Benefits of Sleep in Motor Learning – Prospects and Limitations

by

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During the recent years it has been shown repeatedly that, after initial learning, elapse of time preserves, but sleep enhances performance in procedural motor skills. To date, however, the majority of experimental studies in this area employed some sort of a sequential finger tapping skill as a criterion task. Thus it is unclear yet, if any (and which) other types of motor skills do indeed benefit from sleep. In order to answer this question, and to provide theoretical statements about the memory system regarding benefits of sleep in motor learning, we carried out a series of studies following a "multi-task research strategy". Although we successfully replicated sleep-related improvements in the production of newly acquired sequential finger skills (FT-Task) under different learning conditions (i.e., guided or unguided), we did not find any such effect of sleep in discrete motor tasks requiring precise production of (a) a specific relative timing pattern (Diamond Tapping-Task), or (b) a sub-maximal force impulse (vertical Counter Movement Jump), and we also failed to find any specifically sleep-related effects on subsequent performance in (c) a continuous visuo-motor pursuit-tracking task. These results are considered in relation to other work, and the respective theoretical implications are discussed.

Keywords: sleep, motor learning, tracking-task

Introduction

There is a fast growing body of research in the area of neuropsychology and the behavioral sciences addressing consolidation and optimization of internal representations in the course of motor learning (Blischke & Erlacher, 2007). Particularly, it has been shown that, after initial learning, elapse of time preserves, but *sleep enhances* performance in procedural motor skills. After having established a considerable body of behavioral studies coming up with similar results (e.g. Fischer et al., 2005; Walker, 2005;

Walker et al., 2002), some leading research groups in this area now begin to focus on scrutinizing the functional components and anatomical substrates (i.e., brain structures) underlying the reported sleep-related changes in performance at the cellular and molecular level (e.g. Benington & Frank, 2003; Smith et al., 2004), while others study the effects of daytime naps on motor learning and brain activity (e.g. Nishida & Walker, 2007).

To date, however, the majority of pertinent experimental studies in this area employed some sort of a *sequential finger skill* as a criterion

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Table 1

*Designated learning tasks and features characterizing the respective task domains.*

Task	Finger-Tapping	Diamond Tapping	Hand-Tapping	Pursuit Tracking	Vertical CM-Jump	Golf-Putt	Dice-Stacking
Type	discrete-repetitive	discrete	discrete	continuous	discrete-ballistic	discrete-ballistic	discrete => rhythmic
Range	fine motor task	fine motor task	semi-gross motor task	fine motor task	gross motor task	gross motor task => object control	mixed fine & gross motor task => object control
Criterion: *What has to be learned*	sequence: end-effectors	sequence: time-intervals	sequence: spatial locations	space-time-pattern	force impulse	spatial goal & force impulse	coordination strategy
Memory	partially declarative	partially declarative	partially declarative	predom. non-declar.	none-declarative	partially declarative	partially declarative
Learning Condition	explicit (speeded)	explicit (unpaced)	explicit (speed.-unpaced)	implicit (paced)	explicit (unpaced)	explicit (unpaced)	explicit

task (cf. insert in figure 1). And although changes in brain activation, brain state, functional connectivity, and REM sleep parameters after initial learning of *visuo*-motor tasks were recently reported (pursuit tracking; mirror tracing; cf. Maquet, Schwarz, Passingham & Frith, 2003; Schredl & Erlacher, 2007), it is not clear yet if *performance measures* in these tasks are actually *improved* by sleep-related processes of memory reorganization as compared to memory consolidation during wake. Therefore it is still an open question, which *other* types of motor skills (that is, except sequential finger tapping tasks) do indeed benefit from sleep.

So far, there is no straight-forward answer to this question, for there may be different task-specific systems in the human brain, each composed of a well defined set of components, i.e. processes that achieve their functions. This possibility requires that statements about the *functional components* underlying sleep-related motor memory enhancement be supplied with statements about the *set of tasks* to which they are applicable. Generalization of theoretical statements about the memory system regarding benefits of sleep in motor learning thus calls for a "multi-task research strategy" (Heuer, 1987).

Applying this approach, we set out to investigate the effect of nocturnal sleep on newly acquired motor skills across different task domains. To this end, we conducted a series of laboratory studies, each employing another

Figure 1

Experimental paradigm. For details see text.
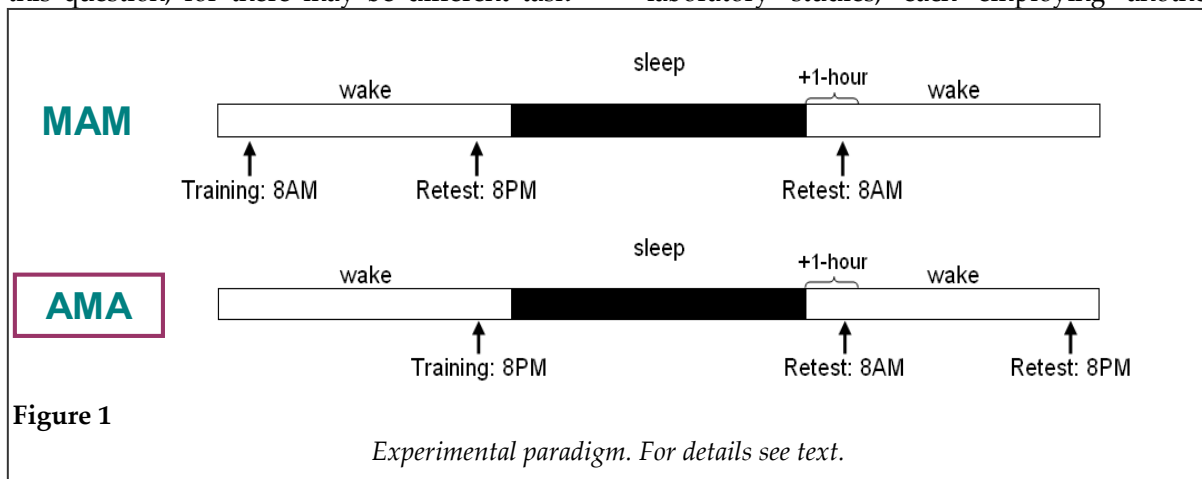
learning task. Tasks were chosen to reflect domain-specific features of motor control and respective memory requirements (see table 1).

