Using two sequential key press sequences, we tested the extent to which subjects' performance on a digital piano keyboard changed between the end of training and retest on subsequent days. We found consistent, significant improvements attributable to sleep-based consolidation effects, indicating that learning continued after the cessation of practice during both the first and second nights of sleep following training. When subjects briefly recalled a learned sequence 1 day after training and then immediately learned a second, similar sequence, there were no observable improvements in subjects' performance of the first sequence after the second night of sleep. We discuss our results in relation to similar findings in neuroscience and cognition.

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Procedural Memory Consolidation in the Performance of Brief Keyboard Sequences

Quite naturally, the topic of memory has long been of interest to musicians and music teachers. Memorization is a central component of musicians' lives, not only with respect to the memorization of repertoire, but also, and more fundamentally, with respect to learning and recalling the motor components of skilled musical execution.

Perhaps the most often cited research on memory in the context of music making is the series of studies by Rubin-Rabson, in which she tested the effects of multiple variables on pianists' memorization of short pieces (Rubin-Rabson, 1937, 1939, 1940a, 1940b, 1941a, 1941b, 1941c, 1941d, 1941e, 1947, 1950). Her early research on the effects of so-called massed versus distributed practice demonstrated that some musicians remembered learned pieces better when the total minutes devoted to practice were distributed across time, com-

pared to when the same amount of total practice was performed in one sitting, but this effect was observed only in what Rubin-Rabson referred to as "less-able learners" (Rubin-Rabson, 1940a). Rubin-Rabson's finding that distributed practice, spaced over 2 days, was superior to both massed practice and to practice time distributed across multiple sessions within a single day is consistent with more recent and more fully elaborated understandings of human memory, in particular the fact that the process of memory formation continues following the cessation of practice and extends to periods of overnight sleep (Walker, Stickgold, Alsop, Gaab, & Schlaug, 2005).

Comparisons of massed and distributed practice have been explored using a number of motor tasks (Lee & Genovese, 1988, 1989; Shea, Lai, Black, & Park, 2000), but the superiority of distributed practice over massed practice has not recently been addressed in music. More recent studies of memory in the context of music learning were investigations of cognitive strategies used by learners to facilitate the memorization of music repertoire (Chaffin & Imreh, 1997, 2002; Ginsborg, 2002; Williamon & Valentine, 2002), dealing primarily with the ability of learners to remember what they have practiced. The processes of memory formation and their effects on the stabilization and fluency of motor skills in music have received little attention to date.

The systematic study of memory formation over the past half-century has revealed that memory is not at all analogous to a blank tape or a computer hard drive. The formation of memories includes the integration of new experiences into the extant organization of the mind. Thus, memories for new events are affected not only by the conditions under which events are experienced, but also by the structural organization of the mind of the learner. Furthermore, memories are not fixed at the time of experience, but continue to change over time, even in the absence of further contact with remembered events and without conscious effort by the learner.

The formation and elaboration of memory involve processes of protein synthesis that lead to physical changes in synaptic structures and the creation and modification of connections among networks of neurons. This neural plasticity has been observed at both macroscopic and microscopic levels, with corresponding behavioral changes observed in both declarative and procedural memories, including motor skills (Walker & Stickgold, 2004).

The process of physical change that occurs following active learning experiences is termed *memory consolidation* and involves not only a reorganization of the neuronal connections that comprise new memories, but also a relocation of memory structures in the brain (Muellbacher et al., 2002; Walker, 2005). Through wake-based consolidation, which begins during initial practice and continues for up to 6 hours following practice, memories become increasingly resistant to interference from competing stimuli. Consolidation of memories also occurs during sleep, when memories of experiences encountered during the day are reorganized and, in some cases, enhanced.

The relevant research regarding declarative memory shows varying degrees of sleep-dependent effects on the performance of verbal memorization skills (Peigneux, Laureys, Delbeuck, & Maquet, 2001; Vertes & Eastman, 2000), though the role of sleep in the formation of declarative memory remains to be fully understood. An extensive and growing body of research shows that sleep plays a critical role in the formation of procedural memories, including the types of motor skills involved in music performance (see Walker, 2005, for a recent review).

