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The sleeping child outplays the adult's capacity to convert implicit into explicit knowledge

Ines Wilhelm[1,2], Michael Rose[3], Kathrin I Imhof[1], Björn Rasch[4], Christian Büchel[3] & Jan Born[1,5]

When sleep followed implicit training on a motor sequence, children showed greater gains in explicit sequence knowledge after sleep than adults. This greater explicit knowledge in children was linked to their higher sleep slow-wave activity and to stronger hippocampal activation at explicit knowledge retrieval. Our data indicate the superiority of children in extracting invariant features from complex environments, possibly as a result of enhanced reprocessing of hippocampal memory representations during slow-wave sleep.

Adult humans have unique capabilities to adapt their behavior to complex and continuously changing environments that are essentially based on conscious understanding, that is, an explicit knowledge of regularities in these environments. Although such understanding in some situations, for example, problems to be solved, can arise from a very sudden gain of explicit knowledge in the form of insight, understanding the complexity of everyday life more often arises from a rather gradual gain of explicit knowledge. In this process, representations of the complex stimulus patterns initially encoded implicitly and without full awareness become transformed and restructured such that more and more invariant and relevant features of these representations are enhanced to eventually enter consciousness[1]. This process of restructuring representations in memory to promote the extraction of explicit knowledge from implicitly encoded information is supported by sleep[2–5]. Indeed, the implicit-to-explicit conversion of knowledge has been proposed to be part of a system consolidation process occurring during slow-wave sleep (SWS), in which newly encoded representations stored temporarily in hippocampal networks are reactivated to be transformed and redistributed to neocortical networks for long-term storage[6].

Adults outperform children in virtually all cognitive domains. However, sleep is deeper in children and they show distinctly greater amounts of SWS as well as peak levels of slow-wave activity (SWA, that is, electroencephalographic (EEG) power in the frequency range of 0.5–4 Hz)[7,8]. Thus, we chose children as a model to study how sleep can facilitate the gain of conscious knowledge about rules and regularities underlying complex stimulus conditions. We trained 8–11-year-old children ($N = 35$) and 18–35-year-old adults ($N = 37$) on a motor sequence task that required them to repeatedly press a sequence of cued buttons (by light), as fast as possible, either in the evening before nocturnal sleep (children, $N = 16$; adults, $N = 16$) or in the morning before a wake period (children, $N = 19$; adults, $N = 21$). Participants were subsequently asked to freely recall the sequence in a recall test 10–12 h later (**Fig. 1a** and Online Methods).

Implicitly training the sequence, as expected, in both children and adults led to a significant gain of implicit knowledge, that is, a decrease in reaction times across training ($P < 0.001$; **Supplementary Fig. 1**). Training-induced sequence-specific knowledge was also confirmed in a separate control group of children, who