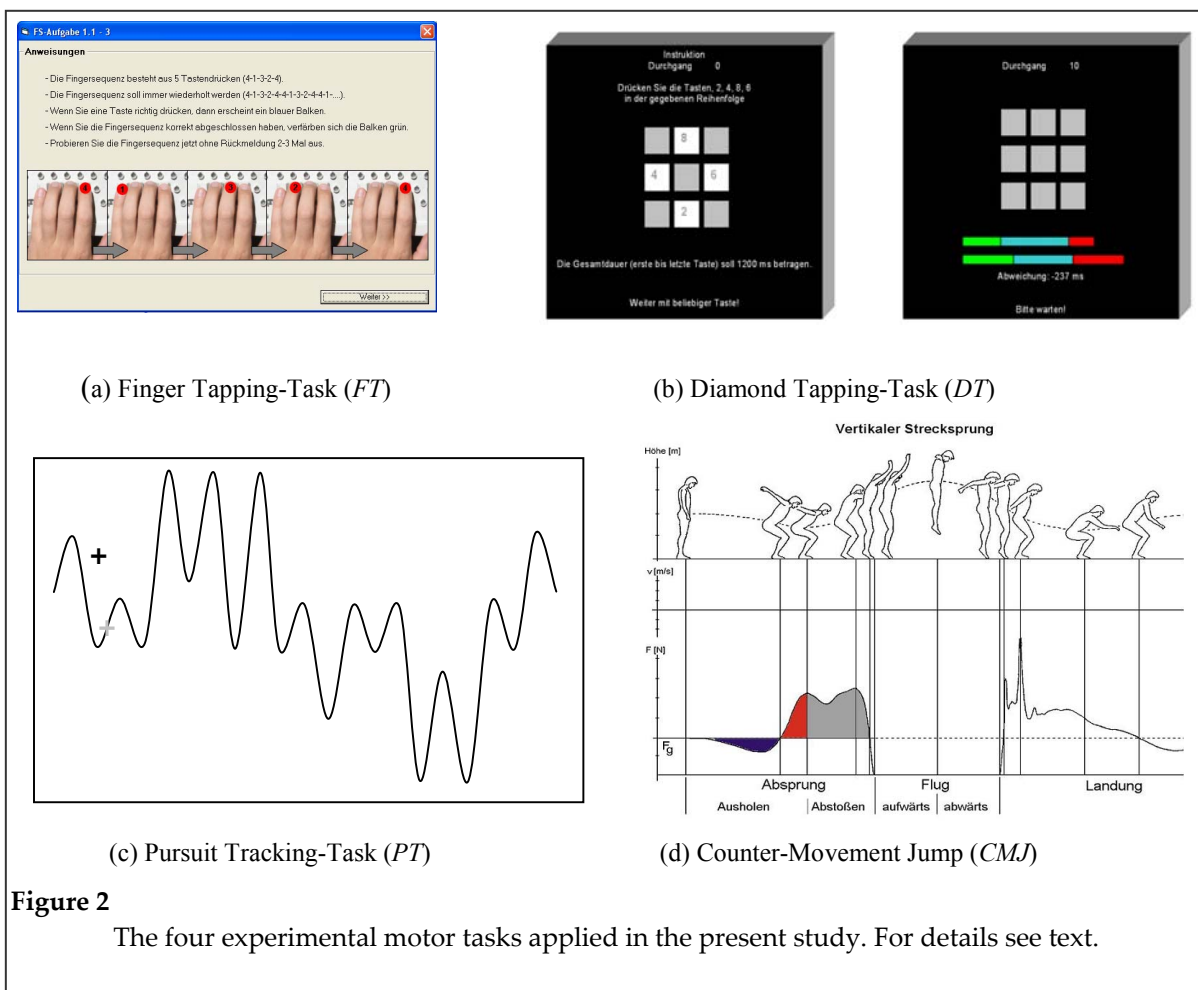## Methods

Experimental protocol

To allow for a comprehensive view on the various results, all studies followed the same basic experimental protocol, which in its basic features resembles the experimental design applied by Walker et al. (2002). In our case it always comprises two groups of subjects (cf. Figure 1). One group (MAM) received training in the morning ("Morgen"), was retested in the evening ("Abend") after a 12h wake period (Retest 1), and was then retested again the next morning ("Morgen") after another 12h period including regular night sleep (Retest 2). The other group (AMA) underwent training in the evening, was retested 12h later in the morning after a regular night's sleep (Retest 1), and then again after another 12h wake interval in the evening (Retest 2). Analysis of changes in criterion task performance across the final block(s) of practice trials (Post Training), Retest 1, and Retest 2 allowed for dissociating memory consolidation during wake from possible memory enhancement during sleep. Comparison of the two groups allowed for control of circadian effects on acquisition and early and late retention. Subjects were required to refrain from daytime naps, alcohol, excessive caffeine-intake, and any other drugs from the night before training session until the end of Retest 2. Since all our subjects were physical education students, sport practice was permitted as usual.

Tasks and procedure

So far, four of the tasks listed in table 1 have been submitted to experimental scrutiny: (a) Finger Tapping (FT), (b) Diamond Tapping (DT), (c) Pursuit Tracking (PT), and (d) Vertical Counter-Movement Jump (CMJ) (cf. Figure 2).