Quite remarkably, sleep-based memory consolidation has been shown rather consistently to *enhance* learned procedural skills absent additional practice. Performance enhancements attributable to memory consolidation during sleep have been observed in both simple and complex motor skills (Kuriyama, Stickgold, & Walker, 2004; Maquet, Laureys, et al., 2003; Mednick, 2003; Vertes & Eastman, 2000; Walker, Brakefield, Hobson, & Stickgold, 2003; Walker, Brakefield, Seidman, et al., 2003), auditory discrimination skills (Atienza & Cantero, 2001; Atienza Cantero, & Dominquez-Marin, 2002; Atienza, Cantero, & Stickgold, 2004), visual discrimination skills (Karni, Tanne, Rubenstein, & Askenasy, 1994; Maquet, Schwartz, Passingham, & Frith, 2003; Mednick et al., 2002; Mednick, Nakayama, & Stickgold, 2003; Stickgold, James, & Hobson, 2000), and verbal skills (Fenn, Nusbaum, & Margoliash, 2003).

During the initial acquisition stage of skill learning, rapid improvements in performance are readily observable as memory undergoes an encoding process leading to long-term memory storage. When the rate of improvement in an initial learning session begins to slow and asymptotic levels of performance improvement are reached, the consolidation process begins (Hauptmann & Karni, 2002; Hauptmann, Reinhart, Brandt, & Karni, 2005; Ofen-Noy, Dudai, & Karni, 2003), continuing for up to 6 waking hours following the termination of practice. During this period, which Walker, Brakefield, Seidman, et al. (2003) label *consolidation-based stabilization,* memories become resistant to interference, and performance levels attained by the end of physical practice are maintained or slightly improved over time. Later, following periods of sleep, larger improvements in motor skill performance are observed, absent additional practice (Brashers-Krug, Shadmehr, & Bizzi, 1996; Hauptmann & Karni, 2002; Hauptmann et al., 2005; Kuriyama et al., 2004; Walker, Brakefield, Hobson, et al., 2003; Walker, Brakefield, Morgan, Hobson, & Stickgold, 2002; Walker, Brakefield, Seidman, et al., 2003; Walker & Stickgold, 2004). Termed *consolidation-based enhancement,* this sleep-dependent process not only increases the stability of procedural memory, but also involves further learning, in that subsequent performances evince enhancements in movement accuracy and speed.

For consolidation to be fully realized, practice of new skills must be followed by a period of sleep. The night of sleep following initial practice is particularly important for establishing procedural memories (Stickgold, James, et al., 2000). Specific stages of sleep, charac-

terized by distinct patterns of neural activity, are believed to play a role in consolidation-based enhancement processes. Karni, Stickgold, and others found that improvements in visual discrimination skills were related to the product of the percentages of time spent in slow-wave sleep (SWS) in the first quarter of the night and rapid eye movement (REM) sleep in the fourth quarter of the night (Karni et al., 1994; Stickgold, James, et al., 2000; Stickgold, Whidbee, Schirmer, Patel, & Hobson, 2000). Improvements in the performance of motor skills have been found to be proportionally related to time spent in non-REM sleep (including stage 2 and SWS periods) (Huber, Ghilardi, Massimini, & Tononi, 2004; Walker et al., 2002).

Depriving learners of sleep following the acquisition of a novel skill may cause significant deficits in memory consolidation. Impairments in learning have also been shown to result from selective deprivation of specific sleep stages, such as SWS early in the night and REM sleep in the last quarter of the night (Beaulieu & Godbout, 2000; Smith, 1995, 1996; Smith, Conway, & Rose, 1998).

Although complete cycles of sleep stages occur most often during extended periods of sleep, overnight sleep is not the only time during which consolidation-based enhancements develop. Even daytime naps have been shown to result in performance enhancements of visual discrimination skills, provided that they include intervals of REM sleep (Mednick et al., 2002; Mednick et al., 2003).

