell whether this is the case. It is therefore as of yet unknown how effort would impact statistical learning.

In the present study, therefore, we ask whether explicit instruction facilitates or impairs the implicit learning of transitional probability in a statistical learning paradigm. We ask this question first in a behavioral study with adults in order to determine whether effortful processing interferes with learning in a linguistic context. Based on previous work with the SRT task, explicit instruction should facilitate learning when the structures to be learned are simple and impede learning when they are complex. We therefore use an artificial language comprised of words that belong to phonologically defined categories and impose a category-specific ordering constraint. Within this language, the words can be thought of as relatively simple and the category structure as relatively complex. We then direct learners to either passively listen to the language (implicit condition), explicitly try to learn the words, or explicitly try and learn the categories. If these ideas are correct, then directing effort toward the simple structure (words) should enhance learning of the simple structure, but likely interfere with the learning of complex structure (categories); directing effort toward the complex structure, on the other hand, should interfere with learning both.

Importantly, the detrimental impact of effort (for learning complex structure) is hypothesized to be a direct consequence of the maturity of the PFC in adults. To determine whether this is the case, we use transcranial theta-burst stimulation (TBS) to temporarily take this region offline. In this way, adults will be temporarily transformed into children, at least in terms of being able to use one side of their prefrontal cortex. Effortful learning under these conditions, unlike in the previous experiment, should therefore incur no cost for learning of both the simple and complex structures.

4.3 Experiment 1

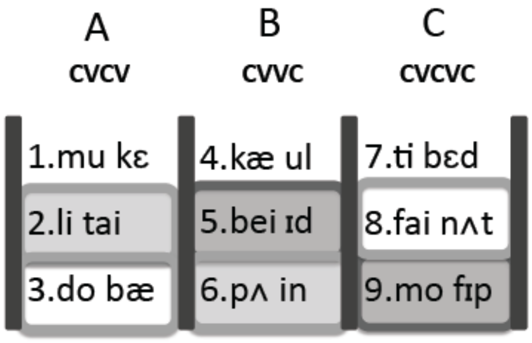
4.3.1 Experiment 1 Methods

Participants

Forty-eight undergraduates at the University of California, Berkeley participated for course credit. Participants were native speakers of English who reported normal hearing.

Stimuli

Experimental stimuli consisted of nine two-syllable words, presented in Figure 1, constructed from a set of 9 consonants (C) and 9 vowels (V). Each word belonged to one of three categories, A, B or C, with each category defined by a distinct, category-specific phonological structure. Words in category A followed a CVCV structure, words in B a CVVC structure, and words in category C a CVCVC structure. Each category was comprised of 3 words.



A cvcv	B cvvc	C cvcvc
1.mu kɛ	4.kæ ul	7.ti bɛd
2.li tai	5.bei ɪd	8.fai nʌt
3.do bæ	6.pʌ in	9.mo fɪp

Figure 1. *Structure of the Artificial Language*

Each of nine words belongs to one of three categories (A, B and C) that are defined by their phonological structure. Some words were not presented in succession; these pairings are indicated with similar shading.

The stimuli consisted of an A word followed by a B word, followed by a C word, which was then followed by an A word, followed by a B word, followed by a C word, and so on, with no pauses whatsoever in the stimuli. This structure (ABCABCABC…) repeated for 9 minutes 37 seconds. As such, B words never followed C words and C words never followed A words. Importantly, each word occurred an equal number of times in the stimuli (45). Additionally, one specific word from each category never followed another particular word from the preceding category. For example, /beiɪd/ from category B never followed /dobæ/ from category A. The withheld pairings are indicated by shading in Figure 1. Other than these constraints, words were presented randomly. Transitional probabilities were therefore 1.0 for word internal syllable transitions and ranged from .33 to .5 across word boundaries (The range is due to the fact that words from the withheld pairings could only be followed by two other words, while words that were not withheld could be followed by three other words). A sample stretch of the input stream is presented here: /mukɛkæultibɛddobæbeiɪdfainʌt/.

This auditory stream was created using the text-to-speech program SoftVoice (Katz, 2005). The synthesizer produced syllables with a monotonic F_0 (fundamental frequency) of 83.62 Hz. All vowels were matched for length and there were no co-articulation effects. We used synthesized speech to allow better control of the above-mentioned parameters. Use of natural speech risks the inclusion of additional segmentation cues through varying degrees of co-articulation, different vowel lengths, amplitudes, frequencies, etc.

Because there were no pauses in the stimuli whatsoever, the only information about word boundaries available to participants was from the TPs, and the only cue to category membership was the syllable structure.

Experimental Manipulation

Participants were randomly divided into three exposure conditions. In the implicit learning condition, participants were told that they were going to listen to a new artificial language. They were instructed simply to listen to the language as best they could, but not to over-think or ignore what they were listening to. To encourage this, participants colored using crayons or markers during exposure. In the word-level explicit condition, participants were told that they were going to listen to a new artificial language and to try as hard as they could to learn the nine words present in the language. They were alerted to the fact that this would be difficult because there were no pauses between the words in the language. They were also asked to indicate their knowledge level in an ongoing way throughout exposure. They were to press one of two buttons (the white one) whenever they had a strong idea or hypothesis about what a word was and were to do so immediately after hearing that word. A second (red) button was to be pressed whenever they were sure that they had learned a word; this too was to be pressed immediately after hearing that particular word. The third condition was the category level explicit condition. In this condition, participants were given the same instructions as in the previous condition, but instead of being told that there were nine words in the language, they were told that there were three kinds of words in the language. They were also asked to indicate their knowledge level via button presses, indicating each time they had an idea about or had learned a category.

After exposure, participants in the two explicit conditions were asked to answer direct questions about the language. Individuals in the explicit-word condition were asked 1) to produce the nine words they had heard, 2) how many words they thought were in a sentence, and 3) how many different kinds of words they thought were in the language. Individuals in the explicit-category condition were asked 1) how many words they thought were in a sentence, 2) how many words they thought were in the language, and 3) to produce any of the words in the language if at all possible. Both groups were also asked how frustrating they thought the learning exercise was (on a scale of 1 to 5) and if they gave up at any point during the learning phase. These questions preceded the standard testing given to all three groups.

Tests

After exposure and the explicit knowledge probes, all participants completed two forced-choice tests designed to test (1) participants' knowledge of words (i.e., whether they had successfully segmented the words using TPs) and (2) their knowledge of the category ordering.