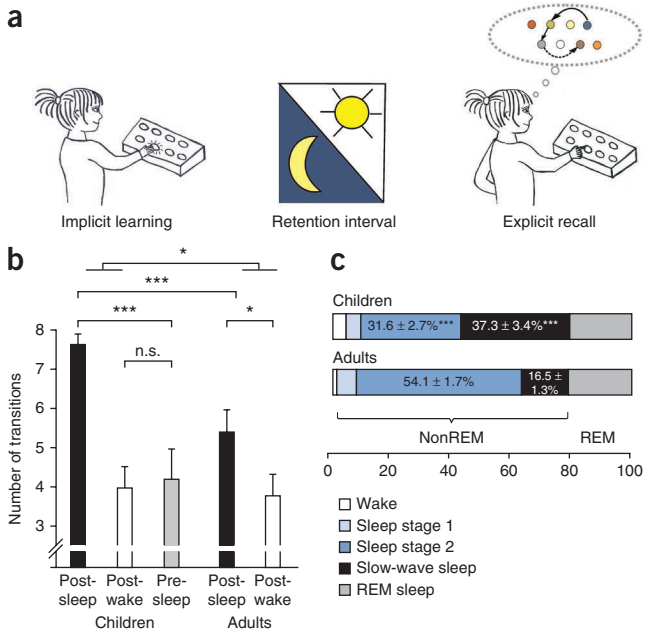

Figure 1 Experimental procedure, explicit sequence knowledge at retrieval testing, and sleep. (**a**) Children and adults were trained in the morning or in the evening on a motor sequence task (button-box task). After a 10–12-h retention interval filled with sleep (children, $N = 16$; adults, $N = 16$) or wakefulness (children, $N = 19$; adults, $N = 21$), retrieval of explicit knowledge about the sequence structure was examined. (**b**) Explicit sequence knowledge, as indicated by the number of recalled element transitions after sleep (black bars) and wake (white bars) retention intervals, and as tested in control children ($N = 14$) immediately after learning. Data are presented as mean ± s.e.m. $^{***}P \leq 0.001$, $^{*}P \leq 0.05$, n.s. = not significant ($P > 0.05$), for planned contrasts between groups. (**c**) Percent time spent in the different sleep stages (white, wake; light blue, stage 1 sleep; dark blue, stage 2 sleep; black, SWS; gray, REM sleep) in children (upper bar) and adults (lower bar).

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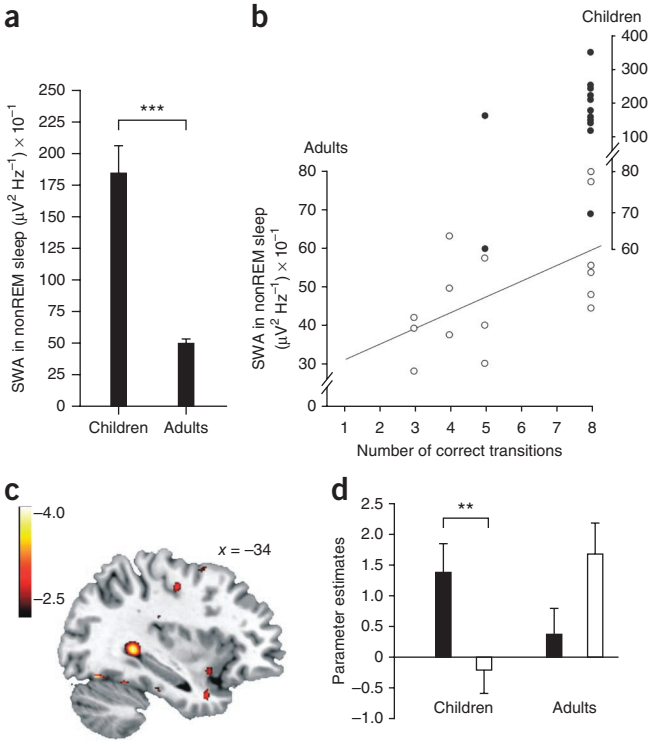

Figure 2 SWA during post-training sleep and BOLD signal responses during retrieval of explicit knowledge. (**a**) SWA during post-training nonREM sleep (recordings from frontal sites in which SWA is maximal) in children ($N = 13$) and adults ($N = 15$). (**b**) In adults (open circles), SWA during nonREM sleep was positively correlated with explicit knowledge during sequence recall after sleep ($r = 0.57$, $P = 0.026$). Because of the ceiling effect in children (filled circles)—that is, almost all showed perfect explicit sequence knowledge after sleep—a correlation with SWA could not be determined for this group. Recordings are from central sites where correlation was highest. (**c**) During retrieval of explicit sequence knowledge after retention sleep (black bars; children, $N = 16$; adults, $N = 16$) compared with wakefulness (white bars; children, $N = 15$; adults, $N = 15$), the left posterior hippocampus [–34, –44, 6] was activated to a greater extent in children than in adults (thresholded at $P_{SVC} < 0.05$). Color bar indicates z score. (**d**) Respective parameter estimates at the coordinates of local maxima. Note: values do not indicate absolute activation, but instead indicate relative increases during retrieval of learned sequences with reference to control task performance. Data are presented as mean ± s.e.m. $^{***}P \leq 0.001$, $^{**}P \leq 0.01$.