The necessity of wake-based consolidation in memory formation and the necessity of sleep-based consolidation in memory enhancement have been demonstrated in both rats and humans. Electroconvulsive shock, the cortical injection of protein synthesis inhibitors, and transcranial magnetic stimulation, applied prior to the completion of consolidation, have all been shown to interrupt the consolidation process and inhibit the formation of procedural memories for newly acquired skills (Graves, Pack, & Abel, 2001; Muellbacher et al., 2002; Trepel & Racine, 1999). When these procedures are introduced within 6 hours of skill acquisition, memory is degraded; when the same procedures are introduced later, after wake-based consolidation has completed, no decrements in memory are observed.

It has recently been demonstrated that when two similar skills are learned in close temporal proximity, the learning of the second skill may interrupt the consolidation of the skill learned first, and thus may inhibit improvements in performance of the first-learned skill, especially following a night of sleep (Brashers-Krug et al., 1996; Walker, Brakefield, Hobson, et al., 2003), a result that has obvious implications for skill learning in music. Moreover, Walker, Brakefield, Hobson, et al. have shown that, in some instances, the simple recall of a previously consolidated memory may return it to an unstable, labile state, thus rendering it susceptible to interference and requiring a period of reconsolidation.

To test the proposition that sleep-based procedural memory consolidation enhances the performance of motor skills, we designed a series of training and retest conditions, similar to experiments con-

ducted by Walker, Brakefield, Hobson, et al. (2003) and using nearly identical motor tasks. We tested the effects of learning two similar skills on the stabilization and enhancement of procedural memories.

Our goal was to study the processes of motor skill learning in the context of music performance, and it seemed an important first step to replicate, using music instruments, relevant research that has been conducted in other contexts. This is the first in a series of experiments that examines consolidation effects in simple and complex motor skills, including skills involved in music performance.

METHOD

Subjects were 49 right-handed nonmusic majors enrolled in music classes at The University of Texas at Austin (M age = 20.2 years; SD = 2.0). Each subject had had fewer than 3 years of formal instruction on a musical instrument and had participated in no music-making activities in the 5 years preceding the experiment. All agreed to abstain from drugs, alcohol, and caffeine 12 hours prior to and during the experiment. The experiment was approved by the Institutional Review Board at The University of Texas at Austin, and subjects received monetary compensation for their participation.

Subjects learned either one or two finger-tapping sequences (2–5–3–4–2 or 4–3–5–2–4), identical to those used by Walker, Brakefield, Hobson, et al. (2003). (Finger numbers above are those typically assigned in piano; i.e., 1 is thumb, 2 is index finger, and so on). Subjects tapped the patterns on a Roland KR-4700 Digital Piano on the keys F3, G3, A3, and B3. The order of the two sequences was counterbalanced among subjects and within conditions, with approximately half the subjects learning 2–5–3–4–2 first and the remaining subjects learning 4–3–5–2–4 first.

Subjects sat at the keyboard and watched a 12-inch computer screen mounted at the level of the keyboard's music rack. The sound of the keyboard was turned off. On the screen were the finger numbers of the target sequence, and below each finger number was a circle that illuminated each time a key was pressed. The circles illuminated in order from left to right, regardless of whether subjects pressed a correct key. Thus, the illuminated circles did not provide accuracy feedback, but were intended only to help subjects maintain their place in the sequence. This procedure is identical to one used in a number of other experiments in which subjects tapped on a computer keyboard (Kuriyama et al., 2004; Walker, Brakefield, Hobson, et al., 2003; Walker et al., 2002; Walker, Brakefield, Seidman, et al., 2003).

Subjects were instructed to play the target sequence with their left (nondominant) hand, using the fingerings indicated, and to repeat the sequence "as quickly and accurately as possible" during 30-second practice blocks. Subjects were tested individually in a small room free of distractions. During the entire procedure subjects wore Bose QuietComfort 2 acoustic noise-canceling headphones.