In the word segmentation test, words were defined as the words (with 1.0 word-internal syllable TPs) to which participants had been exposed. These were compared to either non-words, the first syllable from one word paired with the second syllable from a completely different word, e.g. /mutai/, or part-words, consisting of the second syllable from one word paired with the first syllable from a word in the adjacent category, e.g. /kɛbei/. The non-word comparisons are the easiest: although participants had heard each of the two syllables in the non-word an equal number of times, they had never heard the two syllables in succession. The part-word comparison is more difficult: the syllables comprising the part-words did occur in succession, but they had lower transitional probabilities than the words to which they were being compared (.33 or .5 as compared to 1.0). There were 9 of each type of test item (word vs. non-word and word vs. part-word), yielding 18 test items in total.

The category ordering test was directed at probing participants' knowledge of category structure. These were of three types: order, withheld-generalization, and novel-generalization. In the first test type (order), participants were asked to compare strings that followed the correct order (A-B-C, B-C-A, C-A-B) with strings that did not (A-C-B, B-A-C, C-B-A). In all cases, comparisons were made between items with the same words presented in different orders, and starting with the same word, e.g. A(/mukɛ/)-B(/kæul/)-C(/tibɛd/) vs. A(/mukɛ/)-C(/tibɛd/)-B(/kæul/). There were 21 of these test items. Above chance performance on this test would indicate that participants were aware of the distributional properties of the language. However, in all cases, learners were asked to compare a phrase that occurred in the exposure set with a phrase that did not, so this test could be done based on familiarity alone.

The second test type—withheld-generalization—probes whether participants had actually learned the category distributions more directly. In these test items, participants were asked to compare withheld sequences with those same words placed in the incorrect order. For example, /dobæ/ (from category A) /beiıd/ (from category B) were never adjacent in the exposure set, but adjacency of these items is grammatical, according to the A-B-C order. During test, participants were therefore asked to compare /dobæ/(A)-/beiıd

/(B)-/wordX/(C) with /dobæ/(A)-/beiɪd/ (B)-/wordX/(A) or /wordX/(B). There were nine of these test items, three for each withheld pairing. Each of the possible words not involved in the withheld pairing was used with each withheld pairing. In the example above, each of the three C words was matched with the withheld AB pairing to create a test item. Since neither string occurred in the exposure set, above chance performance on this test would indicate that participants had learned something about the A-B-C order.

Still, participants could perform well on this test based simply on the basis that they never heard an A or B word after a B word. /beiɪd/ for example, was followed by all of the words in category C, but none of the words in category B or A. The between-word TP from /beiɪd/ to any word in category C is therefore .33. However, the between-word TP from any category B word to a category B or A word is 0, since B words can only be followed by C words. A stronger measure of category knowledge is therefore needed to conclude that participants actually learned the syllable structure generalization underlying the ordering. That is what was probed in the final test type—generalization-novel. Three novel words were generated for each category, that is, nine new words were constructed according to the three syllable structure patterns used to create the exposure words, and these words were used to create the test strings. The nine novel words were: category A: /kɪfi/, /mʌpɛ/, /bidu/; category B: /deiot/, /næif/, /bɪʌt/; category C: /lukaib/, /nailæt/, /pɛnum/.[3]

There were two different types of test strings created using the novel words. First, participants were asked to compare novel words placed in the correct position within a string versus the incorrect position within a string. For example, the novel A word /kɪfi/ was placed in the correct and incorrect location (A(/kɪfi/)-B-C vs. B- A(/kɪfi/)-C). As in other test items, participants were asked to compare phrases containing the same words—in this case one of which is novel—in the correct and incorrect order. There were five of these test items. Above chance performance on this test would indicate that learners understood that words of a particular phonological structure occur in particular locations within a phrase.

Still, participants could rely on other information to correctly respond to these items. For the correct item in the above example, any given C word follows any given B word 33% of the time, while a C word never followed the novel A word /kɪfi/. Thus, the correct answer contains at least one familiar pairing, in contrast to the incorrect string. An additional test type was therefore created using these novel items in which participants were asked to compare licit novel items in the correct location to illicit novel items (according to the structure of the category) in the same location. For these items, four additional novel words were generated that followed a distinct phonological structure: two CVCCV words: /naitlæ/, /pɛnmu/ ; and two VCCV words: /ɪbtʌ/, /ibdu/. Importantly, these words were comprised of the same phones (consonants and vowels) that were used to generate the licit novel words to which these items were compared. For example, the novel word following category B structure /bɪʌt/ was compared with the uncategorized novel word /ɪbtʌ/, with each novel item containing exactly the same phones, simply arranged in a different way. These items were flanked by exactly the same words in a phrase. There were four of these test items. Above chance performance on this test type

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[3] We used the same nine consonants and vowels as before in order to ensure that treatment of the words was due to the rules governing their phonological structure and not any novel sound.

would indicate that participants know something about the allowable structure of words in any given phrase and is therefore the most stringent test of generalization.

All of the test stimuli were generated according to the same procedure as the exposure stimuli. Participants completed the word segmentation test prior to the category ordering test. Within each test, items of all sub-types were presented randomly using E-prime software (Schneider, Eschman, & Zuccolotto, 2002). The two items (either words or phrases) were presented one after another with a 700ms pause in between, and participants indicated their selection using a button press. Participants were told that they would listen to pairs of possible words (or sentences) and were asked to "indicate which is more likely to have belonged in the language" they were exposed to. They were encouraged to make their best guess if unsure and were reminded of these same instructions prior to the second test.

After these tests, participants completed a measure of Reading Span. In this test, a sentence appeared on the computer screen, immediately followed by a letter. Individuals were asked to read the sentences and make a judgment as to whether the sentence was true or false. They were also asked to remember the letters in the order they appeared. After a variable set of sentences and letters, a recall screen would appear in which individuals were asked to indicate which letters had appeared in the order they had appeared.

Procedure

Participants came into the lab, read and signed the consent form, and then completed the experiment, comprising exposure and then testing. Exposure and testing were conducted individually in a quiet room. Stimuli and auditory tests were presented via noise-cancelling headphones. After completing the tests, participants filled in a survey probing their demographic and language backgrounds.

4.3.2 Experiment 1 Results

Figure 2 shows performance on the word segmentation test separately for learners in the implicit, explicit-word, and explicit-category conditions. Since performance did not differ for the non-word (TP=0) and part word (TP=.33/.5)) sub-types ($t(47) = -1.78$, $p = .082$), these data were combined for further comparisons. Two questions were considered in analyzing this data. First, is there evidence that participants correctly segmented and therefore learned the words? Second, does this learning differ between the groups? To assess this first question, we compared performance in each group to chance. One sample t-tests indicate that performance is reliably better than chance in each learning group (implicit: ($t(15) = 4.46$, $p < .001$); explicit-word: ($t(15) = 9.84$, $p < .001$); explicit-category: ($t(15) = 5.57$, $p < .001$)). Therefore, participants in all groups appear to have learned the words.