showed faster responses to sequence compared with random button presses (**Supplementary Fig. 1**). In comparison with the wake interval, sleep produced a significant increase in explicit knowledge of the motor sequence that was independent of age ($F_{1,68} = 27.50$, $P < 0.001$, sleep/wake main effect). The benefit from sleep was most notable in children, as almost all of them perfectly recalled the eight-element sequence after sleep (sleep, 7.63 ± 0.26 remembered transitions; wake, 4.00 ± 0.54; $t_{33} = 6.11$, $P < 0.001$; **Fig. 1b**). In the adults, the sleep-associated increase in explicit sequence knowledge was much smaller, although still significant (sleep, 5.44 ± 0.54 transitions; wake, 3.81 ± 0.53; $t_{35} = 2.11$, $P < 0.05$; $F_{1,68} = 3.97$, $P = 0.05$, sleep/wake × age interaction). Indeed, explicit knowledge after sleep was distinctly better in children than in adults ($t_{30} = 3.66$, $P = 0.001$). In contrast, after the wake interval, free recall of the motor sequence, although slightly better on average in children, did not significantly differ between age groups ($t_{38} = 0.25$, $P = 0.80$). Also, the gain in explicit sequence knowledge after sleep in children was highly significant in comparison with performance in control children ($N = 14$) that were asked to freely recall the sequence directly after the evening training (4.36 ± 0.71 remembered transitions, $t_{28} = 4.34$, $P < 0.001$), whereas performance after the wake retention interval did not differ from this control group ($t_{31} = 0.40$, $P = 0.68$). This pattern indicates a critical role of sleep for promoting explicit knowledge about the sequence[2–4].

Sleep was recorded during the night after learning in the sleep groups (**Supplementary Table 1** and **Supplementary Fig. 2a**). The time that children spent in SWS was threefold greater than that of adults (216.64 ± 18.99 versus 63.70 ± 5.04 min, $t_{27} = 7.78$, $P < 0.001$; **Fig. 1c**). Moreover in non–rapid eye movement (REM) sleep, EEG spectral power in the SWA range (0.6–4 Hz) was distinctly higher in children (1,841.19 ± 216.19) than in adults (498.25 ± 34.17, $t_{26} = 6.14$, $P < 0.001$; **Fig. 2a**). In adults, SWA during nonREM sleep was significantly associated with explicit knowledge of the motor sequence after sleep (frontal site, $r = 0.48$, $P = 0.074$; central site, $r = 0.57$, $P = 0.026$; parietal site, $r = 0.51$, $P = 0.055$; **Fig. 2b**). Similar positive correlations with explicit knowledge after sleep were revealed for the slow oscillation frequency band (0.6–1 Hz) for central and parietal sites (central, $r = 0.62$, $P = 0.018$; parietal, $r = 0.56$, $P = 0.039$) but not for frontal sites ($r = 0.18$, $P = 0.54$). In children, the same correlations could not be calculated because they showed nearly perfect motor sequence knowledge after sleep, that is, a ceiling effect (**Fig. 2b**). Thus, to evaluate the relationship between explicit knowledge at recall and SWA in children, we tested an additional group of ten children on a longer 16-element (rather than 8 element) sequence. This sequence prevented a ceiling effect and uncovered a strong correlation between frontal SWA and explicit sequence knowledge after sleep in children, similar to that in adults ($r = 0.79$, $P = 0.006$; for the 0.6–1-Hz slow oscillation band, $r = 0.68$, $P = 0.031$; **Supplementary Fig. 2b**).

We sought to identify the brain areas associated with explicit knowledge in children (sleep, $N = 16$; wake, $N = 15$) and adults (sleep, $N = 17$; wake, $N = 17$) in an additional study using functional magnetic resonance imaging (fMRI). To enable fMRI recording of retrieval-associated neuronal activity, we used an adjusted retrieval procedure in which the presentation of single sequence elements cued recall of the next two buttons (rather than free recall of the whole sequence; **Supplementary Table 2**). Control trials involved pressing buttons adjacent to the cue. Notably, compared with adults, explicit retrieval of sequence knowledge after sleep in children was associated with a higher blood oxygen level–dependent (BOLD) response (recall trials > control trials) in the left posterior hippocampus (MNI coordinates (mm) $x, y, z = -34, -44, 6$; sleep > wake × children > adults, $P_{SVC} = 0.032$; **Fig. 2c,d** and **Supplementary Table 3**). In previous fMRI studies, activation of this area was shown to be linked to the SWS-associated reprocessing and enhancement of declarative memories[9,10]. In addition, superior explicit sequence recall after sleep in children was associated with an increased activation in the superior frontal gyrus [8, –2, 64] and in the cuneus [–28, –64, 8] (sleep > wake × children > adults, $P_{SVC} = 0.016$ and $P_{SVC} = 0.060$; **Supplementary Table 4**), which are known to be involved in the recall of explicit sequence knowledge[11]. Notably, there were no differences in prefrontal cortex activation associated with superior explicit knowledge after sleep in children, although previous studies in adults have suggested that this region crucially contributes to the gain of insight during wakefulness[12,13].

