SLEEPJ, 2022, 1–13

https://doi.org/10.1093/sleep/zsac025
Advance Access Publication Date: 28 January 2022
Original Article

ORIGINAL ARTICLE

A sleep schedule incorporating naps benefits the transformation of hierarchical knowledge

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Abstract

Study Objectives: The learning brain establishes schemas (knowledge structures) that benefit subsequent learning. We investigated how sleep and having a schema might benefit initial learning followed by rearranged and expanded memoranda. We concurrently examined the contributions of sleep spindles and slow-wave sleep to learning outcomes.

Methods: Fifty-three adolescents were randomly assigned to an 8 h Nap schedule (6.5 h nocturnal sleep with a 90-minute daytime nap) or an 8 h No-Nap, nocturnal-only sleep schedule. The study spanned 14 nights, simulating successive school weeks. We utilized a transitive inference task involving hierarchically ordered faces. Initial learning to set up the schema was followed by rearrangement of the hierarchy (accommodation) and hierarchy expansion (assimilation). The expanded sequence was restudied. Recall of hierarchical knowledge was tested after initial learning and at multiple points for all subsequent phases. As a control, both groups underwent a No-schema condition where the hierarchy was introduced and modified without opportunity to set up a schema. Electroencephalography accompanied the multiple sleep opportunities.

Results: There were main effects of Nap schedule and Schema condition evidenced by superior recall of initial learning, reordered and expanded memoranda. Improved recall was consistently associated with higher fast spindle density but not slow-wave measures. This was true for both nocturnal sleep and daytime naps.

Conclusion: A sleep schedule incorporating regular nap opportunities compared to one that only had nocturnal sleep benefited building of robust and flexible schemas, facilitating recall of the subsequently rearranged and expanded structured knowledge. These benefits appear to be strongly associated with fast spindles.

Clinical Trial registration: NCT04044885 (https://clinicaltrials.gov/ct2/show/NCT04044885).

Statement of Significance

Learning of complex material benefits from building on prior knowledge of both the structure and the content of the material to be mastered. Schemas refer to such structures and while their benefits have been evaluated in several contexts, sleep is not one of them. We found that providing a schema helps initial learning of a hierarchical sequence as well as its subsequent transformation. Given a total sleep budget of 8 h over 24 h, a sleep schedule incorporating daily nap opportunities proved superior to the one where only nocturnal sleep opportunity was provided for the learning task used here. Fast sleep spindles but not slow-wave metrics were associated with better memory performance and dynamic transformation of the learned schema. The multiple phases and repeated testing within subjects provide robust support for our findings.

Key words: schema; prior knowledge; nap; memory consolidation; memory reactivation; sleep spindles

Submitted: 24 September, 2021; **Revised:** 14 December, 2021

Introduction

Prior knowledge structures serve as the foundation for the formation of cognitive frameworks or schemas that facilitate learning and memory [1–3]. These dynamic knowledge representations benefit encoding, consolidation, and retrieval of information [4–7]. To sustain continued learning, schemas should accommodate advances in knowledge that inevitably occur [8]. This adaptability involves *assimilation*, the ability to incorporate novel information into existing knowledge structures, as well as *accommodation*, referring to the flexible updating process that entails schema modification to handle incongruent information [4]. Understanding the mechanisms involved in the dynamic transformation of schemas can inform strategies to optimize learning through the building of robust and adaptable knowledge representations. To date, most studies investigating schema-based learning have focused on the cognitive benefits of these knowledge structures, rather than exploring their dynamic adaptation. This is especially relevant in settings that require one to progressively expand and update existing schemas to keep up with advances in knowledge.

The contents of memoranda may be transformed during sleep, prioritizing what was learned [9], drawing out insights [10, 11], and making inferences [12, 13]. Modern lifestyles shorten nocturnal sleep, fueling interest in whether regular daytime naps might compensate for reduced night-time sleep. Recent research conducted in adolescents suggests that mid-afternoon naps which boost attention are beneficial in sleep schedules where nocturnal sleep is suboptimal in duration [14]. Such naps also benefit the learning of organized facts that engage long term memory [15]. However, it remains an open question whether the benefits of naps extend to the integration of altered and expanded knowledge based on previously constructed schemas, and how this may take place over recurrent nap opportunities. Supporting this possibility, it was recently found that schemas may be updated in light of inconsistent information during a 48-h consolidation opportunity that contained sleep [16].

A final topic of interest lies in the electrophysiological mechanisms supporting the accommodation of new knowledge into existing frameworks. Sleep spindles play an active role in memory reactivation, facilitating sleep-dependent memory consolidation [17–19]. The reactivation of overlapping memory traces during sleep may contribute to the formation of schemas [7], and facilitate the abstraction of generalized knowledge frameworks [20]. Moreover, sleep spindles appear to support the integration of novel information into pre-existing knowledge structures [21, 22].

Here we investigated the effects of daytime napping on schema adaptation (accommodation and assimilation) using a dynamic schema-based learning protocol, within a lab-in-a-school setting [23]. We studied adolescents in view of how common inadequate sleep is in this group and the importance of learning and memory to their future success. These were randomized to either an 8 h Nap (6.5 h nocturnal sleep plus a 90-minute mid-day nap) or 8 h No-Nap (nocturnal-only sleep) schedules (Figure 1). We hypothesized that sleep would preferentially facilitate schema-related memory consolidation and that a sleep schedule incorporating mid-day naps would benefit schema accommodation and assimilation. We also predicted that these schema-driven memory benefits would be more consistently associated with sleep spindles rather than slow-wave sleep (SWS).

Methods

Participants

We evaluated 57 healthy adolescents (29 males, aged 15–19 years) with no history of sleep disorders recruited from schools across Singapore. Participants were excluded if they had known psychiatric conditions, a body mass index of ≥ 30, a history of smoking, and if they consumed more than two cups of caffeinated beverages per day. We also excluded habitual short sleepers as assessed with actigraphy (time in bed of <6 h during weekdays and sleep extension of <1 h on weekends). Participants were not allowed to travel across two or more time zones a month prior to study. Full details of the study protocol are described elsewhere [23]. Four participants withdrew due to respiratory infection or for personal reasons during the first three nights prior to the main experiment, resulting in a final sample of 53. These students were randomly assigned to the Nap ($n = 24$) or No-Nap ($n = 29$) groups. There were no significant differences in the baseline demographic characteristics and routine sleep patterns between the two groups (Table 1).

The study was approved by the National University of Singapore Institutional Review Board and was conducted in accordance with the ethical standards of the 1964 Helsinki declaration. All participants and legal guardians provided written informed consent. The study was a registered clinical trial (https://clinicaltrials.gov/ct2/show/NCT04044885).