A one-way analysis of variance (ANOVA) further indicates that performance between the groups differs ($F(2,45) = 5.18$, $p = .006$). In particular, participants who were instructed to learn the 9 words outperformed those in the implicit condition ($F(1,30) = 14.74$, $p < .001$) but not those in the explicit-category condition($F(1,30) = 1.93$, $p = .174$).

Likewise, implicit learners did not differ from explicit-category learners (*F*(1,30) = 3.38, *p* =.076). Learners in all conditions therefore appear to track the statistical information and perform at above chance levels on this word segmentation test. However, learners who were instructed to learn the nine words perform better than learners who are told nothing, while learners who are told to learn the three categories do not, suggesting there is a benefit in learning when individuals are directed to learn items at the level of the word.

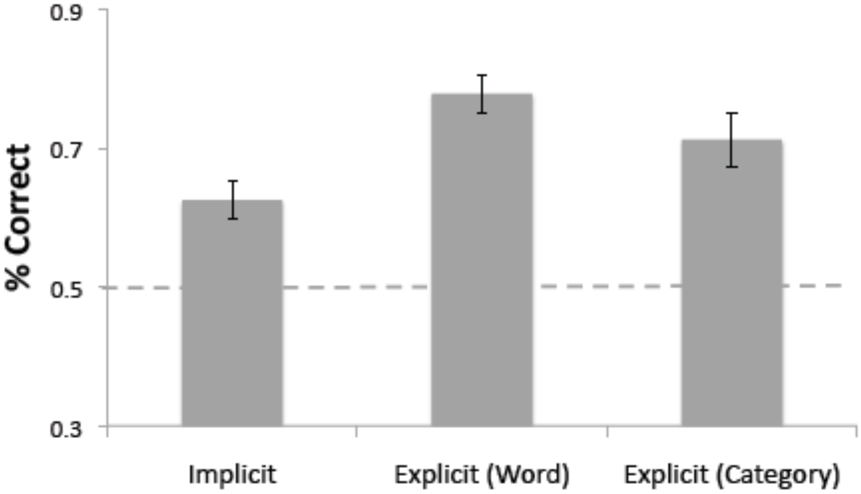

***Figure 2**. Performance on Word Segmentation Test*
Performance is displayed for all three learning groups. The dotted line indicates chance performance. Error bars reflect standard errors of the mean.

Figure 3 shows overall performance on the tests involving category orders (for each subtest considered together), separately for each learning condition. We again were interested in whether people learned and also whether there were any differences in performance between the groups. To assess this first question, we compared performance in each group to chance. Learners from all groups performed significantly above chance (implicit: (*t*(15) = 5.66, *p* <.001); explicit-word: (*t*(15) = 6.12, *p* <.001); explicit-category: (*t*(15) = 2.49, *p* <.001)). These data indicate that learners were able to learn something about the categorical and distributional structure of the artificial language. A one-way ANOVA further reveals a trend toward between group differences (*F*(2,45) = 3.13, *p* =.053), with learners in the explicit-category condition performing significantly worse than learners in the explicit-word condition (*F*(1,30) = 5.34, *p* =.028); there is a trend toward a similar relationship between the explicit-category and implicit learning conditions (*F*(1,30) = 3.41, *p* =.075), although it is not significant. And there appears to be no difference in performance between the implicit learning and explicit-word conditions (*F*(1,30) = .295, *p* =.591). Therefore, while all groups show learning as evinced by above chance performance, the explicit-category group appears to perform the worst on this measure, despite their efforts being directed toward learning exactly this information.

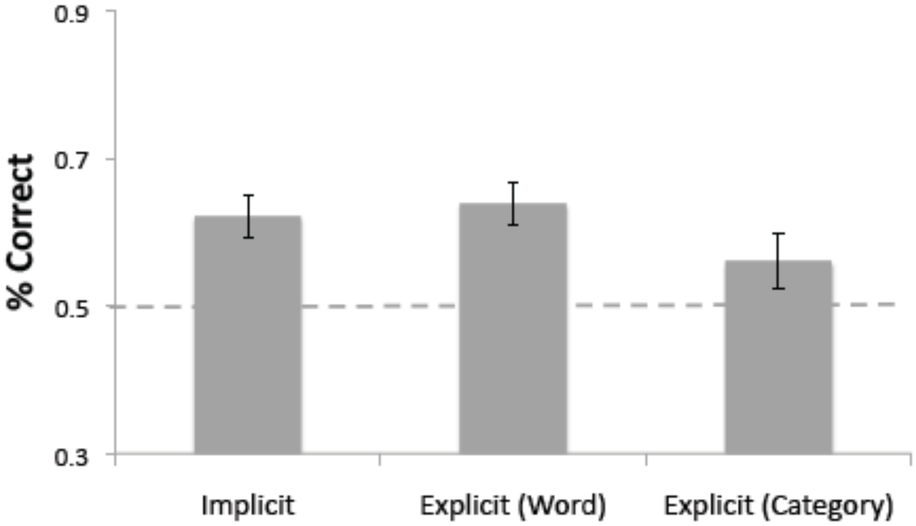

Figure 3. *Performance on the Category Order Test*
Performance is displayed for all three learning groups. The dotted line indicates chance performance. Error bars reflect standard errors of the mean.

Still, there are different types of items within this test that probe different levels of generalization. Figure 4 shows performance on each of these sub-tests, order, generalization-withheld, and generalization-novel, separately for each learning condition.