Training sessions consisted of twelve 30-second blocks of practice, each followed by a 30-second rest interval. Retest sessions consisted of three 30-second practice blocks separated by 30 seconds of rest. Subjects were tested between 9 A.M. and 5 P.M., and individual subjects' Training and Retest sessions were separated by approximately 24 hours (range, 22–26 hours). At the start of each session, subjects reported the number of hours slept and rated their alertness using the Stanford Sleepiness Scale (Hoddes et al., 1973).

Musical Instrument Digital Interface (MIDI) data for both training and retest sessions were recorded using Max/MSP software (Puckette & Zicarelli, 2004). We used as a dependent measure the number of correct key presses per 30-second block (CKP/B), a measure that reflects both the accuracy and speed of subjects' performances.[1] In each condition, the mean CKP/B from the last three training blocks was compared to the mean CKP/B for the three retest blocks using paired t-tests.

RESULTS

Subjects reported an average of 6.53 hours of overnight sleep prior to Training, 6.87 hours' sleep prior to Retest 1, and 7.26 hours' sleep prior to Retest 2. There were no relationships between CKP/B and reported amount of sleep or sleepiness rating at any training or retest session, $p > .25$. We found no relationship between performance improvements at retest (i.e., the difference in CKP/B between Training and Retest 1 or between Retest 1 and Retest 2) and the reported amount of sleep in the preceding night, $p > .33$, nor did we find a relationship between sleepiness ratings prior to training and improvement or percentage improvement in CKP/B at Retest 1, $p > .09$.

There were no systematic differences between groups in terms of hours slept prior to training, $F(5, 53) = 0.56$, $p > .73$, prior to Retest 1, $F(4, 44) = 0.25$, $p > .91$, or prior to Retest 2, $F(1, 18) < 0.01$, $p > .94$. Neither were there systematic differences among the subjects in the five groups in terms of reported sleepiness prior to training, $F(5, 53) = 0.41$, $p > .84$, prior to Retest 1, $F(4, 44) = 1.75$, $p > .16$, or prior to Retest 2, $F(1, 18) < 0.03$, $p > .87$.

We report the results for the five groups below. Each group's label describes the experimental condition. For example, A24B24ab indicates that subjects learned two sequences (A and B) 24 hours apart and were retested on both sequences (a and b) in one session, 24 hours after having learned the second sequence. Recall that the order of the actual sequences learned in all groups (2–5–3–4–2 and 4–3–5–2–4) was counterbalanced among subjects.