Study protocol

The 15-day protocol (depicted in Figure 1) commenced with all participants undergoing two baseline adaptation nights (B1–B2) of 9-h nocturnal sleep opportunity (11:00 pm–08:00 am). The protocol contained two sleep manipulation periods ($M1_1$–$M1_5$) and ($M2_1$–$M2_3$). The manipulation involved how 8 h of sleep opportunity over 24 h was split: in one group (No-Nap) this was all nocturnal sleep: (11:30 pm–07:30 am) while the other group (Nap) received 6.5 h nocturnal sleep (00:15 am–06:45 am) plus a 1.5 h mid-day nap opportunity (2:00 pm–3:30 pm). The first 5-day sleep manipulation period simulated a school week ($M1_1$–$M1_5$), and the two recovery nights of 9-h nocturnal sleep opportunity that simulated weekend sleep ($R1_1$–$R1_2$). This was followed by a second cycle of an attenuated "school week" ($M2_1$–$M2_3$) and "weekend" ($R2_1$–$R2_2$).

The schema-learning paradigm consisted of four phases: Initial learning of the schema ($M1_3$ 9 pm–$M1_4$ 9 am), Schema accommodation ($M1_4$ 9 am–$M1_5$ 9 am), Schema assimilation ($M1_5$ 9 am–$M2_1$ 9 pm), and Schema Restudy ($M2_1$ 9 pm–$R2_1$ 9 pm).

Schema-learning task

We employed a schema-based learning paradigm based on transitive inference [24]. This paradigm incorporates optimal features of a schema-learning task: associative structure, adaptability and schema-driven facilitation of inference [25], and has been previously used and validated [26–28].

Phase 1: Initial schema acquisition

Here, the base schema was introduced. Two learning periods were separated by a 10-minute break. In Phase 1a, the initial

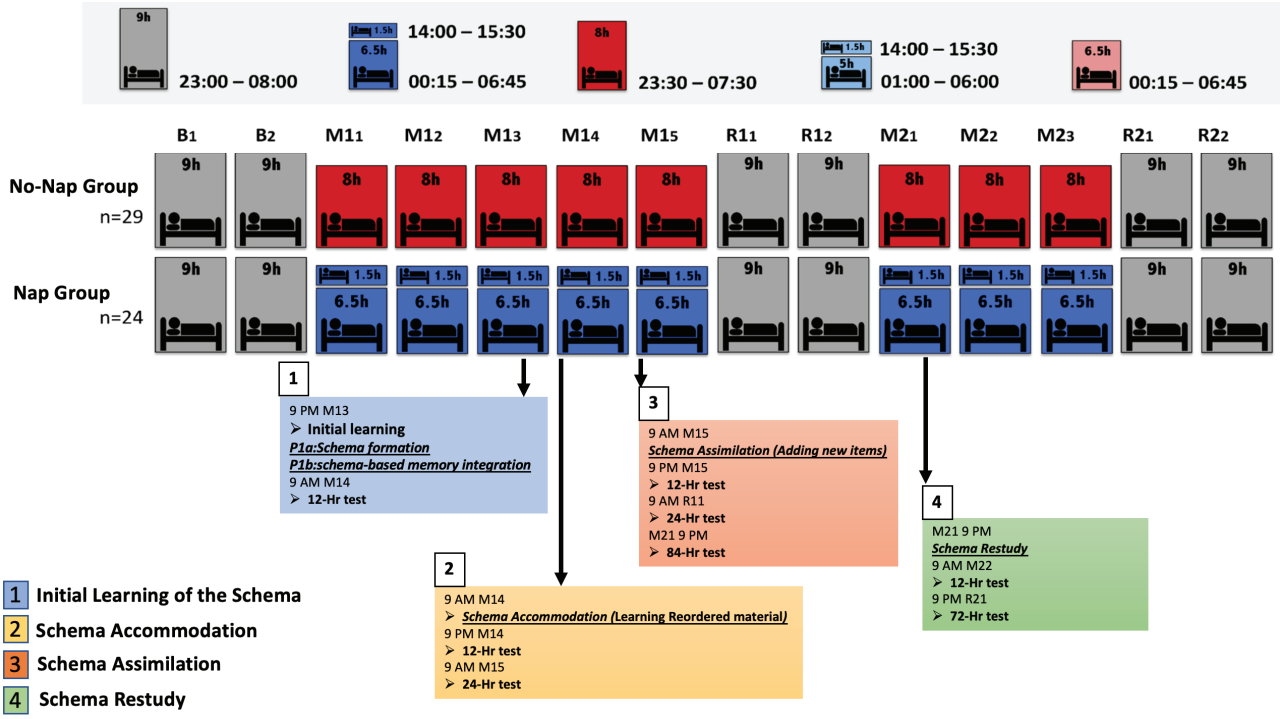

Figure 1. Study protocol and schema-learning sessions. The experiment consisted of two baseline adaptation nights and two sleep manipulation periods which included two recovery nights. Polysomnography was conducted during nights and naps on B2, $M1_5$, $R1_1$, $M2_1$, $M2_3$, and $R2_1$. The schema-learning paradigm consisted of four phases, each involving immediate and delayed test sessions: *Initial learning* (immediate test, 12-h test), *Schema accommodation* (immediate test: 12-h test, 24-h test), *Schema assimilation* (immediate test, 12-h test, 24-h test, 84-h test), and *Schema restudy* (immediate test, 12-h test, 72-h test).

Table 1. Characteristics of Nap and No-Nap groups

	Nap group (N = 24)		No-Nap group (N = 29)	
	Mean	*SD*	Mean	*SD*
Age (years)	16.72	1.16	16.18	0.88
Gender (% male)	45.83	—	48.28	—
Body mass index	20.17	3.13	20.49	3.08
Daily caffeine intake (cups)	0.63	0.82	0.72	1.00
Morningness-eveningness questionnaire	48.83	6.80	49.45	6.18
Epworth sleepiness scale	7.42	3.09	7.66	3.04
Chronic sleep reduction questionnaire	37.00	5.23	36.59	4.04
Pittsburgh sleep quality index				
Weekday TIB (h)	7.36	1.16	7.59	1.38
Weekend TIB (h)	9.10	1.32	8.52	1.32
Weekday TST (h)	6.87	1.22	6.62	1.00
Weekend TST (h)	8.78	2.19	8.43	1.25
Nap TST (min)	58.54	60.00	42.59	53.71
Global score	4.22	1.24	4.48	1.70
Actigraphy				
Weekday TIB (h)	7.22	0.85	7.21	0.74
Weekend TIB (h)	8.40	1.17	8.36	1.04
Weekday TST (h)	5.74	0.84	5.73	0.65
Weekend TST (h)	6.74	1.26	6.65	0.94
Average TST (h)	5.98	0.78	5.97	0.58
Sleep efficiency	79.85	6.87	79.45	6.10

Data collected during the briefing session and participants' sleep were monitored with actigraphy a week before the study began. No significant group contrasts were observed from independent *t*-tests and Chi-squared tests.
TIB, time in bed; TST, total sleep time.

schema was introduced. In Phase 1b, schema-related memory integration took place (Schema condition). Separately, participants also learned a set of completely novel, unrelated faces (No-schema condition). Following the completion of Phase 1b, participants underwent an immediate test and 12 h later, a delayed test session was conducted, the following morning.