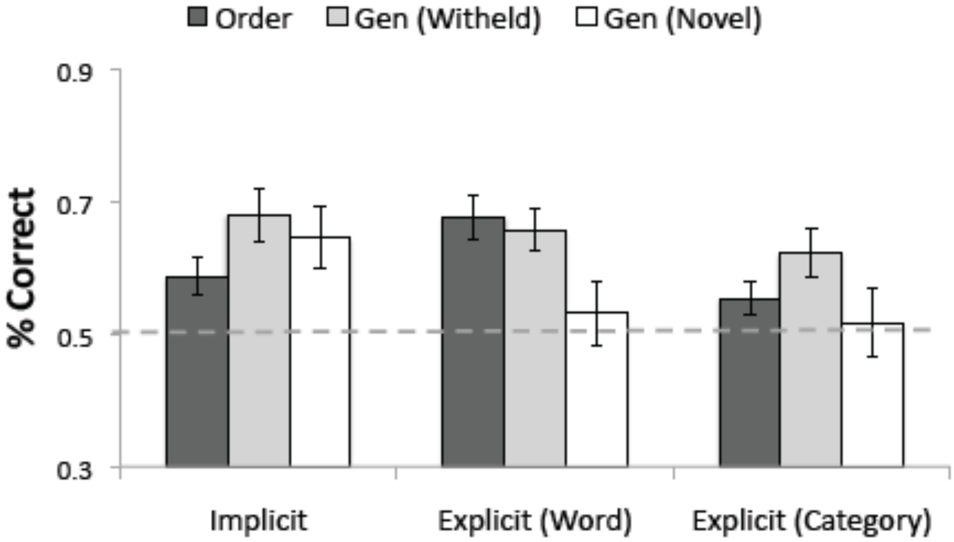

Figure 4*. Performance on Order and Generalization Tests*
Performance is displayed for all three learning groups for the order (dark grey bars), generalization-withheld (light grey bars), and generalization-novel (white bars) tests. The dotted line indicates chance performance. Error bars reflect standard errors of the mean.

As in the other tests reported, we were interested in whether participants learned and also whether there were any differences in performance between the groups. Learners in the implicit condition performed significantly better than chance on all of the sub-tests, including order (*t*(15) = 3.04, *p* =.008), generalization of withheld items (*t*(15) = 4.47, *p* <.001), and generalization of novel items (*t*(15) = 3.20, *p* =.006). Learners in the explicit-word condition were likewise better than chance on the order (*t*(15) = 5.2, *p*<.001) and generalization-withheld items (*t*(15) = 5.13, *p* <.001), but not the generalization-novel items (*t*(15) = .639, *p* =.532). This was also true for the learners in the explicit-category condition: order (*t*(15) = 2.09, *p* =.054), generalization—withheld (*t*(15) = 3.45, *p* =.004), generalization—novel (*t*(15) = .357, *p* =.726). Therefore, only learners in the implicit learning condition displayed learning on the generalization-novel sub-test, suggesting a potential advantage of not exerting effort towards learning this type of information.

Performance differences between groups on these measures were assessed with a repeated measures ANOVA, which revealed a main effect of test type (*F*(2,45) = 4.26, *p* =.017), but no effect of group (*F*(2,45) = 2.52 *p* =.091), or group by test-type interaction (*F*(2,45) = 1.94, *p* =.110). Still, there is reason to believe that between group differences would exist for each of these sub-tests. We therefore compared performance between the groups on each of these sub-tests separately. A one-way ANOVA revealed that performance between learning groups differed for the order test (*F*(2,45) = 4.65, *p* =.015), with the explicitly cued word group performing better than both the implicit (*F*(1,30) = 4.15, *p* =.05) and explicitly cued category (*F*(1,30) = 8.35, *p* =.007) groups, which did not differ significantly from one another (*F*(1,30) = .731, *p* =.399). Performance differences were not observed across groups on the generalization-withheld (*F*(2,45) = .624, *p* =.540), or the generalization-novel tests (*F*(2,45) = 2.09, *p* =.139). However, as mentioned above, only the implicit learning group was significantly different from chance on this most stringent measure of generalization (generalization-novel).

Together, therefore, the data from the word segmentation test suggest that there is a benefit to learners when they direct effort towards learning the words. This manipulation leads learners to perform better than learners in the other conditions on this measure. There also appears to be a benefit from this manipulation for learning the order of words; this group performed significantly better than other groups on the order test. On the other hand, there appears to be no benefit for learners who direct effort towards learning the categories of words in this artificial language. These learners are no different from the implicit group on the word segmentation test. Moreover, they are the worst on measures of category knowledge, despite being cued to learn just that structure. Instead, it appears that the implicit learners are the best at this. This is the only group that is significantly better than chance on the generalization of novel items, although performance on this measure is not reliably different between the groups.

Why is it the case that the implicit group is the only group that is reliably better than chance on this novel generalization test? One possibility is that there is a tradeoff in learning such that an ability to segment the words could mean a highly specific knowledge of those words which leads to an inability to learn the categories. Since the implicit group is not as good at learning the words as the explicit-word group, they may lack this highly specific knowledge and may therefore learn the categorical information with greater ease. To investigate this possibility, we subtracted the overall percent correct on the category test from the overall percent correct on the word segmentation test, producing a difference score for each individual. A positive score would indicate better performance on the word segmentation test, while a negative score suggests the opposite. Scores close to zero show these measures are similar and suggest that there is not a tradeoff, whereas positive scores would be consistent with a tradeoff. These scores are shown in figure 5 for each learning group separately. A one-way ANOVA indicates a main effect of group (*F*(2,45) = 4.217, *p* =.021), such that difference scores are larger in both explicit learning conditions (word: *F*(1,30) = 6.54, *p* =.016; category: *F*(1,30) = 7.41, *p* =.011) as compared to the implicit learning condition, and these are not significantly different from each other (*F*(1,30) = .034, *p* =.855). It therefore appears to be case that there is a tradeoff between word and category learning in explicit but not implicit learning conditions.

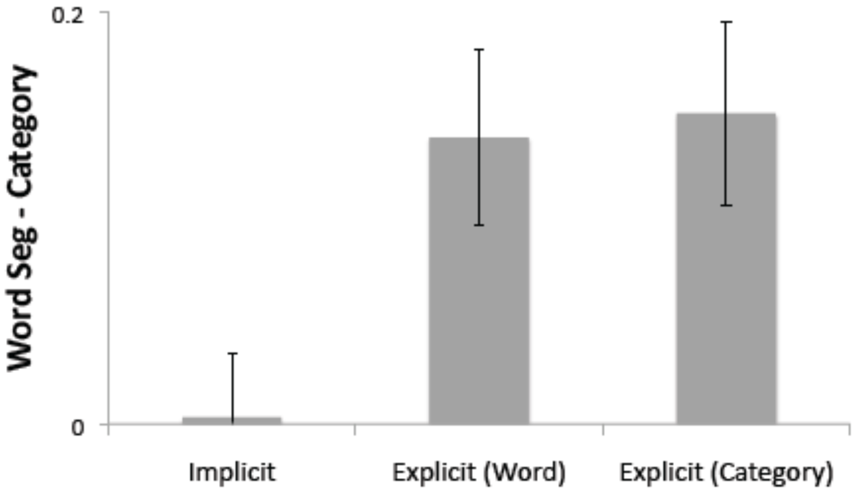

***Figure 5**. Difference in Performance on Word Segmentation and Category Tests by Learning Condition*

Difference scores are displayed for all three learning groups. Error bars reflect standard errors of the mean.