Group A24a. Subjects were trained on one sequence on Day 1 and were retested on Day 2, following a 24-hour interval that included sleep (see Figure 1A). Retest performance indicated a significant increase in mean CKP/B following a night of sleep, from 82.13 ($SE = 6.88$) at training to 95.47 ($SE = 8.21$) at retest (+16.2%), demonstrating overnight consolidation-based enhancements, $t(9) = 2.86$, $p < .019$.
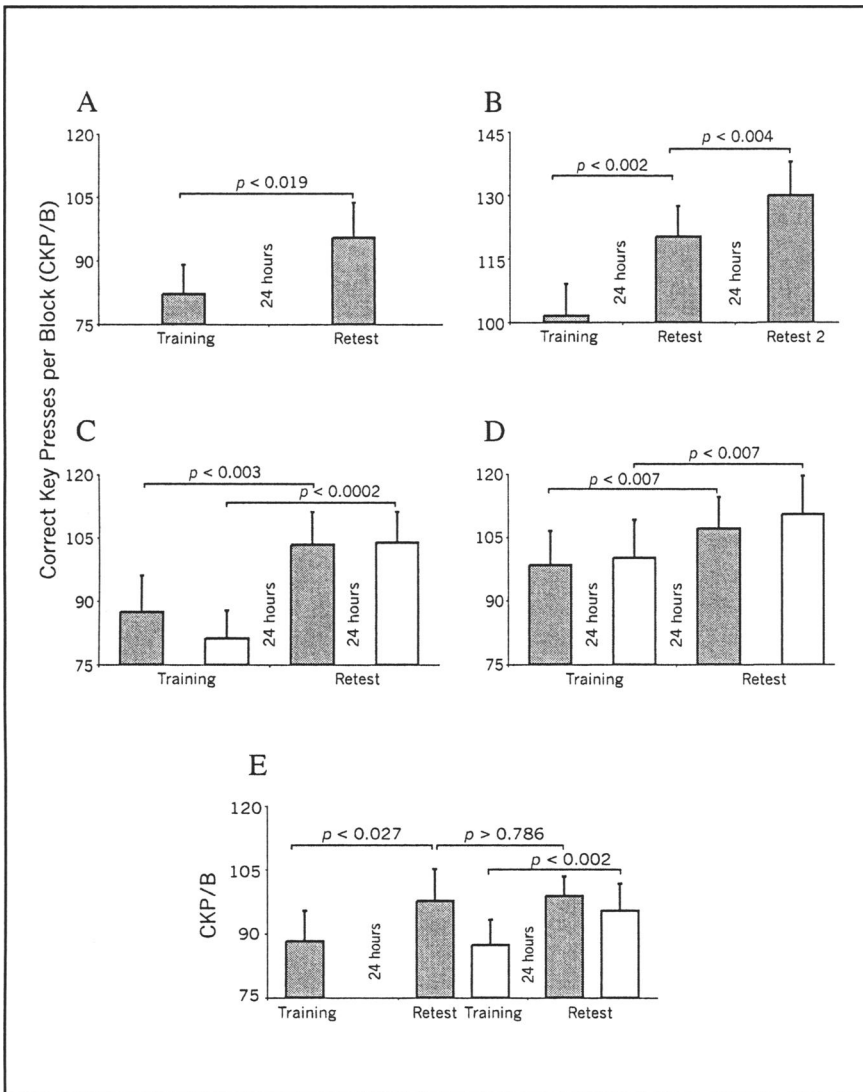
Figure 1. Changes in motor performance from training to retest. A, Group A24a; B, Group A24a24a; C, Group AB24ab; D, Group A24B24ab; E, Group A24aB24ab. Error bars show standard error of the mean.

Group A24a24a. Subjects learned one sequence and recalled it twice, following intervals of 24 and 48 hours after training. Sleep-dependent enhancements were observed in both retests, $F(2, 18) = 28.1$, $p < .0001$. The mean CKP/B at training was 101.60 ($SE = 7.51$). Performance improved to 120.33 ($SE = 7.23$) at Retest 1 (+18.4%),

$t(9) = 4.18$, $p < .002$, and to 130.15 ($SE = 7.97$) at Retest 2 (+8.2%), $t(9) = 3.85$, $p < .004$ (see Figure 1B). The data show that sleep-dependent enhancements occurred over the second night following training, although the second night's improvements were less than those observed after the first night of sleep.

Group AB24ab. Subjects were trained on two sequences on Day 1 and were retested on Day 2, following a 24-hour interval that included sleep (see Figure 1C). Data were used to determine possible interference effects on the consolidation of newly learned skills. Performance on the first sequence improved significantly from 87.48 CKP/B ($SE = 8.61$) at training to 103.41 ($SE = 7.77$) at retest (+18.2%), $t(8) = 4.16$, $p < .003$; performance on the second sequence also improved significantly, and to a greater extent, from 81.26 ($SE = 6.58$) to 103.93 ($SE = 7.30$) (+27.9%), $t(8) = 6.28$, $p < .0002$. Thus, performance seemed to benefit from consolidation-based enhancements in both sequences, but the effect was greater for the sequence learned second.