Phase 1a: Learning the schema to criterion

Participants learned the order of seven individuals' rankings on a hypothetical test. Face pictures were selected from a set of 50 males and 50 females in neutral, frontal pose (Stirling database: http://pics.stir.ac.uk/2D_face_sets.htm). Learning was based on trial and error with active feedback given via alternating learning and test blocks until subjects reached a criterion of > 85% accuracy to facilitate the formation of a schema of the hierarchy. During the learning blocks, participants were presented with faces of two adjacent persons in the hierarchy (A–B, D–C, F–E, B–C, etc., 12 learning trials per block) and were asked: "Who scored higher?". Participants were encouraged to play an active role in learning by responding. Regardless of whether they responded or not, the correct answer was highlighted in green. Nonadjacent pairs (A–C, B–D, etc.) were not presented during learning.

Each learning block was followed by an evaluation block where subjects were tested for the learned adjacent pairs (six per block), and nonadjacent items (inference pairs, four per block) that were not encountered during learning (Figure 2A). Feedback was not provided in test blocks. Transitive inference (that is, if A > B and B > C then A > C) was required to correctly answer the questions on the nonadjacent pairs. Once 85% accuracy was reached, this phase automatically concluded. A provision for up to 20 learning and testing blocks was made to reach this learning criterion. However, participants required (M = 9.2, *SD* = 3.6) learning blocks on average to reach the criterion.

Phase 1b: Schema-related memory integration versus the No-schema condition

Following 10-minute break, participants learned a novel set of rankings under two conditions. In the Schema condition, participants learned a hierarchy where new faces were intercalated with familiar faces from Phase 1a. In the No-Schema condition, participants were presented with a completely novel hierarchy involving new faces. Participants underwent six alternating learning and test blocks for each of the Schema and No-schema conditions. The order of conditions was interleaved. Faces, right/left screen positioning, and presentation order of pairs were counterbalanced and randomized in all phases (Figure 2B).

Phase 2: Schema accommodation (learning the reordered material)

In this phase, and for both groups, the order of four individuals in the ranking hierarchy was updated. They had three alternating learning and test blocks to accommodate the inconsistent information and learn the reordered schema (Figure 3A). The immediate test session was at 9 am on $M1_4$, followed by the 12-h delayed test at 9 pm the same day, and the final 24-h delayed test the next morning at 9 am on $M1_5$.

Phase 3: Schema assimilation (additions to the reordered material)

In this phase 3, new items were added to the previously reordered hierarchies for both Schema and No-schema conditions. Participants had three alternating learning (with active feedback), and test blocks to study the new sets, each comprising 12 items (Figure 3B). Participants underwent four test sessions as follows: immediate test: 9 am $M1_5$, 12-h delayed test: 9 pm $M1_5$, 24-h delayed test: 9 am $R1_1$, 84-h delayed test following the simulated weekend: 9 pm $M2_1$.

Phase 4: Schema restudy (revision of the reordered and expanded material)

Following the simulated weekend, participants were given an opportunity to review the final hierarchy in a single learning block with active feedback. They were then tested over three sessions that were organized as follows: immediate test at 9 pm on $M2_1$, 12-h test at 9 am on $M2_2$, and a 72-h test at 9 pm on $R2_1$.

Polysomnography data acquisition and analyses

Polysomnography (PSG) data were collected on B2, $M1_5$, $R1_1$, $M2_1$, $M2_3$, and $R2_1$ covering naps as well as nocturnal sleep and using a SOMNOtouch recorder (SOMNOmedics GmbH, Randersacker, Germany). Electroencephalography (EEG) was recorded from C3 and C4, referenced to the contralateral mastoids (A1, A2), with Cz and Fpz as common reference and ground electrodes following the international 10–20 system. Electrooculography and electromyography of chin muscles were also recorded for sleep staging. Impedance was < 5 kΩ before the start of recording.

PSG data were first visually inspected for technical deficiencies, before being scored using the Z3Score algorithm (https://z3score.com), which has been previously validated [29] followed by a final manual review. Scoring of the sleep stages (N1, N2 and N3, rapid eye movement, and wake after sleep onset) was performed based on 30-second epochs using the American Academy of Sleep Medicine Manual criteria [30]. Records with higher than 10 percent artifacts were removed from the final analyses. We used Wonambi Python package, v5.24 (https://wonambi-python.github.io) for automatic spindle detection with a well-known algorithm. Previous research [31] suggests that slow (~9–12 Hz) and fast (~12–15 Hz) spindles are functionally and topographically distinct [31, 32]. Slow spindles are more commonly seen in frontal areas and are associated with general cognitive abilities and learning efficiency [33], whereas fast spindles are seen in centroparietal areas and associated with complex cognitive abilities such as fluid intelligence [34]. The (~9–12 Hz), and (~12–15 Hz) criteria for the spindle classification was based on the Mölle algorithm used for automatic spindle detection [31] and has been used in prior studies involving adolescents [35, 36]. Following procedures described previously [37], spindle count and density (counts per minute) were obtained for both N2 and N3 sleep stages. See Supplemental Materials for further details regarding the performance of the selected spindle detection method (Supplementary Figures 1 and 2). Slow-wave activity (SWA), and slow-wave energy (SWE) as integrated power in the delta band (0.5–4 Hz) were calculated [38], and slow oscillations were also identified as events using previously published methodology [31].

Statistical analyses

For each phase, we assessed memory performance (percentage of correct decisions) using mixed analysis of variances (ANOVAs) to investigate consolidation of memories across