Our finding that sleep enhances the extraction of sequence knowledge in implicitly learned materials, together with previous findings[2,4], corroborates the notion of an active system consolidation process during sleep in which newly encoded memory representations undergo qualitative changes that eventually promote the conscious

recollection of invariant structural features of these memories[6,14,15]. Notably, sleep in children was distinctly more effective in producing explicit sequence knowledge than in adults, with this effect being apparently linked to the distinctly higher SWA present in children. There is ample evidence indicating that SWA, particularly the <1-Hz slow oscillations, supports an active system consolidation process that involves the repeated reactivation and transformation of newly encoded hippocampal representations, which are integrated with pre-existing memories[6]. The hippocampus is centrally involved in the encoding of sequence structure, regardless of whether learned explicitly or implicitly, in adults[16] and children[17]. Thus, as SWA during retention sleep, as well as hippocampal activity at sequence recall, were enhanced in children, we propose that the enhanced explicit sequence knowledge is a result of a more effective SWA-driven reactivation and transformation of hippocampal task representations in this age group. This view does not exclude factors other than SWA that contribute to superior explicit knowledge extraction in children.

The capacity of sleep in children to promote the extraction of explicit knowledge about invariant patterns from implicitly encoded complex information is even more notable given that children perform worse than adults in most cognitive tasks. Moreover, previous studies have revealed sleep-dependent benefits in performance on various procedural and declarative memory tasks in children that were smaller or comparable to those seen in adults[18], which suggests that the superior generation of explicit knowledge is a specific advantage conveyed by children's sleep. The ability to generate explicit knowledge from implicitly encoded information is indeed fundamental to adaptive behavioral regulation, as the flexible transfer of knowledge to changing environmental demands is enabled only after explicit knowledge representations have formed[19,20].

METHODS

Methods and any associated references are available in the online version of the paper.

Note: Supplementary information is available in the online version of the paper.

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AUTHOR CONTRIBUTIONS

I.W. and K.I.I. conducted the experiments. I.W., B.R., M.R., J.B. and C.B. designed the experiments and analyzed the data. I.W., J.B. and C.B. wrote the paper.

COMPETING FINANCIAL INTERESTS

The authors declare no competing financial interests.

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ONLINE METHODS

Participants. 49 healthy children (8–11 years, mean ± s.e.m. = 9.58 ± 0.15 years) and 37 adults (23.94 ± 0.49 years) participated in the main experiment. Another 31 children (9.67 ± 0.26 years) and 34 adults (26.21 ± 0.69 years) participated in the supplementary fMRI study and ten children (9.60 ± 0.45 years) participated in the additional control experiment (employing a longer 16-element sequence for motor sequence learning). Interviews with the parents and children and standardized questionnaires ensured that the children had no behavioral problems, cognitive impairments or sleep disorders. Neither the children nor adults had a history of any neurological or psychiatric disorders, nor were they taking any medication during the experiment. Ingestion of caffeine or alcohol was not allowed on experimental days. Subjects were asked (by questionnaire) for individual sleep habits: usual time to go to bed, time getting up, etc. All subjects reported following a regular sleep-wake schedule. None of the adults had been on a night shift for at least 6 weeks before the experiment. Participants of the main experiment were adapted to polysomnographic recordings on a night preceding the experiment proper. The study was approved by the ethics committee of the University of Luebeck and participants and the children's parents gave informed consent before participation. In the main experiment, data from two children and one adult did not enter sleep analyses because of EEG artifacts and data from one additional child did not enter the EEG power analyses because of EEG artifacts in F3 and F4. Data from three adults were excluded from the fMRI analyses because of scanner artifacts. Data from four subjects (one child from the sleep group, one child from the sleep-control group and one adult from the sleep group in the main experiment, and one child from the fMRI experiment) were excluded from analyses of learning performance because of technical problems with data acquisition.