Group A24B24ab. Subjects were trained on one sequence on Day 1, a second sequence on Day 2, and were retested on both sequences on Day 3 (see Figure 1D). Again, significant performance improvements for both sequences were observed following sleep. Mean performance on the sequence learned on Day 1 improved significantly, from 98.47 CKP/B ($SE = 8.08$) at training to 107.22 ($SE = 7.46$) at retest (+8.9%), following 2 nights of sleep, $t(9) = 3.46$, $p < .007$. The sequence learned on Day 2 also showed significant improvements following overnight sleep, from 100.23 CKP/B ($SE = 8.96$) to 110.60 ($SE = 9.12$) (+10.4%), $t(9) = 3.48$, $p < .007$.

Group A24aB24ab. Like subjects in Group A24a24a, subjects learned a sequence and recalled it twice, each time after a 24-hour interval that included sleep. To investigate the effects of learning a competing task on the consolidation of a reactivated memory, we had subjects in this group learn a second sequence on Day 2 immediately after the retest of the sequence that was learned on Day 1. Both sequences were retested on Day 3. We found that by introducing the second sequence following the Day 2 retest of the sequence learned first, we inhibited the overnight consolidation-based enhancement of the first-learned sequence that had been observed on Day 3 of A24a24a. Consistent with the data from our other groups, performance on the first sequence improved significantly, $F(2, 18) = 4.5$, $p < .026$, from 88.30 CKP/B ($SE = 7.11$) at training to 97.70 ($SE = 7.44$) at Retest 1 (+10.7%), $t(9) = 2.63$, $p < .03$, but did not increase between Retest 1 and Retest 2 (+1.3%), following a second night of sleep, $t(9) = 0.28$, $p > .78$ (see Figure 1E). The sequence introduced on Day 2 showed significant sleep-dependent improvements, with mean increases from 87.43 CKP/B ($SE = 5.90$) at training to 95.48 ($SE = 6.32$) at retest (+9.2%), $t(9) = 4.26$, $p < .002$. These data indicate that learning the second sequence on Day 2 inhibited expected sleep-dependent enhancements in the first sequence between Day 2 and Day 3.

DISCUSSION

Our results are consistent with a great deal of research in procedural memory, all of which demonstrates that sleep-based consolidation of procedural skills results in performance enhancements that develop in the absence of practice. Our data replicate what has been shown quite reliably to date, namely, that following the initial acquisition of novel skills, learning continues as memories are stabilized during waking hours following practice; memories are further refined, and in some cases skills are enhanced, during sleep.

Brashers-Krug et al. (1996) and Walker, Brakefield, Hobson, et al. (2003) showed that the consolidation of a newly learned skill could be inhibited by learning a competing skill prior to the consolidation of the skill learned first. We did not find a similar effect. Subjects who learned two skills in one session on Day 1 showed consolidation-based enhancements in both skills at retest, which indicates that the consolidation processes for both skills were unaffected by the proximity of their training sessions. We did observe that the overnight improvements in the sequence learned second were greater than the improvements in the sequence learned first, but this effect may be a result of the fact that subjects performed more poorly on the second sequence than on the first sequence at training (see Figure 1C).

Walker, Brakefield, Hobson, et al. (2003) also found that by training on a new sequence on Day 2, immediately following the recall of a sequence learned on Day 1, subjects' performance of the sequence learned first was diminished at retest on Day 3. Walker, Brakefield, Hobson, et al. interpreted this finding as evidence of a reconsolidation effect; that is, that recalling the first learned sequence on Day 2 returned its memory to a labile state that required a period of reconsolidation and restabilization. Learning the second sequence was thought to have disrupted this reconsolidation process during sleep, as evidenced by the fact that the performance level at retest on Day 3 returned to the performance level observed at the end of training on Day 1. Thus, learning the second sequence eliminated the sleep-based enhancement that had occurred overnight between Day 1 and Day 2.

We did not find the same effect, but we did observe that learning a second sequence on Day 2, immediately after recalling the sequence learned on Day 1, inhibited the sleep-based enhancement in the second night of sleep. When only one sequence was practiced and recalled (A24a24a), we found evidence of sleep-based enhancements after both the first and second nights of sleep following training, although the improvements observed following the second night were smaller than those observed following the first night. But when subjects learned the second sequence following the recall of the first sequence on Day 2, the second night's improvements were not observed. Thus, our findings indicate that learning a new sequence following the recall of an already-learned sequence may interfere with sleep-based enhancement of the sequence learned first.