– The *FT-Task* called for speeded repetitive sequence production with the non-dominant hand. Following a specific serial pattern, the

(a) Finger Tapping-Task (*FT*)

(b) Diamond Tapping-Task (*DT*)

(c) Pursuit Tracking-Task (*PT*)

(d) Counter-Movement Jump (*CMJ*)

Figure 2

The four experimental motor tasks applied in the present study. For details see text.

four fingers had to be quickly activated one after the other for pressing down the keys placed underneath each fingertip. Dependent measures were *speed* (as many correct 5-element sequences as possible per 30 seconds), and *error* (as few wrong sequences as possible per 30 seconds). This task was applied in two different learning conditions, each one comprised of twelve 30-second acquisition blocks separated by a 30-second interval: In the "unguided" conditions, during each 30-second practice trial, subjects were presented a blue bar on a computer screen which increased at each key-press, no matter if correct or incorrect. In the "guided" condition, a blue rectangle popped up on the screen after each correct key-press, and after each incorrect key-press the sequence had to be started all over again. Thus, immediate extrinsic feedback was provided after each key-press. Post-Training measure was calculated from the last two acquisition blocks; Retest 1 and 2 were comprised of two 30-second blocks each.

— The *DT-Task* was conducted on the number-field of a regular computer key board. Four number-keys (2, 4, 8, 6) had to be hit one after the other with the index finger of the non-dominant hand. After each sequence the finger had to be returned to a marked starting position at the lower edge of the keyboard. The number-field was displayed on a computer screen (cf. figure 2). Throughout each trial, the key required to be pushed down next in the sequence was highlighted on the screen. Subjects were asked to produce each sequence in a *total movement time* (TMT) of 2400 ms, following a *temporal pattern* (TP) with the three key-stroke intervals amounting to 10%, 30%, and 60% respectively of the actual over-all duration of the sequence. Dependent measures were total *Percentage of Deviation* (PD [%]) from the TP-criterion (calculated as the sum of deviations from each interval criterion value per trial), and *Absolute Error* (AE [ms]) with respect to the TMT-criterion. Subjects were urged to match both learning-criteria as closely as possible. KR was provided after every second trial. Two hori-

zontal color-bars were presented on the screen, the top one representing the values of both of the learning criteria (overall length = TMT; relative length of its three segments = TP) achieved in the previous trial, the bottom one representing the respective target values. A trial was completed only after all four number keys had been hit in the correct order. Considering the lay out of a traditional computer key board, and visual control allowed for, the actual spatial task requirements in fact were minimal. Acquisition consisted of 100 trials (ten blocks of ten trials, with trial-blocks separated by a 30-second rest interval). Post-Training measure was calculated from the last acquisition block; Retest 1 and 2 consisted of two 10-trial blocks each, one with KR provided on every second trial again, one without any KR. Sequence of KR- and No-KR-blocks was counterbalanced within each treatment group.

— The *PT-Task* required subjects to follow a target cross on a computer screen as closely as possible with a pursuit cross by moving a stylus with their non-dominant hand on an electronic touch-board placed horizontally before them. This set-up thus allowed for concurrent visual feedback. The target cross followed a complex sinusoidal pattern (cf. Figure 2), which was displayed during a 19 second interval. Since subjects only saw the cursor on the screen, but were not presented with the pattern as such, and were not informed of the same pattern being repeated on every practice block (i.e. they were unaware of any regularities in the movement of the target), initial learning can be regarded as predominantly procedural (i.e. non-declarative, or implicit) in nature. It was not checked, however, to what extent subjects did nevertheless acquire some declarative knowledge about the target pattern during initial learning. For acquisition, 30 such practice blocks had to be completed. For dependent measure the *RMS-error* (RMSE) was calculated. Post-Training measure was calculated from the last three acquisition blocks; Retest 1 and 2 included three 19-second blocks each.
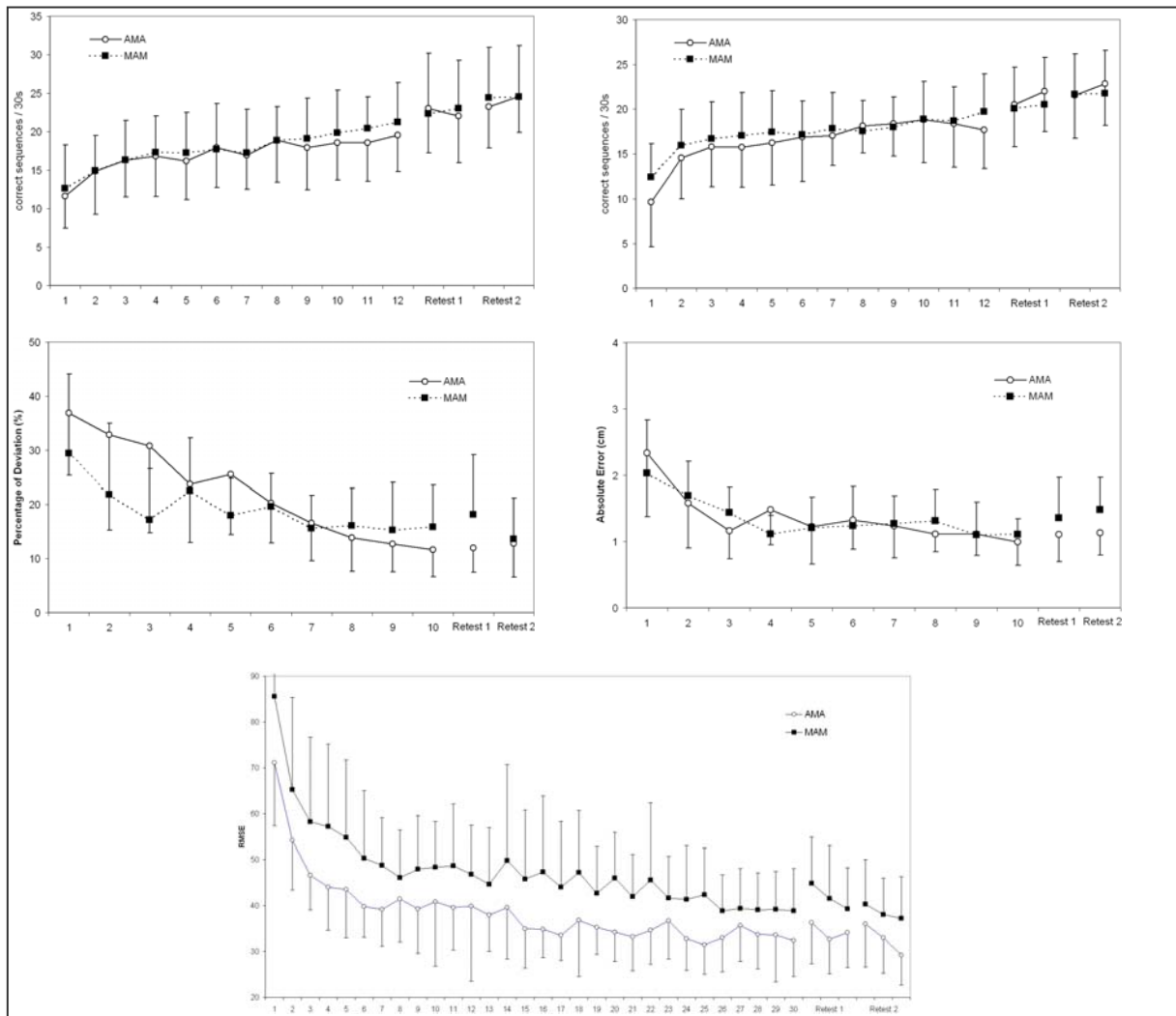
Figure 3