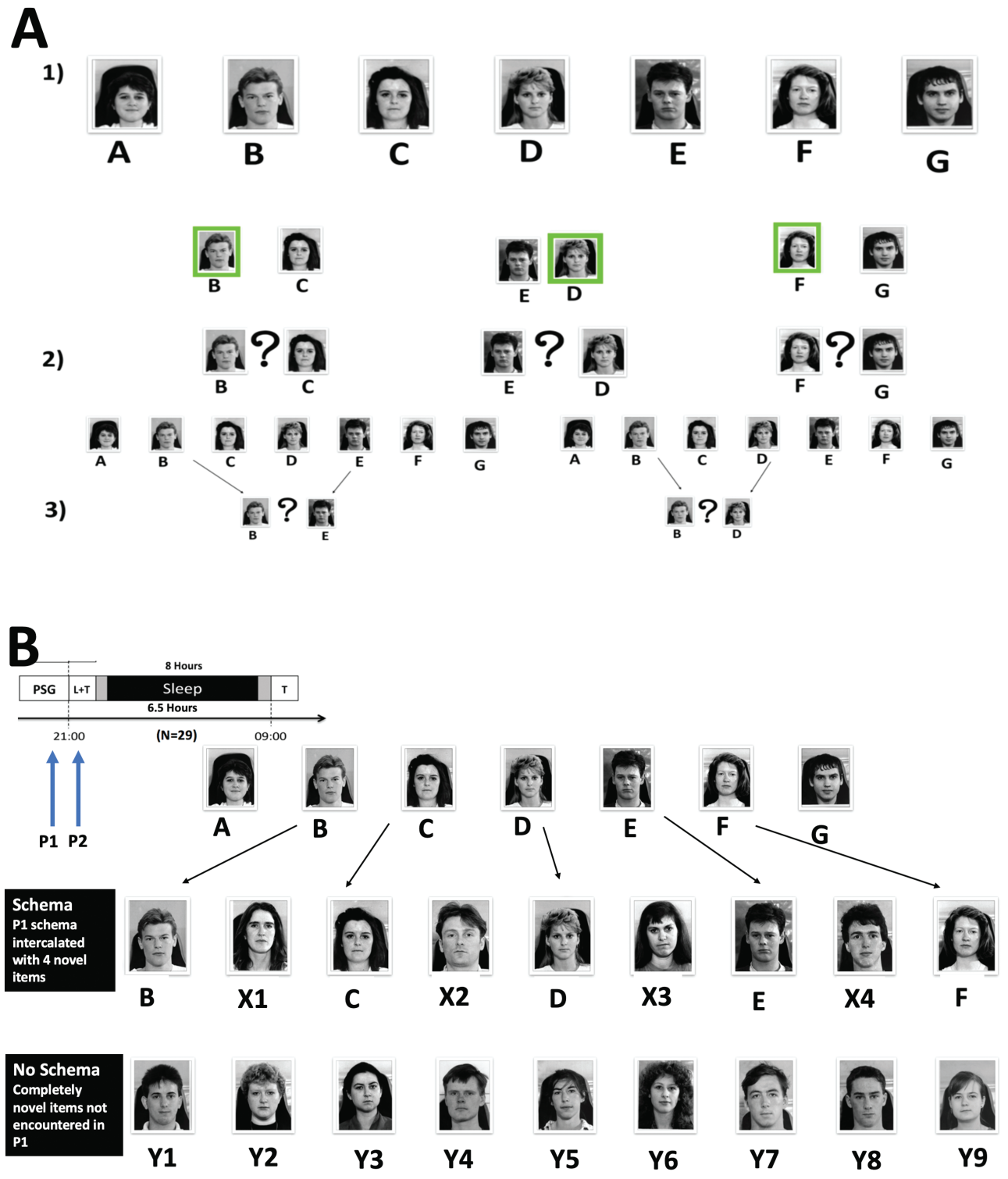

Figure 2. (A) (1) Phase 1a: Learning the schema to criterion. Participants performed learning blocks with active feedback (correct answer highlighted with green). Examples of test trials are shown for (2) phase 1 adjacent pairs, and (3) phase 1 inference pairs. (B) Schema-related memory integration and introduction of the No-schema condition. Participants were shown six alternating learning (with feedback) and test (with no feedback) blocks for the Schema condition. This was repeated for the No-schema condition. L, learning; T, Testing.

sleep schedules with schema condition (Schema, No-schema), and test sessions (immediate, delayed) as the within-subject factors, and sleep schedule (Nap, No-Nap) as the between-subject factor. For each group, the immediate and delayed test results were compared using post hoc paired *t*-tests. We examined associations of sleep stages and spindle measures with the memory performance (difference between delayed and immediate performance) and schema effect (difference

Figure 3. (A) Schema accommodation (learning reordered material). In each condition, the position of four individuals in each hierarchy was changed. (B) Schema assimilation (additions to reordered material). In this phase, three novel items were added to each hierarchy.

between Schema and No-schema condition) for tests following nocturnal and nap sessions using Spearman's correlation analyses. Resulting *p*-values were corrected for multiple comparisons using the Benjamini–Hochberg procedure for controlling the false discovery rate (FDR, p.adjust function in R) [39], and adjusted *p*-values $< .05$ were considered to be significant. MATLAB version R2017b (The Math Works, Inc., Natick, MA), and SPSS 25.0 (IBM Corp., Armonk, NY) was used to pre-process data and run statistical analyses. The stimuli were coded and presented using the E-Prime software.

Results

Initial schema-learning phase and overnight consolidation

Sleep preferentially consolidated schema-related memories in both Nap and No-Nap groups as evidenced by a significant schema condition (Schema, No-schema) by test session (immediate, delayed) interaction ($F_{(1,51)} = 7.79$, $p = .007$, $\eta_p^2 = .133$; Figure 4, Supplementary Figure 3). Initial learning of the schema in $M1_3$ was comparable across sleep groups, even though one group was sleep restricted ($M1_1$–$M1_3$), $t(51) = .757$, $p = .453$. Post hoc *t*-tests indicated significantly higher performance following nocturnal sleep consolidation of learning of schema in both Nap, $t(23) = 2.165$, $p = .041$, and No-Nap groups, $t(28) = 4.01$, $p < .001$. In contrast, no significant nocturnal sleep benefit was observed in the No-Schema condition (Supplementary Figure 3). As predicted, we also found significant main effects of schema, $F_{(1,51)} = 23.41$, $p < .001$, $\eta_p^2 = .315$, and test session, $F_{(1,51)} = 10.83$, $p = .002$, $\eta_p^2 = .175$, reflecting improved performance following a consolidation interval containing nocturnal sleep.

Schema accommodation phase (learning reordered material)

There was a significant main effect of group, whereby the Nap group adjusted better to the reordering of previously learned material, $F_{(1,51)} = 5.38$, $p = .024$, $\eta_p^2 = .096$. There were also significant main effects of schema, $F_{(1,51)} = 15.06$, $p < .001$, $\eta_p^2 = .228$, test session, $F_{(1,51)} = 9.64$, $p < .001$, $\eta_p^2 = .159$, and a significant schema by test session interaction, $F_{(1,51)} = 5.03$, $p = .008$, $\eta_p^2 = .090$, whereby there was less decline in schema-related memories across test sessions compared to the No-schema condition (Figure 4, Supplementary Figure 4).

Critically, despite lesser nocturnal sleep opportunity in the Nap group, both groups reached comparable performance in the initial accommodation test, $t(51) = 1.26$, $p = .214$. Subsequently, there was significantly lower performance in the No-Nap group after 12 h of active wakefulness (mean ± *SD*: 58.76 ± 13.33), compared with the Nap group (M = 67.25 ± 13.57; $t(51) = 2.29$, $p = .026$).

Schema assimilation (additions to reordered material)

The addition of new items to the relearned material resulted in higher initial schema assimilation test scores compared to initial learning of the reordered material, $t(52) = 3.78$, $p < .001$. There was a significant main effect of group, $F_{(1,51)} = 7.39$, $p = .009$, $\eta_p^2 = .127$, whereby the Nap group benefited retention of novel items assimilated into a newly acquired schema (Figure 4, Supplementary Figure 5).

As with initial learning, and accommodation phases, both groups reached comparable performance in the schema assimilation test that immediately followed the learning blocks, $t(51) = 1.29$, $p = .202$. There were significant main effects of schema, $F_{(1,51)} = 8.34$, $p = .006$, $\eta_p^2 = .140$, and test session, $F_{(1,51)} = 5.33$, $p = .002$, $\eta_p^2 = .095$, without significant interaction.

