tion (Gaskell & Marslen-Wilson 1997; Luce & Pisoni 1998; McClelland & Elman 1986; Norris 1994). Hence, an acid test of whether a spoken form has been lexicalized is whether or not it engages in lexical competition, and thereby affects the activity within the mental lexicon. In one of our experiments (Gaskell & Dumay 2003, Experiment 3), adults learned nonsense-speech sequences that overlapped strongly with existing words (such as "cathedruke" for "cathedral"). The influence of the newly learned words on lexical activity, our indirect measure of learning, was then assessed using the pause detection paradigm. Here, participants made speeded decisions as to whether a short silence was present towards the offset of the existing words (e.g., "cathedr_al"). Mattys and Clark (2002) demonstrated that pause detection latencies are positively correlated with the number of words activated in lexical memory on hearing the speech portion preceding the pause. As indicated by a direct two-alternative force choice recognition test (e.g., "cathedruke" vs. "cathedruce"), the 36 exposures to each novel word during learning resulted in a good immediate explicit knowledge, with no significant change when retested one week later (96% of correct responses on both occasions). More crucially, whereas no change in lexical activity was observed in pause detection immediately after learning a new competitor, a clear effect of the novel competitor had emerged during the time interval between exposure and retest, seven days later. This is strong evidence that, in contrast to phonological (episodic) storage, lexicalization (and thus integration) of spoken words requires a substantial amount of time.

In a follow-up experiment (Dumay et al. 2004, Experiment 2), we examined more closely the timecourse of lexicalization, tracking the effect of exposure on lexical activity at three time points: immediately after exposure, 24 hours later, and a week later. Again, there was no evidence of immediate lexicalization, but 24 hours after exposure as well as a week later, pause detection performance on the existing words demonstrated that the new competitor was now contributing significantly to lexical activity. Concurrently, the performance in explicit recognition and free recall improved across sessions (from 82% to 87% and from 8% to 20%, respectively).

From these results, we can therefore narrow down the critical time period for the lexicalization of a spoken word form to somewhere between one and 24 hours after exposure. Whether the integration of new representations into long-term lexical memory is primarily dependent on sleep (or some sleep-specific brain state or states) is still to be determined. However, our findings are clear evidence that both consolidation-based enhancement and integration of new declarative memory representations can be obtained after a posttraining interval that includes sleep. Rather than being a distinct stage in the process of memory formation, enhancement might be the sign that integration has taken place. In fact, it would seem quite uneconomical to engage into some sleep-dependent additional learning if it were not to integrate the corresponding representations in a long-term associative network or repertoire. Walker (sect. 2.2) speculates that the effect of sleep on declarative memory could be more protracted and one of subtle maintenance in order to prevent decay over time. Our data indicate that this may not be the case. They suggest instead that following sleep, newly acquired declarative memory representations are not only enhanced, that is, more easily accessed or specified, but also able to affect a highly automatized perceptual skill, and therefore, its underlying procedural memory system.

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What is consolidated during sleep-dependent motor skill learning?

Luca A. Finelli[a] and Terrence J. Sejnowski[a,b]

[a]*Howard Hughes Medical Laboratory, The Salk Institute for Biological Studies, La Jolla, CA 92037;* [b]*Division of Biological Sciences, University of California, San Diego, La Jolla, CA 92093.* **lfinelli@salk.edu terry@salk.edu http://www.cnl.salk.edu**

Abstract: Learning procedural skills involves improvement in speed and accuracy. Walker proposes two stages of memory consolidation: enhancement, which requires sleep, and stabilization, which does not require sleep. Speed improvement for a motor learning task but not accuracy occurs after sleep-dependent enhancement. We discuss this finding in the context of computational models and underlying sleep mechanisms.

Procedural learning, particularly the investigation of motor skill learning, has attracted renewed attention in memory research over the past few years. Procedural learning refers to a particular set of learning abilities that do not afford conscious memory access but may be expressed through performance. It is therefore an ideal starting point to address objectively the problem of sleep and memory. The model presented in the target article by Walker is based on experimental evidence that primarily comes from motor skill learning experiments. In this context, an important distinction to consider is the dissection of the acquisition process. Similar observations can be extended to perceptual and visuomotor experiments.