4.4 Experiment 2

The previous study indicates that explicit instruction interacts with implicit learning in a statistical learning language paradigm. In particular, instructing subjects to effortfully learn the words was beneficial for learning the words but detrimental for generalizing to novel instances on the category test. Given that generalization is extremely important for language learning and that adults are known to have superior explicit learning abilities, this pattern could help us understand, at least in part, why adults have more difficulty learning language as compared to children. One remaining question, however, is whether this is the consequence of adults' mature prefrontal function. It is crucial for these ideas children outperform adults because of the ongoing development of neural structures that are important for effortful processing. In Experiment 2, therefore, we use transcranial theta-burst stimulation (TBS) in adults to temporarily take the PFC offline. In this way, adults are temporarily transformed into children, at least in terms of being able to use their prefrontal cortex. Only the explicit-word level manipulation was used in this study to determine whether the effects of instruction could be reversed: decreased performance on the word segmentation test and increased performance on the generalization to novel categories test.

4.4.1 Experiment 2 Methods

Participants

Thirty-two undergraduates at graduates at the University of California, Berkeley participated for payment. Ten received TBS on the left DLPFC, ten on the right DLPFC and twelve to a control region, the vertex. All participants were right-handed native English speakers.

Stimuli and Tests

The stimuli and test items for this experiment were the same as in Experiment 1.

Procedure

The procedure was exactly the same as for the explicit-word learners in Experiment 1, except that individuals received TBS in one of three locations prior to exposure: left DLPFC, right DLPFC, or vertex. Continuous theta-burst TMS was delivered using a 70-mm diameter figure-eight coil (Rapid2 stimulator; Magstim, Whitland, UK). The coil was placed tangentially to the scalp, with the handle pointing posteriorly for DLPFC placement and directly above the scalp at 0° angle for the vertex placement. Theta-burst TMS (TBS) consisted three bursts of stimuli repeating at 50 Hz; bursts repeated at 5 Hz. Continuous TBS was applied for 40 sec at 80% of each participant's active motor threshold (AMT) (Huang, Edwards, Rounis, Bhatia, & Rothwell, 2005). The AMT was determined for each individual by measuring the motor evoked potential (MEP) in the right first dorsal interosseus and recording the minimum single pulse intensity required to produce an MEP of greater than 200 μV in this muscle on more than five out of ten trials, while the participant was maintaining a voluntary contraction of about 20% of maximum. Continuous TBS seems to have an inhibitory effect lasting up to 40 minutes post stimulation (Huang et al., 2005; c.f. Muellbacher, Ziemann, Boroojerdi, &Hallett, 2000).

Anatomical images were acquired on a Siemens MAGNETOM Trio 3T MR Scanner 291 at the Henry H. Wheeler, Jr. Brain Imaging Center at the University of California, Berkeley. Images consisted of 160 slices acquired using a T1-weighted MP-RAGE protocol (TR = 2300 ms, TE = 2.98 ms, FOV = 256 mm, matrix size = 256 x 256, voxel size 1 x 1 x 1 mm). For left and right DLPFC, we used MNI coordinates previously reported (Galea, Albert, Ditye, & Miall, 2009; Willingham et al., 2002). To relate this standard position to individual participants, each high resolution structural scan was normalized to the MNI brain using SPM2 (Friston et al., 1991). The inverse transformation for each participant was then applied to the standard coordinates to identify the subject-specific target location for each participant. BrainSight (Rogue Research, Montreal, Quebec, Canada) was used to place the TMS coil at this position. The vertex was defined as the central point on an individuals' skull, between both ears and directly in line with their nose.

4.4.2 Experiment 2 Results

Figure 6 shows performance on the word segmentation test separately for learners who received TBS to the right DLPFC, the left DLPFC, and the vertex (control). One-sample t-tests reveal that learners in all groups were significantly better than chance (right: $t(9) = 8.00$, $p<.001$;left: $t(9) = 5.25$, $p <.001$; vertex: $t(11) = 12.2$, $p <.001$) and therefore appear to have learned the words. Moreover, a one-way ANOVA reveals that performance across groups did not differ on this measure ($F(2,29) = .371$, $p =.693$), suggesting that TMS neither interfered with nor facilitated learning on this test. In further support of this, an ANOVA comparing performance on this test across all six groups (including learners from Experiment 1) reveals a main effect of group ($F(5,74) = 4.5$, $p =.001$), such that performance of individuals who received TBS to the left DLPFC was not different from that of individuals in the explicit-word learning condition ($F(1,46) = .309$, $p =.581$) but was different from individuals in both the explicit-category ($F(1,46) = 4.37$, $p =.042$) and implicit learning ($F(1,46) = 21.54$, $p <.001$) conditions. These comparisons also hold for those who received TBS to the right DLPFC and the vertex: performance does not differ from the explicit-word learners but is better than the explicit-category and implicit learners. As in Experiment 1, therefore, we observe a main effect of instruction such that those who are told to learn the nine words perform better than those who are given other instructions.

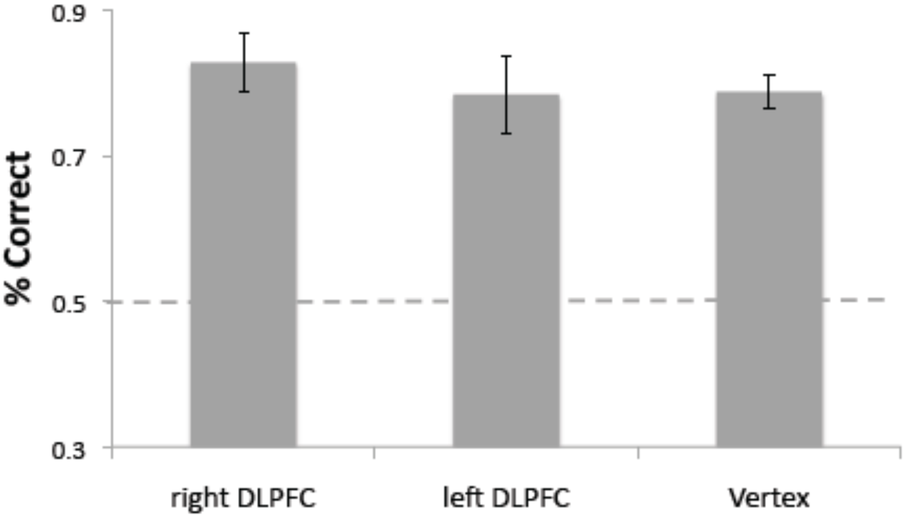

Figure 6. *Performance on the Word Segmentation Test by TBS Location*
Performance is displayed for all three groups. The dotted line indicates chance performance. Error bars reflect standard errors of the mean.