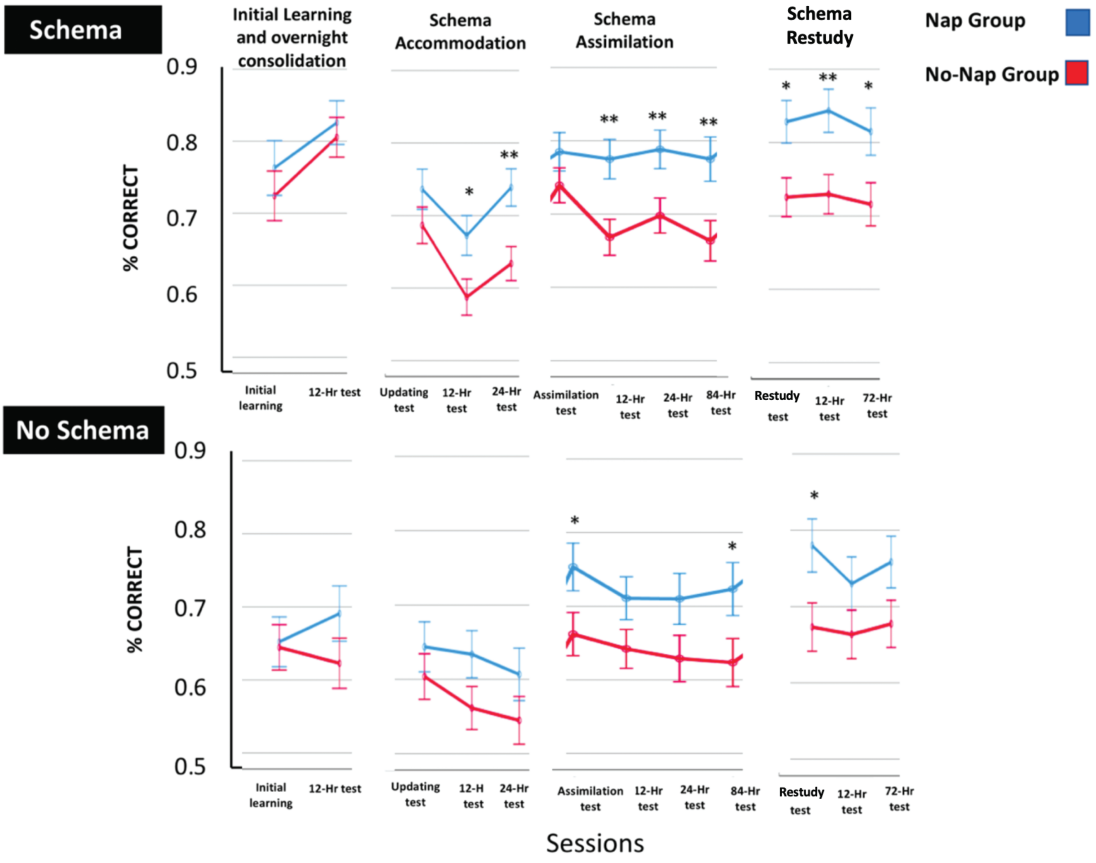

Figure 4. Behavioral results across all phases. Performance on immediate and delayed test sessions for the Nap and No-Nap groups are shown for both the Schema and No-schema conditions. $^{**}p < .01$, $^{*}p < .05$.

Post hoc t-tests indicated significantly higher memory scores for the Schema condition in the Nap group after 12-h (M = 77.50 ± 12.08) and 24-h (M = 78.83 ± 12.62) intervals, compared with the No-Nap group (12-h: M = 66.83 ± 14.08; 24-h: M = 69.79 ± 13.07), $t(51) \geq 2.54$, $p \leq .014$. This benefit extended to the 84-h delayed test session for both schema conditions, $t(51) \geq 2.06$, $p \leq .045$.

Schema restudy phase

Similar to the delayed 84-h assimilation test, the observed learning and memory benefits of the split sleep schedule in the nap group extended to the second manipulation week ($R1_1$, $R1_2$). A mixed ANOVA on memory performance following restudy of the learned material, highlighted a significant main effect of group, $F_{(1,51)} = 6.88$, $p = .011$, $\eta_p^2 = .119$, demonstrating that the nap group retained significantly higher schema-related items compared with the No-Nap schedule (Figure 4, Supplementary Figure 6). In contrast with prior phases, memory benefits were already apparent for both schema conditions in both groups from the immediate restudy test session, $t(51) \geq 2.62$, $p \leq .012$. Furthermore, post hoc t-tests demonstrated significantly higher memory scores for the Schema condition in the Nap group after a 12-h (M = 84.33 ± 14.29), and 72-h interval (M = 81.50 ± 15.19), compared with the No-Nap group (12-h: M = 72.97 ± 14.56, 72-h: M = 71.59 ± 16.33), $t(51) \geq 2.270$, $p \leq .027$. We also observed a significant main effect of schema, $F_{(1,51)} = 9.79$, $p = .003$, $\eta_p^2 = .161$, and a significant schema by test session interaction, $F_{(1,51)} = 3.49$, $p = .034$, $\eta_p^2 = .064$.

Schema versus No-schema across the protocol

As expected, we observed a strong, and consistent schema effect throughout the protocol. However, the difference between the Schema and No-schema condition gradually diminished as the No-schema condition slowly schematized and strengthened following repeated restudy across multiple learning and test sessions.

Nap EEG—memory associations

Sleep macrostructure for nocturnal sleep and naps are summarized in Supplementary Table 1. For naps, the schema-effect (Schema–No-Schema) in assimilation, and restudy phases was significantly associated with higher fast spindle density $r(22) \geq .441$, $p \leq .040$ across all nap sessions ($M1_5$, $M2_1$, and $M2_3$, these are highly conservative FDR-corrected values; see Table 2 for uncorrected p-values). Similarly, for fast spindle density in N2, significant correlations appeared consistently *across all nap sessions containing EEG recordings* ($M1_5$, $M2_1$, and $M2_3$), with the strongest association observed for the schema-effect in the assimilation 12-h test, $r(22) = .605$, $p = .009$. (Table 2, Figure 5). All correlations with memory remained significant in the delayed test sessions after $M1_5$. There were no significant correlations for any analysis that combined both fast (12–15 Hz) and slow spindles (9–12 Hz), $r(22) \leq .341$, $p \geq .120$.

Likewise, there were no significant correlations between sleep stage, SWA, SWE, and change in schema-driven memory performance in $M1_5$ and $M2_3$ nap sessions, $r(22) \leq .343$, $p \geq .177$ (Table 3). $M2_1$ was an exception. Here, longer duration of post-encoding SWS (N3 duration in minutes), was associated with a boost in schema-driven memory performance following restudy, $r(23) = .566$, $p = .012$. No significant associations were observed for the No-schema condition, SWS measures, and other sleep stages, $r(23) \leq .237$, $p \geq .289$.