Design and procedure. Children and adults were randomly assigned to the sleep and wake groups at a fixed ratio of 1:1. All participants performed on the motor sequence learning task (button-box task described below) in their home environment and they also slept at home. In the sleep group, the learning phase of ~15 min took place between 7:00 and 9:15 p.m. for children, and between 10:00 and 12:15 p.m. for adults. Thereafter, participants of both age groups went to bed, so that lights were turned off at the habitual bedtime (between 7:30 and 9:30 p.m. for children, between 10:30 and 12:30 p.m. for adults). In the next morning participants were awakened at their usual time. Retrieval testing took place ~60 min later. The interval between learning and retrieval testing averaged 12 h in children and 10 h in adults. In the wake group, learning took place in the morning ~60 min after awakening from night-time sleep and retrieval was tested after a retention interval of wakefulness that likewise lasted ~10 (adults) or ~12 (children) h. During the wake retention interval participants followed their daily schedules. The parents kept a continuous record of their children's activities (asking for their activities every hour) to control for possible disturbing events or interfering cognitive activities. Adult participants kept this record themselves. Before retrieval testing participants rated their subjective tiredness and motivation (**Supplementary Table 4**). An additional control group of children learned the task in the evening (like the sleep group) but retrieval was tested immediately after the learning phase. A further group of children learned a prolonged 16-element sequence in the evening and explicit sequence knowledge was tested after retention sleep. Procedures of the additional fMRI study were basically similar (see below); however, no polysomnographic recordings were performed when participants slept at home.

Memory task. To investigate memory consolidation, we used the button-box task, which is an implementation of a motor sequence learning task that is specifically adapted to the motor abilities of children. The button box is a white 50-cm × 22-cm × 7-cm box with eight colored buttons placed on its upper panel in two rows, which are consecutively flashed up according to a repeating eight-element sequence (4-2-5-7-6-3-1-8, with the upper buttons referring, from left to right, to the numbers 1, 2, 3 and 4, and the lower buttons to the numbers 5, 6, 7 and 8). In the group of subjects who learned the 16-element sequence, an extended button box with 16 buttons was used. Participants were instructed to press the button flashing up as fast as possible with the non-dominant (left) hand. At learning, participants performed ten blocks (each including five eight-element sequences). After each block, a short break was made to provide the participant with feedback (on a computer screen) about the mean reaction time during this block. For implicit learning, the speed of button press responses was analyzed as mean reaction time in each block.

To assess (at retrieval testing) explicit knowledge of the sequence trained on the button-box task, participants stood in front of the button box and were asked to recall the sequence by pointing at the buttons in the same order as they flashed up during the learning phase. Before recall, subjects were instructed to guess in case they were unable to recall the complete sequence. No additional instructions were given, for example, where to start or when to finish the recall of buttons. As a measure of explicit sequence knowledge, the number of correct transitions, that is, of the correct recall of two buttons in a row was used, yielding a possible maximum score of eight. The validity of this recall procedure as a measure of explicit sequence knowledge was confirmed in separate control experiments in 11 children (8–11 years) in which we compared this recall procedure (after sleep) with a more conservative procedure of explicit knowledge recall, that is, the subjects were asked to freely recall the sequence by naming numbers (1 to 8) that had been attached to the buttons immediately before recall testing. Both measures of recall were highly correlated (Pearson's correlation coefficient $r = 0.98$, $P < 0.001$).

In the fMRI experiment, the button-box task was adjusted to the specific requirements of the magnetic resonance environment, that is, to reduce movement artifacts, the button box was constructed smaller with the distance between the buttons being also shorter (panel size = 24 × 12 cm). The button box was placed on the subject's thighs (fixated by a vacuum cushion). A mirror was integrated in the coil above the head such that the participant saw the buttons on the button box without turning his or her head. At retrieval testing, six blocks of sequence recall alternated with six blocks of a control task, with each block including eight trials. Sequence and control blocks were separated by a 20-s interval during which participants received oral feedback about the average reaction time in the previous block and the information about the type of task (sequence recall versus control task) in the upcoming block. Each trial started with flashing one of the eight buttons of the button box. For the blocks of sequence recall, the participants were asked to imagine the two buttons succeeding this button in the sequence they had trained in the learning phase. After four seconds the button illumination turned off, and only then were participants allowed to actually press the two imagined buttons of the sequence. The next trial started with a variable inter-trial interval of 4–10 s. The amount of explicit knowledge was indicated by the number of correctly retrieved sequence triplets. In the control blocks, participants were asked to press two of the buttons adjacent to the button that had flashed, as soon as the button light had turned off, that is after 4 s. Explicit sequence knowledge was also tested in these participants after scanning via the same free recall procedure as was used in the main experiment.

