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Neural representations for newly learned words are modulated by overnight consolidation, reading skill, and age

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ABSTRACT

Word learning depends not only on efficient online binding of phonological, orthographic and lexical information, but also on consolidation of new word representations into permanent lexical memory. Work on word learning under a variety of contexts indicates that reading and language skill impact facility of word learning in both print and speech. In addition, recent research finds that individuals with language impairments show deficits in both initial word form learning and in maintaining newly learned representations over time, implicating mechanisms associated with maintenance that may be driven by deficits in overnight consolidation. Although several recent studies have explored the neural bases of overnight consolidation of newly learned words, no extant work has examined individual differences in overnight consolidation at the neural level. The current study addresses this gap in the literature by investigating how individual differences in reading and language skills modulate patterns of neural activation associated with newly learned words following a period of overnight consolidation. Specifically, a community sample of adolescents and young adults with significant variability in reading and oral language (vocabulary) ability were trained on two spoken artificial lexicons, one in the evening on the day before fMRI scanning and one in the morning just prior to scanning. Comparisons of activation between words that were trained and consolidated vs. those that were trained but not consolidated revealed increased cortical activation in a number of language associated and memory associated regions. In addition, individual differences in age, reading skill and vocabulary modulated learning rate in our artificial lexicon learning task and the size of the cortical consolidation effect in the precuneus/posterior cingulate, such that older readers and more skilled readers had larger cortical consolidation effects in this learning-critical region. These findings suggest that age (even into late adolescence) and reading and language skills are important individual differences that affect overnight consolidation of newly learned words. These findings have significant implications for understanding reading and language disorders and should inform pedagogical models.

1. Introduction

Word learning depends not only on efficient online binding among phonological, semantic, and orthographic features, but also on consolidation of new word representations into permanent lexical memory (Ashworth et al., 2014). Indeed, across a number of studies researchers have shown that word learning consists of an initial episodic encoding for an isolated encounter, followed by a longer-term, sleep–mediated, consolidation process by which a word becomes lexicalized (Brown et al., 2012; Davis et al., 2009; Davis and Gaskell, 2009a, 2009b; Henderson et al., 2014). Additionally, studies of word learning under a variety of contexts indicate that an individual's oral and printed language skill (e.g., vocabulary knowledge, sight word reading efficiency) can impact the facility of novel word learning in both the printed and spoken domains (cf., Bishop and Hsu, 2015; Litt and Nation, 2014; Warmington and Hulme, 2012). Critically, recent work suggests that these factors (offline sleep-mediated consolidation) and language skill may not be independent. For example, we have found that adults with language impairment have diminished ability to consolidate newly learned speech sounds, even under conditions where initial encoding

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was unimpaired, implicating specific impairments in offline consolidation of newly learned linguistic information (Earle et al., 2015, 2018). With respect to word learning specifically, recent research finds that individuals with specific language impairment (SLI) show impairments in both initial word form learning and in maintaining newly learned representations over time, implicating mechanisms associated with maintenance that may be driven by deficits in sleep-associated consolidation (McGregor et al., 2013; see also James et al., 2017 for theoretical discussion of how sleep and oral language skill may interact).

Neuroimaging studies have the potential to inform these relations given that both the neural systems for word learning (in both typically developing and language impaired populations) and the neural systems associated with overnight consolidation have been well studied independently. The current study seeks to connect these lines of research by specifically investigating how individual differences in language skill modulate patterns of neural activation associated with newly learned words following a period of offline, sleep-mediated consolidation.

1.1. Individual differences in the neurobiological mechanisms for word learning

Neuroimaging studies have been able to provide information about the neural networks that support printed and spoken word learning under varied learning conditions, as well as the plasticity in cortical and subcortical structures that makes this learning possible. For example, Breitenstein and colleagues (2005) examined the implicit acquisition of novel word meanings using fMRI. In their task, adult participants "learned" auditory pseudoword-picture pairings, which co-occurred over ten presentations in the scanner. This was contrasted with a no-learning condition, in which a given picture-pseudoword pair was presented only once. Behavioral performance in the learning condition improved across repetitions, and the imaging data revealed a significant linear decrease in activation across repetitions in the left hippocampus, a critical region for memory formation (cf., Preston and Wagner, 2007) and the left fusiform gyrus, a key region for printed and spoken word representations (e.g., Dehaene et al., 2010; Ludersdorfer et al., 2016; Yoncheva et al., 2010). Further analyses revealed links between activation in the left hippocampus and cortical regions over the course of learning such that individual differences in the magnitude of the decrease in activation levels in the left hippocampus across repetitions were significantly correlated with decreases in activation in left fusiform gyrus and with increases in activation in left inferior parietal lobule (IPL). Moreover, the magnitude of signal decrease across blocks in the left hippocampus was negatively correlated with vocabulary knowledge. This association between vocabulary skill and continued engagement of the hippocampus over the course of implicit learning suggests a relationship between the quality of existing vocabulary knowledge and domain-general mechanisms for learning, providing additional motivation for the exploration of the relationship between language skill and memory consolidation.