Influential computational studies of motor control (Kawato et al. 1987; Shadmehr & Mussa-Ivaldi 1994; Wolpert et al. 1995) have suggested that learning a motor skill requires the formation of an internal model of the dynamic behavior of the motor system in the task. For arm reaching movements in interaction with a mechanical device, the internal model may persist for at least 5 months without further practice, even after a single training session (Shadmehr & Brashers-Krug 1997). A computational framework could help to characterize memory-stage concepts like acquisition and consolidation in the context of neural representations.

The motor skill experiments in the target article employed a sequential motor task involving five stereotyped finger movements in the absence of dynamic constraints. It is reasonable to assume that, in adults, the internal models for each of the five movements need not be learned. It is, in fact, easy to fast finger-tap on a surface. However, this task would be profoundly different to a baby, who takes weeks to learn the internal models for skilled finger movements.

So what is "acquisition" in finger tapping? The largest improvement was obtained within the first three learning trials (3 minutes; Walker et al. 2002), suggesting that the process of acquiring a control strategy for existing internal models is fast. Karni and colleagues referred to this as "acquisition of a task-relevant routine" (fast learning; Karni et al. 1995), which additionally does not generalize even after long-term training. Fischer et al. (2002) also found that the enhancing effect of sleep on motor performance is highly specific to the practiced sequence.

This dissection is important because it helps to define constraints for the search of underlying mechanisms. It also guides thinking about the reorganization of internal motor representations during acquisition and enhancement. The enhancement component of consolidation can thus be interpreted as automatization/optimization of the new control strategy: optimization in terms of speed and/or accuracy of execution, as instructed. Note the absence of additional requirements, for example, rhythm, as would be the case for learning to play musical instruments.

Sleep may have enhancing effects on performance. However, it is not clear what aspects of performance, and consequently of internal motor representation, are enhanced exclusively by sleep. In an experiment designed to determine the effects of several interventions interfering with synaptic plasticity on the ability to learn a new motor memory, performance on day 2 after a night of sleep

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did not improve compared to the last training set in day 1; in addition, total sleep deprivation between day 1 and day 2 did not alter performance compared to sleeping controls (Donchin et al. 2002). This experiment studied arm reaching in interaction with external forces, which is known to require time-dependent consolidation (Shadmehr & Brashers-Krug 1997). Interestingly, performance was quantified with a learning index that measures quality, rather than speed, on task.

Similar observations can be made for finger skills. When motor skill accuracy (error rate) was measured as absolute number of wrong sequences per 30-second trial (Walker et al. 2002), it did not change significantly between 10:00 a.m., 2:00 p.m., 6:00 p.m., and 10:00 p.m.; nor did accuracy change between 10:00 a.m., 10:00 p.m., and post-sleep 10:00 a.m.; nor did it change between 10:00 p.m., post-sleep 10:00 a.m., and post-sleep 10:00 p.m. In contrast, when error rate was redefined as number of wrong sequences relative to number of correct sequences per 30-second trial (Walker et al. 2003b), significant differences could be observed between all pre- and post-sleep conditions above. Interestingly, Fischer et al. (2002) found that performance speed, but not accuracy, significantly improved during daytime awake retention without practice. Consistent with the proposed model is the hypothesis that an adaptive, compensatory response to increased sleep need could take place during extended wakefulness (Finelli et al. 2000).

In summary, these findings suggest that sleep may not have a uniform effect on all constituents of memory. Rather, specific aspects, or types, of internal representation may be selectively enhanced by mechanisms characterizing the sleep process. Understanding which features of behavioral performance are enhanced will help uncover the specific mechanisms influenced by sleep.

Hypotheses concerning the putative mechanisms that may underlie the consolidation of memory traces during sleep have focused on the role of either REM or non-REM sleep (Maquet 2001). The evidence in favor of one or the other hypothesis requires careful consideration of experimental design and method (Peigneux et al. 2001a). Walker's (2002) hypothesis makes no a priori assumptions about the sleep state that may be exerting an effect on memory consolidation. Thus, he and coworkers were able to infer post hoc a correlation between relative amount of stage 2 non-REM sleep and performance improvement after sleep. The independent study by Fischer et al. (2002) that used a similar task and design confirmed most results, except for dependence on stage 2, showing instead a correlation between amount of REM sleep and performance gain after sleep. For both studies the amount of time spent in one sleep stage across the night at best accounted for less than 44% of the variance in performance gain (the other stage accounted for less than 14%). Therefore, none of those factors can explain entirely the relation between sleep and performance improvement (see also Gais et al. 2000; Stickgold et al. 2000b). Factors other than time related to sleep staging (e.g., electrophysiological variables) should also be tested.

