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Sleep-based memory processing facilitates grammatical generalization: Evidence from targeted memory reactivation

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ABSTRACT

Generalization—the ability to abstract regularities from specific examples and apply them to novel instances—is an essential component of language acquisition. Generalization not only depends on exposure to input during wake, but may also improve offline during sleep. Here we examined whether targeted memory reactivation during sleep can influence grammatical generalization. Participants gradually acquired the grammatical rules of an artificial language through an interactive learning procedure. Then, phrases from the language (experimental group) or stimuli from an unrelated task (control group) were covertly presented during an afternoon nap. Compared to control participants, participants re-exposed to the language during sleep showed larger gains in grammatical generalization. Sleep cues produced a bias, not necessarily a pure gain, suggesting that the capacity for memory replay during sleep is limited. We conclude that grammatical generalization was biased by auditory cueing during sleep, and by extension, that sleep likely influences grammatical generalization in general.

1. Introduction

The ability to *generalize* is a key aspect of many basic types of learning, such as motor learning and perceptual learning (e.g., Fenn, Nusbaum, & Margoliash, 2003; Shadmehr & Moussavi, 2000). Generalization involves abstracting regularities from specific examples and applying these regularities to new instances or situations. In contrast to rote learning or to episodic encoding, generalization allows learners to respond adaptively to stimuli that fall outside the original conditions of training. Generalization therefore represents a powerful learning mechanism whereby the learner can transfer acquired knowledge to never-before-experienced stimuli and situations.

Generalization also plays a central role in language acquisition. A hallmark feature of language is that it allows a virtually infinite set of meaningful and grammatically correct utterances to be produced (Hauser, Chomsky, & Fitch, 2002; Pinker & Jackendoff, 2005). Because language is open-ended, language users must be able to generalize common linguistic principles to new combinations of words, rather than relying upon memory of meanings of individual phrases and sentences that they have already heard. This ability to generalize depends upon rules or regularities that are found in virtually every linguistic subsystem, including phonology, morphology, semantics, and syntax. During language acquisition, these overarching linguistic rules or patterns are abstracted over multiple learning episodes, and then applied in order to comprehend and produce novel phrases and sentences. For example, learners of English exposed to a sufficient number of plural nouns will eventually learn that the morpheme –*s* is typically used to denote plurality, and can then apply this rule to novel words. The "Wug Test" is a well-known demonstration of this phenomenon (Berko, 1958). Research using this test has shown that young children are able to correctly produce the plural form of a made-up pseudoword (*wug*), providing evidence that they have extracted generalizable rules from linguistic input, rather than simply memorizing words that they have heard (Menn & Ratner, 2000).

Processes contributing to the generalization of rules from input operate not only during online learning, but during sleep as well. Sleep has been shown to facilitate generalization processes involved in a number of different aspects of language, including speech perception (Fenn et al., 2003), grammar learning (Batterink, Oudiette, Reber, & Paller, 2014; Gómez, Bootzin, & Nadel, 2006; Nieuwenhuis, Folia, Forkstam, Jensen, & Petersson, 2013), and speech production (Gaskell et al., 2014). These experimental results have often implicated generalization above and beyond any improvement in rote or exemplar-based learning. In an artificial grammar learning task, sleep leads to improvement in classification driven specifically by an enhancement of rule

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abstraction, and not by the strengthening of memory for "chunks," the bigrams and trigrams that make up parts of the presented sequences (Nieuwenhuis et al., 2013). Similarly, infants who were exposed to an artificial language consisting of nonadjacent dependencies and then napped showed greater rule abstraction, whereas infants who remained awake showed improved veridical memory for specific nonadjacent word pairs (Gómez et al., 2006). Sleep also leads to generalization of phonetic constraints in speech production, an effect that is specifically associated with slow-wave sleep (Gaskell et al., 2014). These findings dovetail with numerous results from nonlinguistic tasks demonstrating the importance of sleep for the extraction of overarching rules or patterns (e.g., Djonlagic et al., 2009; Durrant, Cairney, & Lewis, 2013; Durrant, Taylor, Cairney, & Lewis, 2011; Ellenbogen, Hu, Payne, Titone, & Walker, 2007; Wagner, Gais, Haider, Verleger, & Born, 2004). Generalization may be promoted by sleep through simultaneous reactivation of individual memories that share common elements, leading to strengthening of the shared connections (Lewis & Durrant, 2011).