While there was no effect of TBS location as measured by the word segmentation test, we hypothesized that TBS to the DLPFC would selectively facilitate generalization ability. To assess learning on this test, we first compared performance on each of the sub-tests—order, generalization-withheld, and generalization-novel, to chance. This is shown in Figure 7. One-sample t-tests revealed that performance of individuals who received TBS to the right DLPFC was not significantly different from chance on any of the measures: order ($t(9) = 2.15$, $p = .06$), generalization-withheld ($t(9) = 1.66$, $p = .131$), or generalization-novel ($t(9) = 1.08$, $p = .307$). However, individuals who received TBS to the control region—the vertex— performed at above chance levels on the measure of order ($t(11) = 3.08$, $p = .011$), but not for either of the generalization measures: withheld ($t(11) = 1.63$, $p = .131$) or novel ($t(11) = 1.54$, $p = .153$). Interestingly, those who received TBS to the left DLPFC showed a different pattern, with no evidence of learning on either the measures of order ($t(9) = 1.2$, $p = .078$) or generalization-withheld ($t(9) = .721$, $p = .489$), but they did show above chance performance on the most stringent measure of generalization: novel ($t(9) = 4.02$, $p = .003$).

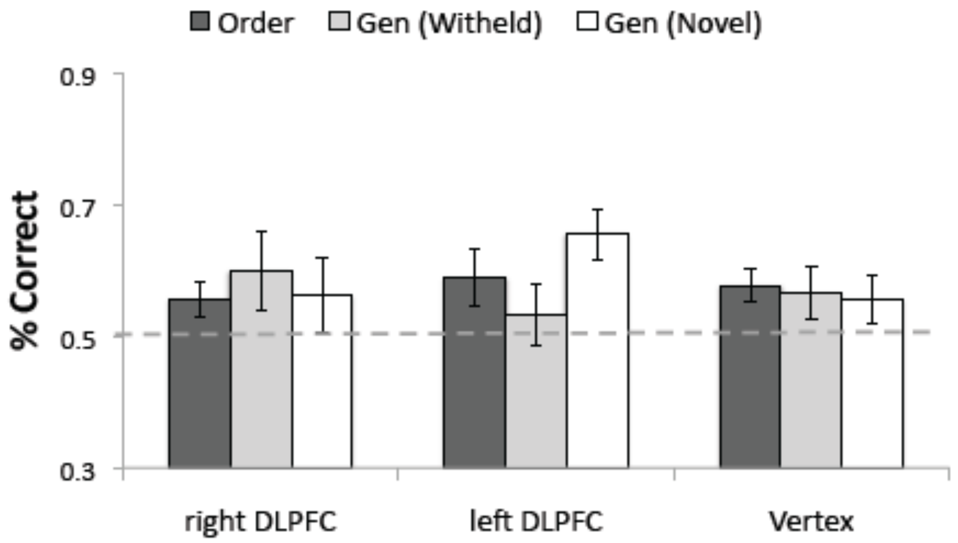

Figure 7. *Performance on Order/Generalization Tests by TBS location*
Performance is displayed for all groups for order (dark grey bars), generalization-withheld (light grey bars), and generalization-novel (white bars) tests. The dotted line indicates chance performance. Error bars reflect standard errors of the mean.

In comparing performance to chance, an interesting pattern therefore seems to emerge such that participants in the control (vertex) condition uniquely display learning on the order test and participants who received TBS to the left DLPFC uniquely display learning on the generalization-novel test.

To compare performance on these tests across groups, a repeated measures ANOVA revealed that there was no effect of test type (*F*(2,29) = .222, *p* =.802) or TBS group (*F*(2,29) = .523, *p* =.598) and no group by test type interaction (*F*(2,29) = .893, *p* =.474). However, each test type was designed to assess a different aspect of category knowledge, so despite not finding an effect of test-type across groups, we ran separate one-way ANOVA's to probe group differences on each of the sub-tests. Here again, no group differences were observed on any test: order (*F*(2,29) = .229, *p* =.797), generalization-withheld (*F*(2,29) = .444, *p* =.646), or generalization-novel (*F*(2,29) = 1.60, *p* =.220). In sum, only individuals who received TBS to the vertex showed evidence of learning the order and only individuals who received TBS to the left DLPFC showed evidence of generalizing to novel instances, as shown by the comparisons to chance. However, these differences were not observed across groups in the omnibus ANOVA.

To better understand this potentially unique ability on the part of the left DLPFC TBS group, we conduced a repeated measures ANOVA, additionally including the learning groups from Experiment 1. This again revealed that there was no effect of test type (*F*(5,74) = .248, *p* =.620) or group (*F*(5,74) = 1.97, *p* =.093) and no group by test interaction (*F*(2,29) = 1.961, *p* =.094). Comparing data from the present experiment to

Experiment 1, however, reveals interesting qualitative differences. The only group to perform significantly better than chance on the novel generalization test were the implicit learners. Here we observe that this is also uniquely true of learners in the left DLPFC TBS group. These data therefore suggest that TBS to the left DLPFC could enhance generalization ability to the level of implicit learners.

4.5 General Discussion

In this study we asked whether the sensitive period for language learning is related to protracted PFC development—a structure known to be crucial for effortful processing. To explore this possibility, we first investigated the role of effort in extracting statistical structure from speech, both for segmenting words and categories. We then linked this more directly to PFC function by taking this region temporarily offline in adults using TBS. In so doing, we asked whether there is a casual link between the use of this region and learning outcomes in adults.

Our results indicate that effort can indeed be detrimental (but also beneficial) for extracting statistical structure from speech in adults, especially for more complex structures. While all groups of learners were able to learn the words, learners who were directed to effortfully learn the nine words learned the words better than if they were told nothing at all or if they were told to learn the categories. This finding is in line with previous work in implicit learning, showing that effort can facilitate implicit learning when learners are directed to the correct structure (Reber, 1993) or when the structure to be learned is simple and within a learner's executive capacity limitations (Fletcher et al., 2005; Unsworth & Engle, 2005). Here, we extend this work by additionally showing that effort can be beneficial for the learning of first-order statistical structure to find units akin to words in the auditory domain.