It has recently been proposed that sleep spindles, by virtue of a pattern of excitation-inhibition that provokes massive Ca entry that specifically activates Ca-dependent molecular gates in the spindling cells, could open the door to subsequent long-term changes in cortical networks (Sejnowski & Destexhe 2000). This hypothesis is consistent with the correlation observed by Walker (2002). Prominent in non-REM sleep stage 2, spindles >13 Hz have been shown to have their maximal expression in an area surrounding the head vertex, that is, in close correspondence with the motor cortex (Finelli et al. 2001). Sleep is a regulated process whose timing, duration, and intensity depend on the interaction of homeostatic (the prior sleep-wake history) and circadian factors (Borbély 1982). Would a non-dramatic extension (or reduction) of some stage of sleep cause a better (or worse) improvement in performance? Sleep deprivation prior to new acquisition and sleep-induced enhancement would increase slow wave sleep, and would probably not alter stage 2. However, EEG power density in the range of spindles would be significantly reduced (Finelli et al. 2001). The concept of memory enhancement through sleep could be tested in experiments of this kind.

Sleep and memory: Definitions, terminology, models, and predictions?

Jonathan K. Foster[a] and Andrew C. Wilson[b]

[a]*School of Exercise, Biomedical and Health Sciences, Edith Cowan University, Joondalup, and School of Paediatric & Child Health, University of Western Australia, Princess Margaret Hospital, Subiaco, Western Australia, Australia;* [b]*Department of Respiratory Medicine, Princess Margaret Hospital, Subiaco, Western Australia, Australia.* **j.foster@ecu.edu.au andreww@ichr.uwa.edu.au**

Abstract: In this target article, Walker seeks to clarify the current state of knowledge regarding sleep and memory. Walker's review represents an impressively heuristic attempt to synthesize the relevant literature. In this commentary, we question the focus on procedural memory and the use of the term "consolidation," and we consider the extent to which empirically testable predictions can be derived from Walker's model.

In recent decades, there has been increasing research focus on the topic of sleep and memory, transcending once and for all the "sleep and memory tapes" anecdotal speculation of yesteryear. Walker hails from one of the scientific hotbeds of contemporary sleep-memory research. His starting point is that neuroscientific evidence indicates that sleep plays a role in learning and memory, but that the mechanisms involved are currently unclear. In this heuristic review, Walker seeks to clarify the current state of knowledge, in the process formulating a model whereby, it is argued, sleep impacts favourably on specific elements of memory processing.

In his review, Walker focuses predominantly on procedural memory, proposing that learning in this domain comprises an acquisition phase which is followed by two specific stages of consolidation (the first involving a process of stabilization and the second involving a process of enhancement; the latter is proposed to underlie delayed learning). Walker argues that acquisition and stabilization of procedural information do not rely fundamentally on sleep. By contrast, he argues that procedural memory enhancement does appear to rely on sleep, presenting evidence for specific sleep-stage dependencies. Walker adduces relevant evidence from the sleep/memory literature and nominates potential candidate mechanisms at the molecular, cellular, and systems levels.

In the initial reading of Walker's article, there is some apparent confusion regarding the notion of consolidation. Presumably the sentence towards the end of the Abstract which begins "In contrast, the consolidation stage . . . does appear to rely on the process of sleep" should in fact read "In contrast, the enhancement phase," given that Walker has already stated that the stabilization phase of consolidation is not modulated by sleep per se.

Of interest is the manner in which Walker characterises the distinction between declarative and procedural memory; for example, in section 2.1 he refers to declarative memory in terms of "one or two readings of a text" or "one exposure to an event" and procedural memory in terms of being "passive." It is not entirely clear that these dichotomies are appropriate with respect to the extant literature. For example, a recent search of the Institute of Scientific Information Science and Social Science Citation Indexes found no association between the notions of procedural memory and passive processing. Although this point perhaps does not bear directly on the theoretical framework that is being articulated by Walker, it is germane to some of the neurocognitive mechanisms which he cites. Furthermore, we find the use of the term "consolidation" in this context to be potentially confusing, given its much more frequent use in the declarative memory literature (again evaluated via Institute of Scientific Information Science and Social Science Citation Indexes), and given the sleep-related distinction that is here being attempted by Walker between declarative and pro-

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