Changes in performance across acquisition and retests in four different tasks. Top panel: FT-Task (left: unguided; right: guided); middle panel, left: DT-Task; middle panel, right: CMJ-Task; bottom panel: PT-Task. group means per block of trials; filled squares: MAM-groups, open circles: AMA-groups, bars: standard deviations.

— The *CMJ-Task* required subjects to produce a sub-maximal vertical force impulse of precisely 60% of the individual maximum, the learning criterion thus being defined as 60% of each individual's maximal vertical COM-elevation as expressed in cm. As is known from previous experiments (e.g., Blischke, 2001), in order to learn this task subjects are dependent on externally provided information on the movement outcome (KR), but they do not acquire any declarative representation of this learning criterion. Therefore, learning this task results in an essentially procedural memory representation. For acquisition, subjects completed 100 tri-

als (ten blocks of ten trials, with trial-blocks separated by a two-minute interval, and trials within each block separated by about six to eight seconds). KR (actual COM-elevation in cm) was provided acoustically after every second trial. For dependent measure, *Absolute Error* (AE [cm]) was calculated. Post-Training measure was calculated from the last acquisition block; Retest 1 and 2 consisted of two 10-trial blocks each, one with KR provided on every second trial again, one without any KR. Sequence of KR- and No-KR-blocks was counterbalanced within each treatment group.

Subjects:

In all four experimental studies, subjects participating were physical education students from University of Heidelberg, and from Saarland University. In each study, subjects were randomly assigned to both the MAM- and the AMA-group. Differences between group-samples reported below resulted from dropouts or from subjects being eliminated from further data processing because of insufficient compliance with the above stated task requirements. Since previous studies showed that performance in all four tasks is unaffected by gender, we did not balance experimental groups with respect to sex of participants. 47 right-handed students took part in the *FT-Task* study, 23 (age: $\bar{x}$ [years] = 24.61; $s = \pm$ 2.13; 11 men, 12 women) in the "unguided" condition (MAM-group: n = 12; AMA-group: n = 11), and 24 (age: $\bar{x}$ = 24.16; $s = \pm$ 1.66; 11 men, 13 women) in the "guided" condition (MAM-group: n = 12; AMA-group: n = 12). There were 20 right-handed participants (age: $\bar{x}$ [years] = 22.4, $s = \pm$ 2.08; 14 men, 6 women) in the *DT-Task* study (MAM-group: n = 10; AMA-group: n = 10). 32 right-handed subjects (age: $\bar{x}$ [years] = 24.03; $s = \pm$ 1.56; 18 men, 14 women) were enrolled in the PT-Task study (MAM-group: n = 16; AMA-group: n = 16). 23 students (age: $\bar{x}$ [years] = 22.43, $s = \pm$ 2.39; 15 men, 8 women) participated in the *CMJ-Task* study (MAM-group: n = 12; AMA-group: n = 11).

Hypotheses

For all four experimental tasks, during acquisition considerable increase in performance was expected (hypothesis *H1*) . After acquisition was completed, according to the prevailing theoretical conceptions (e.g. Walker, 2005), further significant improvements in performance should be observed following a night of sleep, no matter, if subjects slept during the first or the second 12h interval of a 24h retention period (hypothesis *H2*). However, performance should remain unaltered during the respective 12 h retention intervals of wake following the Post-Training or the Retest 1 measure (hypothesis *H3*).

Statistics

For every performance measure, group means were calculated from individual subjects' means of number of trials performed per practice block during acquisition, as well as in Post Training, Retest 1, and Retest 2 respectively. We used Two-way ANOVAs to assess performance changes during acquisition, with one repeated measures factor ("within"-factor: "practice blocks"; "between"-factor: "Group"[MAM, AMA]). With respect to the retention period, statistical analysis is based on One-way ANOVAs for repeated measures (Post-Training, Retest 1, Retest 2) conducted separately for each experimental group (i.e. MAM & AMA). In addition, for each experimental group, two-tailed paired t-tests were calculated to evaluate performance differences across each 12 h interval separately (i.e. Post Training vs. Retest 1, and Retest 1 vs. Retest 2), whenever ANOVAs turned out to be significant. In case of violation of the sphericity assumption in ANOVAs incorporating a repeated measures factor, *df*-correction according to Huynh-Feldt was applied as provided by the statistics program. Regarding the Post Training-, Retest 1-, and Retest 2-blocks, there were no missing values in our data. Except for two data points in the PT-Task there was no further necessity to correct for outliers. Level of significance was set at α = 5%. Calculations were conducted with SPSS-PC, version 15.0.