A core question of this work was to probe the role of effort for learning the categorical structure present in the artificial language; such structure is an important hallmark of language, the learning of which has received substantial attention (e.g. (Bloom, 1970). Effort appears to hinder extraction of this categorical structure. In fact, both the learners who were told to learn the three categories present in the language and those who were told to learn the nine words were not better than chance on the test probing their ability to generalize to novel items. However, learners who were told nothing at all were able to generalize. This finding is again in line with previous work suggesting that effort is detrimental when learning complex structure (Fletcher et al., 2005). Here we show that this is true for the learning of categories in the auditory domain. This is an important discovery in the study of why children are better at learning language as compared to adults. It has been noted that the learning of morphosyntax is especially compromised in adult learners (Johnson & Newport, 1989; Newport, 1990; C. Weber-Fox & H. Neville, 1996). This deficit in appears to be specifically related to the advanced executive abilities of adults.

This finding is especially noteworthy, since even the learners who were directed to learn exactly these categories were not able to do so. This could be because the instructions were vague and learners were therefore attempting to find a kind of structure that was not present in the auditory stimulus. Recall that when Reber simply told learners to find structure when in a Markov chain grammar, they were worse than when they were told nothing at all; however, given a cartoon of a similar grammar, they improved (Reber, 1993). The failure to learn in the present experiment could have to do with the fact that learners were not sure what to look for. Future investigations should probe the impact of more specific instructions for this kind of learning.

Another explanation for the failure of this group to learn has to do with the complexity of the categorical structure itself. In order to perform well on the generalization-to-novel-items test, learners would have had to know that words with a particular phonological form could only appear in particular locations relative to one another. So while the rules governing the phonological structure of the categories were not complex by themselves, this overall structure was complex because of nested relationships. In order to learn this categorical information, one must know something about the words. Knowing something about these would in turn allow analogies to be made across the words, allowing a representation of the category to be formed. It could therefore be the case that directing effort toward learning the categories caused learners to fail since they first neede to learn the words. If this were the case, however, one would expect performance to be poor on the word segmentation test. However, explicit-category learners were no worse on the word segmentation test than the implicit learning group, suggesting that their failure to learn the categories was not a consequence of the failure to learn the words but rather the rules governing the distribution of similarly formed words.

Still, the relationship between learning on each of these tests is worth further discussion. Although learning the words may be an important initial step for learning something about the categories in some cases, the opposite has also been argued. Adults' superior processing capacities may enable them to learn precisely what they are exposed to rather well, but perhaps because of this effective learning, they fail to learn the internal structure and therefore fail to generalize (Pitts Cochran, McDonald, & Parault, 1999; Rohde & Plaut, 2003). To explore the relationship between effective learning of words and categories, we therefore computed a difference score by subtracting the mean performance on the category test from the mean performance on the word segmentation test for each individual. We found that this difference in performance was significantly greater in both of the explicit learning conditions compared to the implicit condition, suggesting that there might be some exchange between the learning of the words and the categories when individuals effortfully learn a language, but not when no effort is put forth. However, more careful investigations need to be undertaken to determine to what extent this exchange is causal.

In conclusion, data from Experiment 1 show that effort is detrimental for learning the categories but not the words in an artificial language. In addition, benefits in word learning might have a cost for learning the categories. In Experiment 2, we further explored the extent to which these disadvantages in learning are related to mature PFC function. Does taking this region offline reduce the cost of exerting effort? To test this, the effects of TBS administration to either the left or right DLPFC or the vertex (control region) were determined for the explicit-word condition. There was no overall effect of TBS on the word segmentation test. Learners who received TBS to each location performed significantly better than chance at levels analogous to those in the explicit-word condition from Experiment 1 and, as in that group, better than the implicit learners in Experiment 1. In Experiment 2, therefore, we again observed the benefit of directing learners to learn words for learning the words.

Of particular interest, however, was the effect of TBS on the learning of categories, since explicit-word learners failed to generalize to novel instances in the first experiment. On this measure, learners who received TBS to the right DLPFC or the vertex were not significantly better than chance. TBS to these locations therefore did not change the findings reported in Experiment 1. In contrast, learners in the TBS to the left DLPFC group were significantly better than chance on the novel-generalization test. Taking the left DLPFC offline, therefore, appears to diminish the cost of trying to learn to words for learning the categories. The left DLPFC in particular has been shown to be important for effortful processing of linguistic stimuli, suggesting that this region, more than the right DLPFC, would have an impact on learning outcomes (Fiebach, Rissman, & D'Esposito, 2006). This suggests that when it comes to learning language, having a mature left DLPFC might be detrimental, especially in situations where learners exert effort.

Taken together, these data show that effort can harm the extraction of statistical regularities from speech, but only 1) when effort is directed to learning higher order regularities (categories), or 2) when effort is directed toward learning first order regularities (words) and knowledge of the higher order regularities is probed. Moreover, taking the left DLPFC offline ameliorates the cost of this effort. These data contribute to our understanding of the sensitive period for language learning by showing that adults' learning difficulties are due, at least in part, to mature prefrontal function and effortful processing abilities.

Chapter 5. Concluding Remarks

This collection of studies was designed to test the NCNA theory, which attempts to explain, at least in part, why children consistently surpass adults in their ultimate attainment of language. This theory first suggests that an expert neural system for language processing is built in a nested way, with commitments made first to aspects of language that are learned early. Once built, this system—though expert in processing one's native language—is ineffective in processing other languages, particularly those that differ in these early-learned aspects of language (such as sound structure). The second part of this theory suggests that asynchronies in the development of neural substrates supporting learning contribute to sensitive period phenomena. One consequence of the vast differences in the maturation of various substrates important for learning is that children have an abundance of implicit learning mechanisms relative to explicit. Since much of language learning is likely to occur via these implicit mechanisms, the result is that children might simply be better built to learn language.