Nocturnal sleep EEG—memory associations

There were robust and significant associations between the increased nocturnal fast spindle density in N2, with stronger schema effects across all manipulation nights, $r(50) = .389$, $p = .010$; $r(48) = .537$, $p < .004$; $r(49) = .310$, $p = .030$; and $r(49) = .375$, $p = .010$ for $M1_5$, $R1_1$, $M2_1$, and $R2_1$ (Figure 6, see Table 4 for uncorrected p-values). No significant associations were found for any analysis that combined both fast (12–15 Hz) and slow spindles (9–12 Hz), $r(49) \leq .242$, $p \geq .094$.

There were no significant correlations between SWS, SWA, SWE, other sleep stages, and change in schema-driven memory performance on the four nights when EEG recordings were performed, $r(50) \leq .293$, $p \geq .164$. Similarly, we did not find any significant associations between memory, SWS measures, and sleep stages in the No-schema condition, $r(49) \leq .193$, $p \geq .188$ (Table 5).

Homeostatic sleep pressure

Accumulation of homeostatic sleep pressure was investigated based on the nocturnal N2 latency, sleep efficiency, and SWE (0.6–4Hz). We found significantly lower SWE and decreased stage N2 sleep latency on manipulation nights preceded by naps, indicating dissipation of homeostatic sleep pressure in the Nap group (ps < .034).

Discussion

Building up of a schematic knowledge framework of ordered memoranda and then using this as the basis for remembering subsequently reordered and expanded items was beneficial for the recall of updated contents. This benefit extended up to 84 h after the expansion of updated memoranda. Napping preferentially facilitated schema-related learning and benefitted the dynamic adaptation of prior knowledge structures. Specifically, splitting up an 8 h sleep allocation into a shorter nocturnal sleep and a mid-afternoon nap yielded superior memory performance compared to obtaining a continuous 8h stretch of nocturnal sleep. Better memory consistently correlated with higher fast spindle density during sleep across multiple nap and nocturnal sleep opportunities. We did not find robust associations between the schema-driven benefits and the amount of post-encoding SWS. However, daytime napping significantly relieved nocturnal homeostatic sleep pressure and this could contribute to learning performance. Finally, similar to prior work on the transformation of associative schemas across time [40]; the large initial schema advantage for associative memory and inference diminished at the end of the experiment.

Our findings extend previously reported benefits of naps for fact-learning in educational settings [15] to schema-based learning. The higher schema adaptability in the Nap group have been the result of stronger consolidation of recently acquired knowledge structures following napping. This is consistent with

Table 2. Correlations between schema-effect (Schema–No-Schema) and nap spindles

	Slow spindle count (N2 + N3)	Slow spindle density (N2 + N3)	Fast spindle count (N2 + N3)	Fast spindle density (N2 + N3)	Fast spindle count (N2 only)	Fast spindle density (N2 only)
M15 (*N* = 22)						
Assimilation 12 h test	*r* = –.253 *p* = .257	*r* = –.186 *p* = .408	*r* = .321 *p* = .146	**r = .441** **p = .040** **p* =.040**	*r* = .346 *p* = .114	**r = .605** **p = .003** **p* = .009**
M21 (*N* = 23)						
Restudy immediate test	*r* = –.240 *p* = .258	*r* = –.175 *p* = .413	*r* = .365 *p* = .087	**r = .483** **p = .020** **p* = .030**	*r* = .493 **p = .017** **p* = .036**	**r = .514** **p = .012** **p* = .018**
M23 (*N* = 22)						
Restudy 72-h test	*r* = –.109 *p* = .629	*r* = –.216 *p* = .334	*r* = .444 **p = .039** *p** =.117	**r = .503** **p = .017** **p* = .030**	**r = .479** **p = .024** **p* =.036**	**r = .465** **p = .029** **p* = .029**

Significant Spearman's correlations ($p < .05$) are presented in bold.
p^*: FDR-corrected p-values.
Density was defined as the number of spindles per minute.

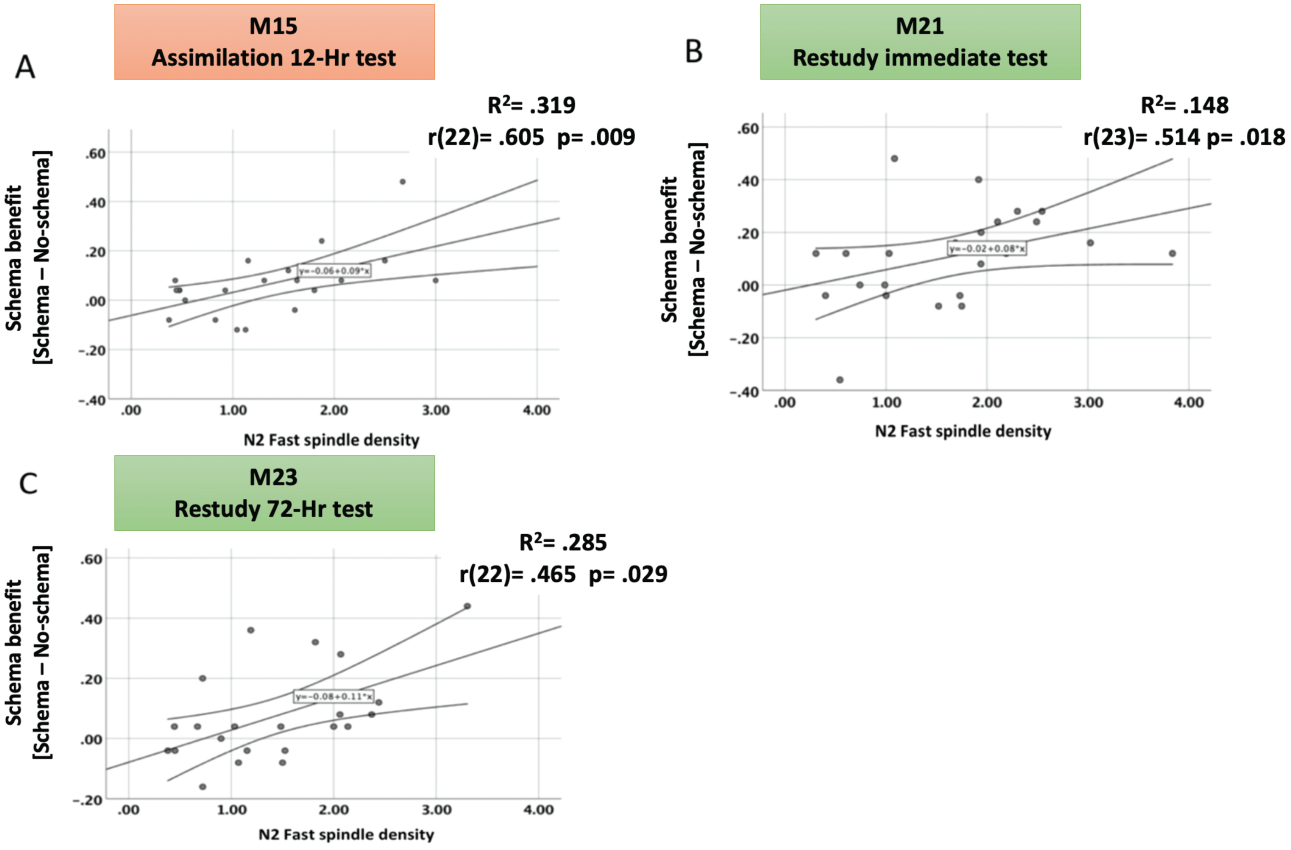

Figure 5. Correlation between schema benefit and spindle density across multiple nap sessions. Higher schema-driven memory benefits after assimilation were associated with increased N2 fast spindle density across naps ($M1_s$, $M2_1$, $M2_3$).

the notion that sleep may dynamically update such schemas [16] in addition to passively protecting newly encoded memories from interference [41].