Results

Acquisition

For all four experimental tasks, performance improved exponentially during the first three to four acquisition blocks, and progressed only slowly and more or less linearly thereafter until the end of acquisition (cf. Figure 3). Performance increases during acquisition were significant in all four experiments, as is shown by the repeated measures "within"-factor's results ($F_{[unguidedFTacquis-blocks: "speed"]}$ (4.711, 98.922) = 16.625, $p < .001$, $\eta_p^2 = .422$; $F_{[guidedFTacquis-blocks: "speed"]}$ (5.480, 120.599) = 28.290, $p < .001$, $\eta_p^2 = .563$; $F_{[DTacquis-blocks: TP]}$ (3.214, 57.853) = 18.907, $p < .0005$, $\eta_p^2 = .512$; $F_{[DTacquis-blocks: TMT]}$ (3.541, 63.744) = 7.59, $p < .0005$, $\eta_p^2 = .297$; $F_{[PTacquis-blocks: RMSE]}$ (7.395, 192,272) =

33.600, $p < .001$, $\eta_p^2 = .564$; $F_{[CMJacquis-blocks: AE]}$ (6.101, 128.114) = 14.168, $p < .0005$, $\eta_p^2 = .403$). There was no significant "between"-main effect "Group"$_{[MAM, AMA]}$ in any case ($p > .350$) except for the *PT-Task*, where a significant group difference was found for the acquisition period ($p = .004$), but no group-by-block interaction. Thus, in each experiment, acquisition proceeded quite similar in each of the two test groups (MAM and AMA). However, performance did not fully reach an asymptote in any of the tasks when considering both MAM- and AMA-groups combined. Altogether, these results confirmed our hypothesis *H1* in all four studies.

Retention

In the *FT-Task*, error- and speed-data for all experimental groups produced nearly identical results. Thus, for brevity, and following publication practice of most of the sleep research groups cited above, only the latter (i.e. the speed-data) are reported here. The ANOVAs yielded significant results for the "unguided" as well as for the "guided" condition ("unguided" condition: $F_{[speed-AMA]}$ (2, 20) = 10.800, $p = .001$, $\eta_p^2 = .519$; $F_{[speed-MAM]}$ (2, 22) = 6.763; $p = .005$, $\eta_p^2 = .381$; "guided" condition: $F_{[speed-AMA]}$ (2, 22) = 16.195, $p < .001$, $\eta_p^2 = .596$; $F_{[speed-MAM]}$ (2, 22) = 5.327, $p = .013$, $\eta_p^2 = .326$). Direction of within-group mean differences supported our theoretical expectations, that is: performance always increased considerably after a night of sleep (see hypothesis *H2*), but showed only little if any improvements after a 12h wake period either right after acquisition or during the day following the sleep interval (supporting hypothesis *H3*). This over-all picture was fully confirmed by the á-priori t-tests for the "guided" learning condition (i.e. significant performance improvements following a night of sleep; non-significant performance increments during daytime wake). In the "unguided" condition, however, sleep-induced improvements for the MAM-group sleep failed to reach the level of significance, although the respective p-value of .087 still indicates a trend in favor of our hypothesis *H2* (cf. Figure 4).

In the *DT-Task*, examination of both dependent measures (i.e. TP- and TMT-data) again produced very similar results. Therefore, only the outcome with respect to the *relative timing* structure of the sequence (i.e., its *Temporal Pattern*) will be reported here, as expressed by the percentage of deviation (PD) from the criterion TP of the movement sequence. Group-means of PD reached in the Post Training block of trials remained about the same for the next 24 h, when KR was provided during the retention tests. For both experimental groups, ANOVAs yielded only non-significant results ($F_{[PD-AMA]}$ (2, 18) = .392, $p = .681$, $\eta_p^2 = .042$; $F_{[PD-MAM]}$ (1.421, 12.792) = 1.456, $p = .262$, $\eta_p^2 = .139$), as did the respective paired t-tests ($p_{[two-tailed]} > .08$). Thus the temporal pattern (with KR provided) remained stable for at least 24 h at the quality reached after 100 practice trials, but was not enhanced by a night of sleep. KR-withdrawal in Retest 1 did not affect PD-scores in any of the two groups, as compared to the Post Training scores (paired t-tests$_{[Post\ Training-Retest1]}$; $p_{[two-tailed]} > .60$). No-KR-performance also remained stable during the second 12 h retention interval in both groups, as was confirmed by a 2 x 2-ANOVA with "Test" as a repeated measures factor (main effect$_{[Retest1-Retest2]}$: $p = .929$; interaction$_{[Group\ x\ Test]}$: $p = .177$). Thus, once again sleep as compared to wake did not exert any differential effect on the PD scores during a 24h retention period. (While Retest scores in the KR condition could be influenced by active learning again to some extent, only skill reproduction in the No-KR condition allowed assessment of the "pure" memory-based level of performance.) Altogether, these results are well in line with hypothesis *H3*, but do not support our hypothesis *H2*.

