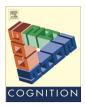
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Brief article

Sleep restores loss of generalized but not rote learning of synthetic speech



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ABSTRACT

Sleep-dependent consolidation has been demonstrated for declarative and procedural memory but few theories of consolidation distinguish between rote and generalized learning, suggesting similar consolidation should occur for both. However, studies using rote and generalized learning have suggested different patterns of consolidation may occur, although different tasks have been used across studies. Here we directly compared consolidation of rote and generalized learning using a single speech identification task. Training on a large set of novel stimuli resulted in substantial generalized learning, and sleep restored performance that had degraded after 12 waking hours. Training on a small set of repeated stimuli primarily resulted in rote learning and performance also degraded after 12 waking hours but was not restored by sleep. Moreover performance was significantly worse 24-h after rote training. Our results suggest a functional dissociation between the mechanisms of consolidation for rote and generalized learning which has broad implications for memory models.

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1. Introduction

The acquisition of complex skills depends on the ability to generalize beyond exact situations experienced during learning. It has been argued that the ability to generalize is the defining feature of adaptive learning, and the quality that distinguishes it from simple associative memory (Poggio & Bizzi, 2004). Many models of memory suggest that generalized learning relies on the same underlying associative mechanisms as learning of specific experiences; generalization depends on abstraction from associations acquired during training (e.g., Goldinger, 1998; Hintzman, 1986; McClelland & Rumelhart, 1985). In contrast, other theories suggest that memory involves both specific representations and abstract representations (cf. Anderson et al., 2004; Grossberg, 1986; Posner & Keele, 1968). Evidence

suggesting that there may be different mechanisms underlying rote and generalized learning would present a challenge for models that posit only specific representations and would provide support for models that allow for both specific and abstract representations. Here we report that the two forms of learning show different patterns of sleep-dependent consolidation.

Memory consolidation research suggests that sleep consolidates procedural and perceptual skills (see Margoliash & Fenn, 2008; McGaugh, 2000; Walker, 2005, for reviews) but the vast majority of this research has emphasized tasks wherein learning is restricted to the exact information encountered during training. Tasks used to study procedural consolidation typically focus on learning one motor pattern (cf. Fischer, Hallschmid, Elsner, & Born, 2002) or discrimination of one visual pattern (cf. Karni, Tanne, Rubenstein, Askenasy, & Sagi, 1994) which may be considered rote procedural learning. In rote motor learning, sleep is reported to enhance learning; performance is

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significantly better after sleep than after training, an effect not seen after an equal interval of wakefulness (cf. Fischer et al., 2002; Walker, Brakefield, Hobson, & Stickgold, 2003). Although several studies have reported this effect, recent work has argued that apparent memory enhancements may be explained by reactive inhibition (Rickard, Cai, Rieth, Jones, & Ard, 2008) or circadian differences at test (Cai & Rickard, 2009).

Although some of the work in rote procedural learning has been questioned, there is strong evidence that sleep consolidates generalized learning and promotes abstraction of information. In generalized procedural learning, performance degrades across waking retention and is restored by sleep. Sleep also inoculates memory against subsequent degradation (Brawn, Fenn, Margoliash, & Nusbaum, 2008; Fenn, Nusbaum, & Margoliash, 2003). Consistent with this, we have reported that after controlling for reactive inhibition, rote motor learning follows the same general pattern of waking degradation and restoration after sleep (Brawn, Fenn, Nusbaum, & Margoliash, 2010). Other studies that have investigated generalized learning and sleep have shown that sleep can restructure information acquired during waking. Of note, Wagner, Gais, Haider, Verleger, and Born (2004) trained participants on a complex algorithm that contained a hidden rule that allowed the problem to be solved in fewer steps. Participants were more likely to become aware of the hidden rule if tested after sleep than after a waking interval. Similarly, infants who were exposed to an artificial language showed evidence of generalization and abstraction of the rules of the language after a nap. In contrast, after a waking interval, infants showed stronger veridical memory, but did not show any evidence of abstraction or generalization (Gomez, Bootzin, & Nadel, 2006). Thus, there is strong evidence that sleep consolidates generalized learning and promotes abstraction or restructuring of information.

Given that sleep consolidates both rote and generalized learning, the potential difference in consolidation of these types of learning can be used to investigate whether different mechanisms underlie these two forms of learning. Consolidation in rote skills may be confined to lower-level cortices (cf. Karni & Bertini, 1997) whereas generalized learning may depend on the interaction of broader networks of neural activity (Ahissar & Hochstein, 2004; Poggio & Bizzi, 2004). Generalized skills may receive a different benefit from consolidation processes and may be more susceptible to waking interference.

The effects of sleep on rote and generalized learning have only been compared across substantially different tasks, complicating interpretation of differences. We compared rote and generalized learning in a synthetic speech learning task and tested the effect of waking retention and sleep on performance.

2. Method

2.1. Participants

We recruited 67 right-handed native English speakers who had no history of speech, hearing, or memory disor-

ders. Nine participants were excluded from all analyses for not being native English speakers (n=4), or for consuming alcohol on the study evening (n=1), or for not completing the experiment (n=4). The remaining 58 participants (32 female) had a mean age of 20.6 ± 3.6 (s.d.) years. All were students or employees at the University of Chicago and were financially compensated.

2.2. Materials

Seven hundred monosyllabic words were generated by rsynth, a text-to-speech synthesizer based on Klatt (1980). The intelligibility of this synthetic speech is relatively low, but listeners show significant improvement after one training session (Fenn et al., 2003). The words were taken from phonetically balanced lists, approximating the distribution of phonemes in English (Egan, 1948). Words were chosen based on the distribution of phonetic properties in English and were derived from a diverse set of syntactic categories (nouns, verbs, adjectives, and adverbs). The words were divided into four (100-word) test sets and one (300-word) training set. The test sets were balanced to establish comparable difficulty, based on pilot testing. Participants received each of the four tests in one of the following positions: Pretest, Posttest I, Posttest II, and Posttest III. Test order was counterbalanced across participants. In addition, twenty of the training words were added to each test so each test included 100 novel words and 20 words that repeated throughout the experiment (i.e. during training and every test).

2.3. Design

All participants completed three experimental sessions. The first session contained a pretest, training, and posttest. The second and third sessions contained only a posttest. Each session was separated by a 12-h retention interval. The first session was conducted at 09:00; the second session was at 21:00 (after waking retention), and the third session was at 09:00, after a retention interval that included sleep (see Supplementary Fig. 1). We did not test for circadian differences because our previous research demonstrated that time of day effects are negligible (Fenn et al., 2003). Participants were randomly assigned to one of two training procedures that have been found to produce rote or generalized learning respectively (Greenspan, Nusbaum, & Pisoni, 1988). One group (rote-trained) was trained on 20 words. Words were presented in pseudorandom order 15 times throughout training. The other group (generalization-trained) was trained on 300 unique stimuli. Twenty of the training stimuli for this group were used as the full training set for the rote-trained group and were used in each of the tests. The remaining 280 were novel words that did not appear in any of the tests.

An additional control group (n = 12) was trained exactly as the rote-trained group but was tested only on the 20 repeated stimuli during each posttest, to reduce interference during the tests and to ensure that performance in the rote-trained experimental group was not affected by the inclusion of novel items during testing. Because the rote-trained group experienced only 20 stimuli during training

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