Napping also benefited retention of novel items assimilated into a newly acquired schema. This is based on finding that at the initial schema assimilation test, there was no significant difference between the groups but on subsequent testing, a difference emerged. Thus, while we cannot deny that the accumulated benefits of having a schema to aid memory assimilation made a difference, the nap clearly did contribute to the observed improvement in memory.

Our findings converge with previous work highlighting the contribution of sleep spindles to the integration of novel information into pre-existing knowledge networks [22, 42]. Having a foundation of prior knowledge has also been shown to support fast spindle-dependent memory reactivation during sleep

Table 3. Sleep stage correlations with change in memory performance following nap

		SWA	SWE	SO count	SO density	N3	N3%	REM	REM%
M15 (*N* = 22)									
Assimilation	Schema	*r* = .054	*r* = .031	*r* = .250	*r* = .275	*r* = .096	*r* = .132	*r* = –.293	*r* = –.262
(12-h test–Immediate test)		*p* = .812	*p* = .892	*p* = .261	*p* = .215	*p* = .671	*p* = .558	*p* = .186	*p* = .239
	No-schema	*r* = –.065	*r* = –.112	*r* = –.237	*r* = –.138	*r* = .057	*r* = .030	*r* = .004	*r* = .012
		p = .774	*p* = .620	*p* = .289	*p* = .540	*p* = .800	*p* = .894	*p* = .985	*p* = .957
M21 (*N* = 23)									
Restudy	Schema	***r* = .427**	***r* = .422**	*r* = .351	*r* = .324	***r* = .566**	***r* = .529**	*r* = –.298	*r* = –.250
(Immediate restudy–Assimilation 84-h test)		***p* = .047**	***p* = .050**	*p* = .093	*p* = .142	***p* = .004**	***p* = .009**	*p* = .178	*p* = .262
		*p** =.141	*p** =.150			***p** =.012**	***p** = .027**		
	No-schema	*r* = –.041	*r* = –.105	*r* = .194	*r* = .187	*r* = –.049	*r* = .007	*r* = .014	*r* = .042
		p = .856	*p* = .642	*p* = .365	*p* = .404	*p* = .829	*p* = .975	*p* = .950	*p* = .854
M23 (*N* = 22)									
Restudy	Schema	*r* = .070	*r* =–.057	*r* = –.170	*r* = .023	*r* =–.124	*r* =–.343	*r* = .252	*r* = .277
(72-h test–12 h test)		*p* = .755	*p* = .802	*p* = .451	*p* = .922	*p* = .871	*p* = .177	*p* = .271	*p* = .223
	No-schema	*r* = –.097	*r* =–.177	*r* = –.083	*r* =.–.121	*r* =–.114	*r* = .006	*r* = –.006	*r* = .042
		p = .667	*p* = .430	*p* = .712	*p* = .603	*p* = .615	*p* = .980	*p* = .981	*p* = .855

Significant Spearman's correlations ($p < .05$) are presented in bold.
*p**: FDR-corrected *p*-values.
Subjects with more than 10 percent artifacts removed.
SWA, slow-wave activity, SWE, slow-wave energy; SO, slow oscillation; REM, rapid eye movement.

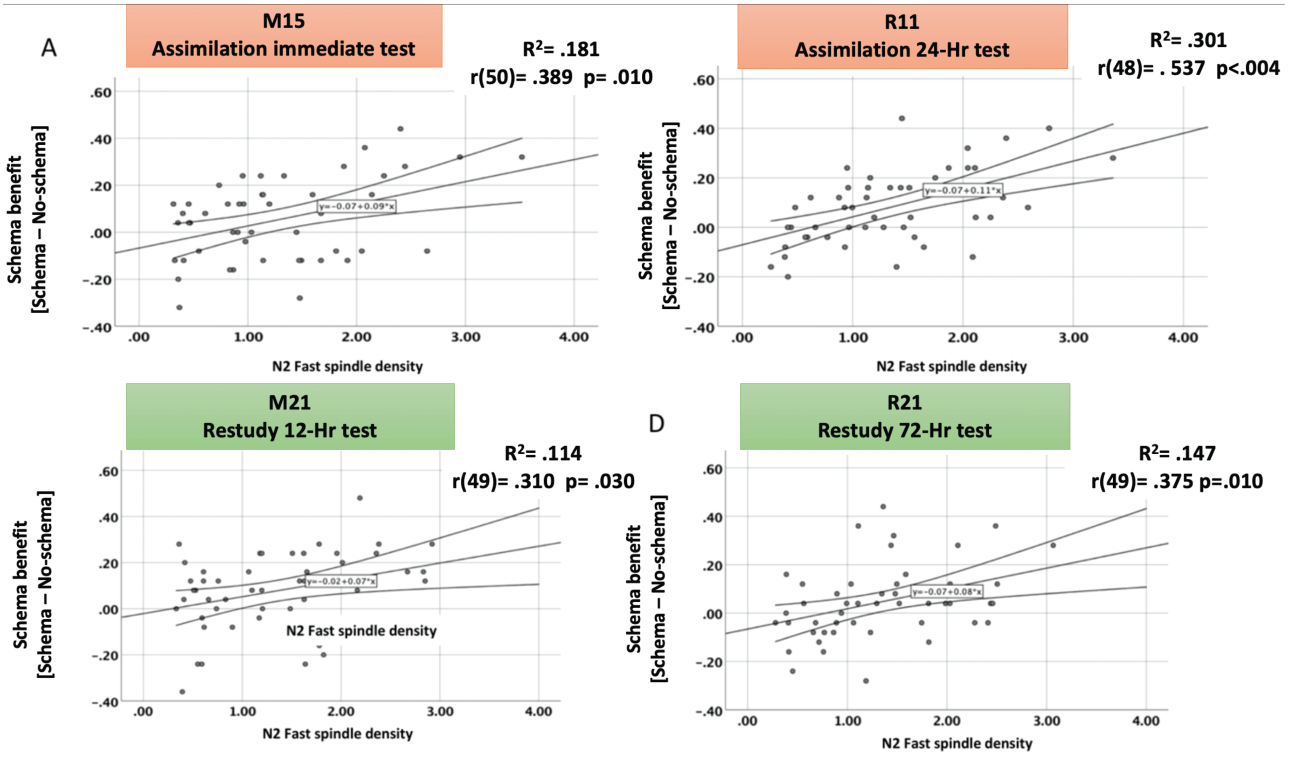

Figure 6. Correlation between schema benefit and spindle density across multiple nights of sleep. Higher schema-driven memory benefits after assimilation and restudy were associated with increased N2 fast spindle density across manipulation nights ($M1_S$, $R1_1$, $M2_1$, and $R2_1$).