In the *PT-Task*, visual inspection of the RMSE-group means suggested performance in both groups to somewhat decrease during the first 12h retention interval, and then to increase again up to the post training level during the second 12h retention interval. These changes obviously were uninfluenced by the succession of wake and sleep periods, and covering the full 24h retention period, they in either group failed to reach level of significance, as was statistically confirmed for the AMA-group ($F_{[PT-AMA]}$ (2, 30) = 0.903, $p = .416$) as well as for the MAM-group ($F_{[PT-MAM]}$ (2, 30) = 3.150, $p = .057$). However, in the MAM-group, final compensation of performance losses suffered during the first 12h
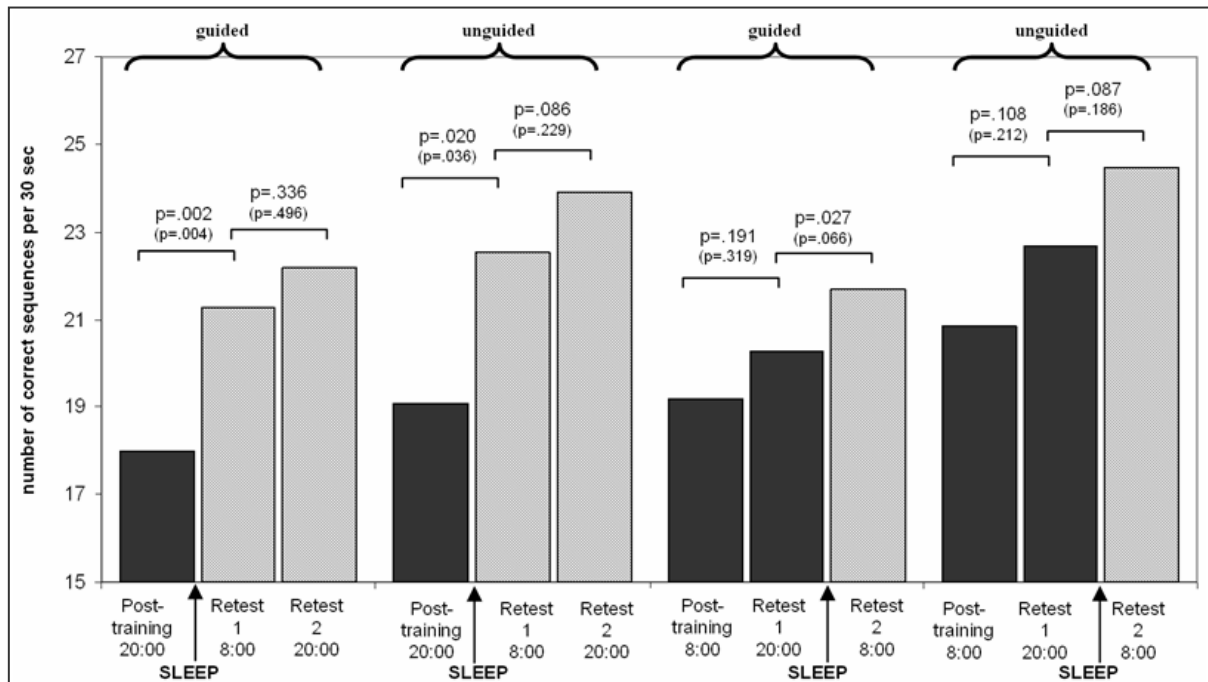
Figure 4

Differential effects of sleep and wake on retention scores across 24 h for the FT-task in the guided and unguided condition. Subjects in the AMA groups, trained in the evening (closed bars) immediately showed a significant improvement just 12 h after acquisition, following a night of sleep (Retest 1, hatched bars), but displayed no further significant improvement with an additional 12 h of wake (Retest 2, hatched bars). Subjects in the MAM groups demonstrated no significant improvement in performance following 12 h of wake (Retest 1, closed bars). However, following a night of sleep (Retest 2, hatched bars), performance improved significantly in the guided condition but not for the unguided condition. (P values in parentheses represent t-tests using an expected difference of 0.28 sequences (guided) and 0.46 (unguided), based on two trials of task repetition; cf. Walker et al., 2002).

retention interval (paired t-tests[Post Training-Retest1]; $p_{[two-tailed]}$ = .097) even turned out to be significant (paired t-test[Retest1-Retest2]: $p_{[two-tailed]}$ = .036). And for the AMA-group this final compensation effect still amounted to what might be regarded as a statistical trend (paired t-test[Retest1-Retest2]: $p_{[two-tailed]}$ = .078). As can be seen from development of performance scores per trial blocks across acquisition and retests (cf. 3), during retests subjects always started out at a level well below the one acquired at the end of the preceding Post Training- or Retest 1-block, and then exhibited marked improvements until the end of the respective test session. Thus we cannot rule out the appearance of warm-up decrements, namely after daytime retention intervals. This effect may also have contributed to the violation of hypothesis *H3*. However, a post-hoc correction for this possibility of transient warm-up decrements by excluding the very first trial block of

each retention test from further calculations did not alter the general results: Still, for both groups (MAM as well as AMA) the respective ANOVAs failed to reach significance ($p > .10$), and in both groups again performance exhibited slight performance increments during the last 12h retention interval again, independent of wake or sleep. This improvement was significant this time for the AMA-group only (paired t-test[Retest1-Retest2]: $p_{[two-tailed]}$ = .035). In total, these results once again go against our initial central hypothesis *H2* (sleep, and *only* sleep, should have affected performance in *both* experimental groups in the same way), and are hard to reconcile with hypothesis *H3*.