A related neuroimaging study of *printed* word learning by Pugh and colleagues (2008) examined in–scanner repetition learning of visual word forms in relation to reading skill. During scanning, good readers and reading disabled (RD) participants were presented with printed real words that were displayed once or repeated six times across a run. Both groups became both faster and more accurate at identifying the words across repetitions; however, whereas good readers showed expected patterns of repetition suppression in a number of language and reading relevant left hemisphere regions (consistent with what Breitenstein et al., 2005 found for spoken words), struggling readers instead showed increased activity in these same regions, including the left fusiform/occipito-temporal gyrus and left superior temporal gyrus, suggesting repetition-associated engagement. Although this study did not examine activation or behavioral measures of reading on subsequent days after the scanning session, other behavioral research suggests that these short-term online repetition gains observed during reading instruction may not translate into longer-term stability for individuals with language or reading disorders (cf. McGregor et al., 2013), possibly due to a failure of the mechanisms involved in overnight, sleep associated consolidation. Findings from this study motivate further exploration of how individual differences in reading impact the neural circuitry that supports word learning over a longer duration of time that includes a period of offline sleep.

A third relevant imaging study of *printed* word learning by Sandak et al. (2004) explored three types of repetition learning of novel printed words prior to fMRI scanning. During exposure, some words were learned via orthographic training (participants made judgments about consonant-vowel patterns), others were learned via phonological training (participants made judgments about pronunciations), and still others were learned via semantic training (through novel picture-pseudoword pairings). Behaviorally, participants showed evidence of better learning (faster naming) for words learned under semantic and phonological training conditions relative to orthographic training. At the neural level, patterns of activation for trained pseudowords were more like those elicited by real words than those elicited by completely novel items across a number of language critical left hemisphere regions (e.g., middle and superior temporal gyrus [MTG, STG], inferior frontal gyrus [IFG], and the supramarginal gyrus [SMG]), suggesting that trained items had become at least partially lexicalized. With respect to training type, phonological training was associated with relatively reduced activation in a number of left hemisphere regions that are important for phonological processing (e.g., SMG and inferior frontal gyrus [IFG]), suggesting greater efficiency of phonological processing for these items. In contrast, semantic training resulted in a pattern of relatively enhanced activation in bilateral MTG and STG. These findings suggest that although different training foci (here, semantic or phonological) can result in similar patterns of word learning at the behavioral level, the neural circuits that support these training mechanisms are, in fact, quite distinct.

These studies raise questions and motivate the current exploration of the neural bases of learning and consolidation of novel form-meaning pairs as a function of reading skill. The current study combines the auditory paired associated learning approach taken by Breitenstein et al. (2005), the out-of-scanner training used by Sandak et al. (2004), and the focus on individual differences in Pugh et al. (2008; reading) and Breitenstein et al. (2005; vocabulary) with the addition of an overnight design to explore the effects of overnight consolidation on the neural systems for representing newly learned spoken form-meaning pairs.

1.2. The role of sleep-associated consolidation in word learning

The idea that a period of sleep or rest facilitates retention of newly learned information is not a new one. In the early 20th century, Müller and Pilzecker (1900) noted that the recall of a list of nonsense syllables was more accurate when tested after a period of time rather than immediately after list learning. Based on research beginning in the late 1980s, a two-stage complementary learning systems (CLS) model was proposed for acquisition and neural instantiation of new semantic memories, including words (see Davis and Gaskell, 2009a, 2009b; McClelland et al., 1995; Norman and O'Reilly, 2003). The CLS model postulates separate systems for encoding during the awake state supported by the hippocampus, and for longer-term storage supported by the cortex. Patient data in which one system remains intact after damage to the other provides some support for the independence of these two systems (Squire, 1992), and connectionist models have provided a hippocampal learning and cortical consolidation framework to support these findings (McClelland et al., 1995). The role of sleep specifically was initially explored in animal models, with studies finding that firing in hippocampal place cells in particular areas of awake rats was