The first study addresses the first part of the NCNA theory. In this study, I asked if a commitment to one's native language sounds might carry a cost for adults attempting to learn a new language with a phonology that is distinct from their native language. To this end, twenty adult native English speakers learned one of two miniature artificial languages (MALs) over the course of four days, after which their brain activity was recorded while assessing the grammaticality of MAL and English sentences. Crucially, the phonological inventory of one MAL was English-like (EP), while the other was maximally distinct (NEP). The MALs shared the same grammar, which was different from English and so had to be learned. Participants successfully learned all components of the languages, regardless of condition. However, NEP learners were worse overall on measures of vocabulary and on novel tests of verb agreement and noun class. Neural recruitment also differed for the two groups. Neural recruitment for processing the EP language, but not the NEP language, overlapped substantially with English in Broca's region. This difference is noteworthy, since recruitment of this region, across learning groups, is predictive of learning scores and accuracy in grammaticality judgments. In addition, NEP learners recruited regions important for auditory and phonological processing to a greater degree than EP learners. Together, these behavioral and neural data suggest that learning of a new grammar is affected by the phonological and auditory scaffolding that support it. Because the NEP phonology is different from English, learners are less able to take advantage of their existing phonological knowledge and its corresponding neural circuitry. Therefore, having an expert neural system for language that is based, initially, on sound structure appears to be detrimental for learning a new language comprised of different sounds. Taken together, these data suggest that sensitive period phenomena could arise in part from the use of an inappropriate system that is expert in something else, the native language of the learner.

While the use of a neural circuit that is specialized for one's native language appears to contribute to age-related language-learning differences, developmental changes in neural structures that are important for learning in general are also likely to play a role. As yet, however, very little is known about the functional consequences of this maturational change for learning construed more broadly. Determining this is an important first step before direct links to language learning can be made. The second study therefore, addresses the impact of developmental changes on working memory function. Working memory (WM)—the ability to hold information in mind that is no longer present in the environment—comprises a set of cognitive processes required for many, if not all, forms of learning. A critical neural substrate for working memory (the prefrontal cortex) continues to mature through early adulthood. What are the functional consequences of this late maturation for working memory? Using a longitudinal design, we show that although individuals recruit prefrontal cortex as expected during both early and late adolescence during a working memory task, this recruitment is correlated with behavior only in late adolescence. The hippocampus is also recruited, but only during early, not late, adolescence. Moreover, the hippocampus and prefrontal cortex are coactive in early adolescence, irrespective of task demands or performance, in contrast to the pattern seen in late adolescents and adults, in which these regions are coactive only under high task demands. Together, these data demonstrate that the neural circuitry underlying working memory changes during adolescent development. The diminishing contribution of the hippocampus in working memory function with age is an important observation that informs questions about how children and adults learn differently. For language learning in particular, it could be the case that even when children direct effort towards learning, they recruit a distinct subset of neural substrates as compared to adults. These data suggest, at the very least, that the circuitry recruited for effortful processing is very different earlier in life.

This leads one to ask what the impact of effortful processing is for adults learning language. Do such differences in effortful processing make a difference for language learning? The third study addresses this question directly, asking whether children's language-learning advantage could be the result of their ongoing neural development, the slow development of the PFC (as outlined in study 2) in particular. I first explore the relationship between effortful processing and the ability to extract structure from an artificial language in adults and second, use transcranial theta-burst stimulation (TBS) to determine whether this effort-learning relationship is directly related to mature neural function. Participants in this study were exposed to an artificial language comprised of statistically defined words belonging to phonologically defined categories. When instructed to passively listen to the language, subjects learned both the words and the categories. However, when learners were told to explicitly try to learn the words or the categories, they failed to learn the categories. Administering TBS to the left PFC prior to exposure, however, ameliorated the cost of this effort. These data contribute to our understanding of the sensitive period for language learning by showing that adults' learning difficulties are due, at least in part, to mature prefrontal function and effortful processing abilities.

To conclude, this dissertation provides initial support for both aspects of the NCNA theory: a neural commitment to one's native language appears to carry a cost for adults attempting to learn a new language, and advanced explicit abilities (which are the result of mature neural function) appear to hurt adult language learners. Of course, many aspects of this theory remain untested. On the commitment side, it should be shown that these learning difficulties and differences in neural representation are either not present or less profound in children, who are more plastic. Differences in neural representation and learning difficulties should increase monotonically with younger children showing fewer learning and neural differences across the two language types as compared to older children. We should also observe individual differences within children, with larger differences for those who have a greater command of their native language; as in all areas of plasticity, there should be both a benefit and a cost: greater plasticity should mean a greater ability to learn new languages but also less advanced command of one's native language. There is some evidence for this: children who are more committed to the sounds of their language (as measured by categorical perception) are also better, in terms of number of words known, later in life (Kuhl et al., 2005). Also on the commitment side of NCNA, it remains to be shown that certain aspects of language matter more than others. In the first study, I showed that an earlier learned aspect of language—sound structure—matters a lot. However, the aspects that matter the most (and in what order) are still unknown. The theory predicts that earlier learned aspects should matter more than later learned aspects. Future investigations should comprehensively change one aspect at a time. Informed by all of this work, different training studies should also be conducted in adults to see if staged exposure matters; adults should learn better if they are trained slowly on early-learned aspects before confronting complex language structures. This should, in turn, be associated with more native-like neural processing for each of the subcomponents that are learned. In sum, while the first study of this dissertation suggests that a commitment to one's native language plays a role in age-related learning differences, much work remains.

Further work is also required on the asynchronies side of the NCNA theory, the most immediate of which would be to characterize the role of effort for statistical learning in children. Since we show that effort can be detrimental for adult learners, it is important to also understand the impact of instructing children to do the same. Based on the NCNA, we would predict that effort would not produce the same result in children, especially very young children who have limited executive abilities. More broadly, implicit learning mechanisms need to be better characterized in children. Especially missing from the literature is a characterization of how explicit and implicit systems interact during childhood. There is a growing literature showing how they interact in adults, showing that effort can be harmful when the information to be learned is complex or adults are made to “look” for the wrong structure. Is this also true for children? On the one hand, since more phenomena would be considered complex for children, it could be the case that the explicit system interferes more in children. On the other hand, it could be the case that since more phenomena are considered complex, the explicit system stops “trying” much more quickly and therefore does not interfere with implicit processes. These possibilities need to be explored in much more detail, both with regard to basic learning and language more specifically. Careful links also need to be made to the anatomical development of other substrates that are known to be important for learning. I have highlighted the importance of the PFC in studies 2 and 3 of this dissertation, but these predictions extend to many other neural regions and networks, each of which could mediate this implicit-explicit relationship in different ways.

Finally, these different aspects of the theory are presented together in order to provide a full explanation for why we observe sensitive periods for language learning in humans. Although this dissertation does not directly test the relationship between these nested aspects and asynchronies in development, they are likely to interact in important ways. Ultimately, answers to questions such as these are crucial for arriving at a complete understanding of sensitive period effects for language learning.

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