Finally, in the *CMJ-Task*, when KR was provided during retention tests, for both experimental groups ANOVAs did not reach level of significance ($F_{[CMJ-AMA]}$ (2, 22) = .882, p = .428, η_p^2 = .074; $F_{[CMJ-MAM]}$ (2, 20) = 2.522, p = .106, η_p^2 = .201),

and neither did any of the respective paired t-tests ($p_{[\text{two-tailed}]} > .20$). Again the level of performance acquired during 100 practice trials remained stable at least across a 24h retention interval, regardless of intermittent wake or sleep periods, as long as KR was provided on every second test trial, too. The slight increases of mean AE-scores observed in Retest 1 thus proved to be statistically irrelevant. However, in this force-parameter learning task, KR-withdrawal in Retest 1 and Retest 2 impaired performance significantly in both the AMA- and the MAM-group, as compared to the Post Training scores ($p_{[\text{AMA\_two-tailed}]} = .029$, $p_{[\text{MAM\_two-tailed}]} = .032$; paired t-tests$_{[\text{Post Training-Retest1}]}$). Only for the second 12h retention interval, performance across the No-KR retention test blocks remained stable again in both groups, as confirmed by a Two-way ANOVA with "Test" as a repeated measures factor (main effect$_{[\text{Retest1-Retest2}]}$: $p = .768$; interaction$_{[\text{Group x Test}]}$: $p = .182$). Clearly, the effect of sleep did not differ from that of wake in this experiment, no matter if KR was provided during retention tests, or not. Again, these results may be counted as evidence in favor of hypothesis *H3*, but do not support our central hypothesis *H2*.

Discussion

As becomes evident from our results, we successfully *replicated* sleep-related improvements in the production of newly acquired *sequential finger skills* (*FT-Task*) under different conditions (i.e., guided or unguided), when sleep followed initial learning within 24 h (i.e. either during the first, or during the second 12h retention interval). However, we *failed* to find any such effect of sleep in discrete motor tasks requiring precise production of (a) a specific relative *timing* pattern, or (b) a sub-maximal *force* impulse, and we also failed to find any specifically sleep-related effects on subsequent performance in (c) a continuous *pursuit-tracking* task. In these three tasks, performance either remained stable throughout the whole 24h retention period (*DT-Task; CMJ-Task*), or slightly decreased during the early and then improved again during the late 12h interval, no matter, if subjects slept or stayed awake (*PT-Task*).

Thus, temporal patterns (time domain), force parameters (proprioceptive domain), and non-speeded pursuit-tracking (visuo-motor domain) might not be amenable to sleep-related performance enhancements at all. That is, processes which control task features outside the spatial domain and other than sequencing activation of different muscle groups (as in the *FT-Task*) are possibly connected to memory systems, in which consolidation takes place just during the elapse of time, and where off-line learning is either absent, or at least independent from sleep. (It should be remembered here, that in our *DT-Task* spatial requirements were minimal and only one and the same finger was involved in pressing down all four keys in a row.)

There may be an additional, more general feature in these tasks preventing sleep-related processed to exert any specific effect on overt performance. This is the predominantly procedural type of memory representation, which is inherent to the *CMJ-Task*, and is induced by the implicit learning condition in the *PT-Task*. This notion is in line with the results obtained by Maquet et al (2003), who also used a visuo-motor pursuit-tracking task. As the authors state themselves, their study "was not designed to evaluate whether consolidation occurs exclusively during sleep", but was aimed at documenting sleep-related changes in brain activity following initial trajectory-learning by comparing the effect of sleep vs. sleep-deprivation (*not* vs. wake!). Moreover, in this study performance even improved after sleep-deprivation, i.e. throughout wakefulness.

The above conclusion also is supported by results from a number of recent studies, all employing though sequential finger tapping in form of a serial reaction time task, and all following an implicit learning paradigm. In this paradigm, unknown to the subjects, a regular pattern is interspersed with random sequences. The learning measure then is calculated from the difference in reaction time to the regularly patterned as compared to the random sequences. For this type of task Robertson et al. (2005) were able to prove development of explicit knowledge, i.e. *awareness* of the sequence structure, being prerequisite for off-line learning becoming strictly sleep-dependent (see also Robertson et al., 2004). Also, only for the explicit learners, overnight improvements of skill correlated positively with the amount of non rapid

eye movement (NREM) sleep, and negatively with the duration of REM sleep. However, in the implicit learning condition, performance enhancements equal in amount were found following any 12h retention interval, i.e. independent of wake or sleep. No correlations with sleep parameters were found here.

These findings have been corroborated very recently by several studies. For example, Song et al. (2007), showed that general skill (i.e., reduction of reaction times independent of patterned or random sequences) improved over daytime only, while sleep did not enhance general skill nor sequence-specific learning, when probabilistic motor finger tapping sequences were acquired implicitly. And Yordanova et al. (2008), whose subjects implicitly learned a finger tapping sequence in form of a number reduction task, showed slow wave sleep (SWS) early at night to turn implicit knowledge acquired during initial learning into an explicit sequence representation in some of their subjects, and REM sleep late at night instead to mainly stabilize the respective implicit representations without changing their structure.

Implicitly acquired movement sequences, which are characterized by predominantly non-declarative, procedural memory representations, according to these findings do not depend on sleep for any off-line learning. Performance enhancements without further practice in such skills, if they do occur at all, seem to just follow the elapse of time, and might to some extent be attributed to general skill improvement independent of any goal-specific regularity. If the subtle changes in performance observed in our *PT-Task* during the second 12h retention interval also result from such pattern-independent, general variations in the quality of eye-hand control, or if they rather have to be attributed to enhancement of some kind of effector-specific memory representation (see below), can presently not be decided on: Since we did not apply the typical implicit learning paradigm in our study, there were no random movements of the target cross at any time to assess general skill improvement. Also, we did not employ any task transfer to the untrained hand during retests in order to differentiate abstract and effector-specific representational codes.