In the present study, we tested whether effects of sleep on rule generalization could be manipulated or enhanced by experimentally inducing reactivations of linguistic patterns during sleep. A series of recent studies has shown that presenting memory cues associated with a prior learning episode during non rapid-eye-movement (NREM) sleep benefits consolidation of both declarative and procedural memories (e.g., Antony, Gobel, OðHare, Reber, & Paller, 2012; Bendor & Wilson, 2012; Diekelmann, Büchel, Born, & Rasch, 2011; Fuentemilla et al., 2013; Rasch, Buchel, Gais, & Born, 2007; Rihm, Diekelmann, Born, & Rasch, 2014; Rudoy, Voss, Westerbrg, & Paller, 2009; Schreiner & Rasch, 2014). For example, re-exposure of an odor during slow-wave sleep that had been previously presented as context during an object-location learning task improved later memory for object locations (Rasch et al., 2007). Individual memories for object-location associations can also be selectively strengthened, when auditory cues associated with individual objects are presented again during sleep (Creery, Oudiette, Antony, & Paller, 2015; Rudoy et al., 2009). Procedural memories also benefit from cueing; presenting a previously learned melody during sleep results in improved performance on a melody production task for the cued relative to the non-cued melody (Antony et al., 2012; Cousins, El-Deredy, Parkes, Hennies, & Lewis, 2014; Schonauer, Geisler, & Gais, 2013). Collectively, these cueing procedures are referred to as *targeted memory reactivation* (TMR; Oudiette & Paller, 2013). Although TMR has been shown to have clear benefits in terms of strengthening associative memories, whether it also results in qualitative changes to memory with improvements in rule abstraction and generalization is unknown.

The goal of the present study was to examine whether TMR influences rule abstraction and generalization in a language-learning context. Participants gradually acquired the grammatical rules of an artificial language through an interactive, trial-and-error-based learning procedure. They also completed a second learning task involving passive exposure to a tone sequence following a probabilistic pattern, which has been previously shown to be sensitive to sleep (Durrant et al., 2011, 2013). By including two learning tasks we hoped to control for nonspecific effects of cueing on consolidation. Each participant was randomly assigned to one of two cueing conditions, involving either the presentation of auditory recordings of the artificial language (grammar-cued condition) or segments of the tone sequence (tone-cued condition). After initial learning, participants took a 90-min nap, during which auditory cues from the selected task were covertly presented during slow-wave sleep. Upon awakening, participants were tested on both learning tasks.

Our central hypothesis was that participants in the grammar-cued condition would show enhanced acquisition of the grammatical rules relative to participants in the tone-cued condition. In addition, we also examined potential mechanisms whereby TMR may influence grammar learning. As laid out by theoretical frameworks of artificial grammar learning (AGL), classification performance on the AGL task can be driven by abstract, rule-based knowledge and by knowledge of chunks (e.g., Knowlton & Squire, 1994, 1996; Lieberman, Chang, Chiao, Bookheimer, & Knowlton, 2004; Meulemans & Van der Linden, 1997). Adopting this reasoning, we examined whether "chunk strength"—the degree of superficial similarity between training items and test items (Knowlton & Squire, 1996)—interacts with cueing improvements. Given previous evidence that sleep specifically benefits the abstraction of grammar rules without enhancing the effect of chunk knowledge (Nieuwenhuis et al., 2013), we hypothesized that TMR would primarily enhance rule knowledge. Finally, we tested whether oscillatory and spindle activity during sleep predicts cueing-related gains in grammar acquisition by examining correlations between sleep physiology and behavioral improvements on the grammar task.

2. Methods

2.1. Participants

We recruited 44 participants from the university community (30 female; mean age = 22.4 years) for this study. Participants were randomly assigned to one of two sleep-cueing conditions (grammar-cued condition versus tone-cued condition). Of the 44 participants, 35 were successfully cued, 17 in the tone condition and 18 in the grammar condition. The 9 remaining participants were not successfully cued, either because insufficient slow-wave sleep (SWS) prevented cueing from being attempted ($n = 3$), or because cueing attempts resulted in arousals ($n = 6$).

2.2. Artificial language task

2.2.1. Stimuli

The artificial language was composed of 20 monosyllabic nonsense words (e.g., *pilk*). Sixteen of these words were taken from previous artificial language studies (Saffran, 2001, 2002). Each of the nonsense words was assigned to one of six categories (denoted here by A–F), with each category containing 2, 3, or 4 different words (Table 1). An artificial grammar was created using five rules:

Rule 1: A → B → C
Rule 2: A → D → B → C
Rule 3: A → B → C → E
Rule 4: A → D → B → C → E
Rule 5: A → B → F → C

This artificial grammar was designed to be characteristic of natural languages and contained both optional elements and predictive dependencies between word categories. For example, D is an

Table 1
Word categories from the artificial language.

Category				
A	biff	hep	mib	rud
B	cav	lum	neb	sig
C	dupp	jux	loke	vot
D	klor	pell		
E	pilk	tiz	gak	
F	tood	kice	zic	