Analysis of behavioral data. Statistical analysis of reaction times during implicit learning was based on 2 × 2 × 10 analyses of variance (ANOVA) including the two group factors age (children, adults) and sleep/wake representing the two kinds of retention intervals, and a repeated measures factor block representing the ten blocks of training. Retrieval of explicit sequence knowledge after the retention interval was analyzed using a 2 (age) × 2 (sleep/wake) ANOVA. *Post hoc* comparisons and comparisons of sleep parameters between children and adults were performed using *t* tests. Sleep parameters were correlated with explicit sequence knowledge at retrieval using Pearson's correlation coefficients.

Sleep and EEG recordings. Sleep was recorded by standard polysomnography, including electroencephalographic (EEG), electromyographic and electrooculographic recordings. EEG was recorded from F3, F4, C3, C4, P3 and P4 (according to the International 10–20 System) in the main experiment, and from F3, F4, Fz, C3, C4, Cz and Pz in the group of children tested with the prolonged 16-element sequence. Recordings were referenced to an electrode attached to the nose. To ensure high sleep quality, we recorded the subjects' sleep at their homes using a portable amplifier (SOMNOscreen EEG 10–20, Somnomedics). EEG signals were sampled at 256 Hz and filtered between 0.03 and 35 Hz. Recordings were visually scored offline according to standard criteria[21].

Power spectral analysis of the EEG signal was performed using Fast Fourier Transformation on all recording sites and separately for periods of nonREM (stages 2, 3 and 4) and REM sleep. The spectra were calculated for successive 8-s artifact-free intervals (2,048 data points) using a Hanning window to taper the data. Power density ($\mu V^2\ Hz^{-1}$) was computed for three frequency bands of

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interest: SWA (0.6–4 Hz), theta activity (5–8 Hz) and spindle activity (11–15 Hz). Average power for these bands was calculated first over all bins in the frequency range of interest; averages were then calculated for the succeeding 8-s intervals. For statistical analyses, log-transformed power values were subjected to ANOVA that included factors representing the three frequency bands and two age groups. For correlation analyses between SWA and explicit knowledge, means over all frontal, central and parietal electrodes, respectively, were calculated.

In the sleep groups of the additional fMRI experiment, adult participants themselves kept a record about sleep duration and quality in the night after the learning phase. For children, their parents kept this record. On these nights, children slept on average 9.6 ± 0.3 h and woke up 0.7 ± 0.3 times per night. Adults slept 8.0 ± 0.76 h and woke up 1.2 ± 0.3 times per night.

fMRI data acquisition and processing. Functional imaging was performed on a 3T Siemens Trio MR scanner with a 12-channel phased array head coil. We acquired 40 axial slices using an echo-planar (EPI) T2* weighted imaging sequence with a voxel size of 2 × 2 × 3 mm (repetition time = 2.56 s, echo time = 30 ms, flip angle = 90°, field of view = 208 mm^2, matrix = 104 × 104).

The five initial scans were discarded from the analysis to account for magnetic saturation effects. Preprocessing and data analysis were performed using Statistical Parametric Mapping (SPM8, Wellcome Department of Cognitive Neurology, University College London) under Matlab R2008a. Images were realigned, normalized into standard anatomical space (MNI) and smoothed with a Gaussian kernel of 6 mm full width at half maximum. For each participant, evoked hemodynamic responses to event types were modeled with a delta (stick) function corresponding to the stimulus presentation convolved with a canonical hemodynamic response function within the context of a general linear model. The onsets were synchronized with the illumination of the cue button. The data were filtered using a 128-s cut-off high-pass filter to account for low-frequency drifts. Individual contrast images (recall trials > control trials) from all volunteers were entered into a second-level (random effects) analysis. Linear contrasts were used to analyze main effects (recall trials > control trials) and interactions of the two factors sleep/wake and age (sleep > wake; sleep > wake × children > adults; sleep > wake × adults > children). Statistical inferences were performed for all contrasts at a threshold of $P < 0.05$ (family-wise error rate corrected) correcting for multiple comparison in volumes of interest. Areas of interest (10-mm sphere) were taken from previous studies focusing on effects of sleep on consolidation of motor sequences[22,23]. Additional coordinates were taken from a study that applied a comparable approach (a generation task) to test explicit knowledge on a motor sequence learning task[24].

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In the version of this article initially published online, author names Björn Rasch and Christian Büchel were misspelled Björn Rasch and Christian Büechel. The error has been corrected for the print, PDF and HTML versions of this article.