Aside from the declarative-procedural dissociation with regard to general type of memory discussed above, there are even further reasons to differentiate wake- and sleep-dependent mechanisms of off-line learning, as has been shown by Cohen et al. (2005). Again, in this study a finger-tapping task was applied, in which subjects had to respond to visual cues as fast as possible (serial reaction time task). Subjects first implicitly acquired the 12-element sequence with the dominant (right) hand, and then were tested and retested 12h (main experimental groups) or 24h (diurnal groups) later using their non-dominant (left) hand. The 12h retention interval was either over day (wake), or over night (i.e., filled with sleep). During test and retest, half of the subjects were to reproduce the sequence according to the same spatial configuration as it had been initially learned with their right hand. To do this with their left hand now, they had to change the order of finger movements. The other half of subjects with their left hand were to obtain the original order of finger movements they had practiced with their right hand before (thus using homologous muscles in both hands). To do this, they now had to produce a spatial configuration different from the one initially learned, i.e. its mirror-version. This procedure resulted in a double dissociation: Off-line learning in the first group (identical spatial pattern) developed exclusively over a night of sleep, however, in the second group (homologous muscle activation pattern), although to a much lesser extent, exclusively over day (wake).

That is, motor skills organized according to an *abstract spatial representation* (or "goal") represented in an allocentric frame of reference might be facilitated only by *over-night sleep*, even if subjects do not have any explicit knowledge of that goal structure. *Effector-specific representations* of the same skills, to the contrary, might be facilitated only during a *daytime wake* period, as long as learning remains implicit. Interestingly, main experimental groups (12h retention periods) and the respective diurnal groups (24h retention periods) in the study by Cohen et al. (2005) yielded almost identical results. And as was shown by Cohen and Robertson (2007) in a follow-up study which incorporated the same task again, after a retention pe-

riod of 24 h effector-specific representations were fostered only, if acquisition took place in the morning (i.e. was immediately followed by a wake-period), while reproduction of the spatial sequence pattern improved only, if initial learning took place in the evening (i.e., was followed by night-sleep very soon).

It is suggested here (cf. Verwey & Clegg, 2005; Willingham, 1998), that learning and encoding spatial goals (i.e. successive target locations in allocentric space) at an abstract level largely recruits the parietal and – particularly - prefrontal cortices, while encoding effector-specific memories (reflecting e.g. locations in body-centered space) predominantly engages the primary motor cortex (M1). While the former show sleep-related activity changes, the latter decisively contributes to skill improvements over the day (Robertson et al., 2005). According to Willingham (1998), this differentiation of brain structures dominantly involved is also common to the dissociation of declarative and procedural memory systems discussed above. This view has been shared and elaborated by Keele et al. (2003). Based on an integrative review of numerous studies in the field of motor and neurosciences, these authors claim the existence of two distinct cortical networks engaged in developing different types of memory representations relevant to controlling motor skills. While the so-called "dorsal pathway" (including parietal cortex, supplementary motor area and primary motor cortex) is thought to be capable of forming intradimensional associations, the so-called "ventral pathway" (including occipital, temporal, prefrontal and lateral premotor cortex) is hypothesized to support the formation of interdimensional associations. Representations formed within unidimensional modules attributed to the more dorsal neural areas are inaccessible to awareness and thus linked to purely implicit learning, or leaning under dual-task conditions. Learning under conditions typically calling the multidimensional system into action is greater when accompanied by awareness, as is usually the case in explicit learning conditions, or with single-task practice. However, this more ventral multidimensional system can also be engaged during implicit learning. Therefore, according to the authors and challenging the implicit-explicit

distinction, the *crucial* system differences are to be seen in the respective *representational code* and its relation to attentional processes: While attention modulates the access of information to the multidimensional system (only attended stimulus- and response-regularities will be associated and then be *categorically* represented), the unidimensional system is able to extract unattended contingencies, but the respective representation then is *precategorical*, incorporating the "raw" stimulus or response features. Introducing this perspective on differences in representational code and the respective distinct neural memory systems to the problem-area of off-line motor memory consolidation might open up a promising avenue to provide an integrative theoretical basis, which would allow for uniting those seemingly diverse effects of learning conditions (implicit vs. explicit) and representational mode (abstract-spatial vs. effector-specific) on off-line performance improvements during sleep and/or wake, and thus could effectively stimulate future research.

All in all, sleep-related enhancements of motor learning then might be confined to skills, which require (a) *sequential* movements to different (b) *spatial* targets represented (c) *categorically* in an *allocentric* reference frame, or/and which are supported by a sufficiently (d) *declarative* memory component. Skills governed by precategorical memory representation, on the other hand, appear more apt to be enhanced by off-line learning during wake periods only, or may not even be improved at all without any further practice.

However, there still remain a number of unsettled issues. Two such questions waiting for further scrutiny we want to briefly address here. For one, it is unclear yet if the present picture might be extended to gross motor skills made up of composite *whole-body movements*. Although Erlacher et al. (in prep.) found a significant increase in amount of stage REM sleep ($p_{\text{[two-tailed]}}$ = .04), after 22 novices initially learned to perform a sequence of whole-body movements on a trampoline, but not after they had spent an equivalent amount of time cycling on an ergo meter, since behavioral data were not collected in that study, the significance of this result still needs to be clarified. Notwithstanding the considerable methodological expense it

thus seems pertinent to combinedly assess behavioral and sleep data in future studies of this kind. Following the research program outlined in the introduction section of this paper, we plan to systematically address this question of possible off-line learning in gross motor tasks in the near future.

The other issue to be commented on here has been raised again recently in a paper by Sheth et al. (2008). These authors, based on a detailed examination of the time course of performance across sleep in the finger tapping task, claim that practice beyond the initial fast improvements usually observed over the first three to four trial blocks in the acquisition phase, may cause a transient decrement in learning efficacy. Sleep-dependent performance enhancements then should be re-interpreted as a *restoration of the rehearsal-induced synaptic "fatigue"* of the neural circuitry specialized on that task. Clearly, this issue is still debated. However, if the proposed explanation holds true, this might explain why – at least until today – sleep-related enhancements in performance have only been found in the speeded *FT-Task*, but has been absent entirely in all those task which do *not* require successive activation of (different) muscle groups as fast as possible.

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