We propose that recalling a recently consolidated skill memory may render it susceptible to interference from competing stimuli, but that this interference affects only the extent to which the memory is enhanced during sleep. Contrary to Walker, Brakefield, Hobson, et al.'s hypothesis, our data do not support the notion that reactivated memories must be reconsolidated, a topic that is undergoing continuing scrutiny (Alberini, 2005). Rather, interfering stimuli may inhibit a memory's further improvements across an additional night of sleep.

The differences between our findings and those reported by Walker et al. are in some ways puzzling. Recall that Walker, Brakefield, Hobson, et al. (2003) is the only experiment which demonstrates that learning competing skills in temporal proximity can interfere with consolidation and reconsolidation in humans. The tasks in our experiment were identical to the tasks used by Walker, Brakefield, Hobson, et al. in every respect except one: Rather than tapping on a computer keyboard, as Walker's subjects had done, our subjects tapped the sequences on a piano keyboard with weighted keys. Thus, our task required more physical effort and led to slower performance speeds overall than did Walker's, but it is difficult to discern how this could have led to different effects on the consolidation processes observed. Clearly, further research is required to resolve the discrepancies in the findings.

Although we found significant differences in the mean performance levels between the end of training and subsequent retests, there was considerable variability among individuals in the amount of change across a night of sleep. We are unable to reject the possibility that variables encountered following the testing phase may have affected individuals' retention of the newly learned sequences. Our observations are consistent with those of Walker et al. (2002), though, in that within groups, individual subjects' performances changed at considerably different rates across sleep.

In this and other studies, performance change has not been found to be related to subjects' total amount of sleep prior to retest. However, strong correlations have been found between the percentage of overnight improvements in performance and both the total percentage of time spent in Stage 2–NREM sleep and the percentage of Stage 2–NREM sleep in the fourth quarter of the night (Walker et al., 2002). With regard to the present study, we can only speculate as to whether the extent of performance changes among subjects was related to different amounts of time spent in Stage 2–NREM sleep.

The majority of extant research examining the effects of sleep on motor learning has focused on visual and motor skill acquisition and retention, but recent findings describe similar phenomena in the development of auditory memory. There remains a need to test the effects of auditory components on the learning and retention of motor skills. Also, whereas existing research offers reliable evidence of processes implicated in the learning of simple skills, it is not clear whether rates of learning during practice and consolidation vary with the complexity of skills. Further study will expand our understanding

of sleep-based consolidation effects in unskilled subjects and in skilled performers (i.e., trained musicians). Studying the effects of learners' expertise on skill learning is necessary to gain a more complete and useful understanding of procedural memory in music.

Of course, it is tempting to extrapolate from these data and make recommendations about musicians' practice, but such extrapolations are unwarranted at this time. Experienced musicians, being the beneficiaries of learning that has been passed on through centuries of human experience, know a great deal about how to practice skills. Whether research results like those reported here will make music practice more efficient is an open question. The effects we observed are small, and it is unclear whether they would be noticeable in the context of actual music practice over time. Yet, these preliminary investigations are certainly relevant to the study of music, as they begin to explain more fully the processes through which motor memories are recorded, retained, and recalled.

When it comes to learning, much is known in music about what works; much less is known about how and why learning proceeds the way that it does. The questions of how and why seem the most in need of careful research that explains the phenomena that we experience as musicians and teachers.

NOTE

1. We measured correct key presses per block, because this measure includes *both* accuracy and speed in a single assessment. After reviewing previous research and while designing our study, we were concerned about measuring speed and accuracy separately, since a given subject may, for example, increase speed and make more mistakes, or may increase accuracy by going slower. We believe that the number of CKP/B is the measure that best accounts for changes in performance (i.e., how well someone performs), because it is affected by both accuracy and speed.

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