[43]. Moreover, sleep spindles induced using optogenetics may facilitate hippocampus-dependent memory consolidation [44]. Lastly, pharmacologic enhancement of spindles has also improved declarative memory performance following both naps and nocturnal sleep [45, 46].

Higher fast spindle density may promote stronger schema-related memory integration via a higher rate of memory replay [28, 47]. As our paradigm involved repeated restudy and testing of materials, this could favorably increase the replay of overlapping memory traces [48, 49], and facilitate the incorporation of additional schema-relevant memoranda [7, 50, 51]. Sleep spindles may also aid the generalization of memories, a key element of schemas [52]. In line with these accounts, sleep spindles and replay-related phenomena could have facilitated hippocampal-medial prefrontal cortex crosstalk during sleep, resulting in memories more resilient to forgetting [53].

Table 4. Correlations between schema-effect (Schema–No-schema) and nocturnal spindles

	Slow spindle count (N2 + N3)	Slow spindle density (N2 + N3)	Fast spindle count (N2 + N3)	Fast spindle density (N2 + N3)	Fast spindle count N2	Fast spindle density N2
M15 (*N* = 50)						
Assimilation immediate test	*r* = –.241 *p* = .092	*r* = –.253 *p* = .076	**r = .344** **p = .014** **p*** **= .028**	**r = .383** **p = .006** **p*** **=.012**	**r = .328** **p = .020** **p*** **= .040**	**r = .389** **p = .005** **p*** **= .010**
R11 (*N* = 48)						
Assimilation 24-h test	*r* = –.447 *p* = .001	*r* = –.460 *p* = .001	**r = .431** **p = .002** **p***=.008	**r = .485** **p < .001** **p*** **< .004**	**r = .475** **p = .001** **p*** **= .004**	**r = .537** **p < .001** **p*** **< .004**
M21 (*N* = 49)						
Restudy 12-h test	*r* =-.226 *p* = .118	*r* =-.227 *p* = .116	**r = .306** **p = .032** **p***=.042	**r = .321** **p = .024** **p*** **=.032**	**r = .290** **p = .043** **p***= .043	**r = .310** **p = .030** **p*** **= .030**
R21 (*N* = 49)						
Restudy 72-h test	*r* = –.163 *p* = .264	*r* = –.099 *p* = .500	*r* = .252 *p* = .081	*r* = .255 *p* = .077	*r* = .293 **p = .041** **p***= .043	**r = .375** **p = .008** **p*** **= .010**

Significant Spearman's correlations ($p < .05$) are presented in bold.
*p**: FDR-corrected *p*-values.
Density was defined as the number of spindles per minute.

Table 5. Sleep stage correlations with change in memory performance following nocturnal sleep

		SWA	SWE	SO count	SO density	N3	N3%	REM	REM%
M15 (*N* = 50)									
Accommodation (24-h test–12-h test)	Schema	*r* = .147 *p* = .314	*r* = .158 *p* = .277	*r* = .008 *p* = .954	*r* = .065 *p* = .657	*r* = .215 *p* = .548	*r* = .293 *p* = .164	*r* = –.071 *p* = .628	*r* = –.054 *p* = .710
	No-schema	*r* = –.067 *p* = .647	*r* = –.087 *p* = .551	*r* = –.036 *p* = .802	*r* = .061 *p* = .677	*r* = .101 *p* = .490	*r* = .063 *p* = .668	*r* = .108 *p* = .460	*r* = .160 *p* = .271
R11 (*N* = 48)									
Assimilation (24-h test–12-h test)	Schema	*r* = .043 *p* = .784	*r* = .049 *p* = .754	*r* = -.046 *p* = .745	*r* = .014 *p* = .925	*r* = .081 *p* = .583	*r* = .177 *p* = .229	*r* = –.256 *p* = .316	*r* = –.255 *p* = .352
	No-schema	*r* = –.082 *p* = .581	*r* = –.095 *p* = .522	*r* = –.115 *p* = .418	*r* = –.107 *p* = .477	*r* = .053 *p* = .723	*r* = .014 *p* = .926	*r* = .051 *p* = .733	*r* = .008 *p* = .959
M21 (*N* = 49)									
Restudy (Immediate restudy–Assimilation 84 h test)	Schema	*r* = .116 *p* = .433	*r* = .127 *p* = .390	*r* = .113 *p* = .419	*r* = .049 *p* = .741	*r* = .194 *p* = .182	*r* = .124 *p* = .397	*r* = .104 *p* = .628	*r* = .053 *p* = .720
	No-schema	*r* = –.193 *p* = .188	*r* = –.171 *p* = .245	*r* = –.052 *p* = .709	*r* = –.030 *p* = .842	*r* = –.100 *p* = .494	*r* = –.110 *p* = .451	*r* = .078 *p* = .594	*r* = .100 *p* = .493
R21 (*N* = 49)									
Restudy (72 h test–12-h test)	Schema	*r* = .065 *p* = .677	*r* = .071 *p* = .646	*r* = .054 *p* = .707	*r* = –.013 *p* = .930	*r* = .013 *p* = .931	*r* = .009 *p* = .950	*r* = –.186 *p* = .402	*r* = –.184 *p* = .412
	No-schema	*r* = –.055 *p* = .722	*r* = –.085 *p* = .582	*r* = .147 *p* = .314	*r* = .041 *p* = .777	*r* = .052 *p* = .722	*r* = .047 *p* = .748	r= –.115 *p* = .430	*r* = –.072 *p* = .622

Subjects with more than 10 percent artifacts were removed.
SWA, slow-wave activity; SWE, slow-wave energy; SO, slow oscillation; REM, rapid eye movement.

In contrast to the findings related to fast spindles, we found no direct association between the amount of SWS, measured either via duration or amplitude, on memory performance. However, SWS could still benefit learning by providing an additional opportunity to relieve sleep pressure [15]. Such relief of homeostatic sleep pressure is theorized to help restore learning capacity, benefiting performance in the Nap group.

In relation to this latter point, a study of 929 young adults failed to detect significant correlations between deep sleep and memory consolidation, suggesting overestimation of the association strength in prior works with smaller samples [54, 55]. A similar null finding involving 159 participants has also led to the suggestion that slow-wave mediated memory benefits may be task-dependent, less long-lasting, and may only be observed under certain boundary conditions [56]. Moreover, adolescents restricted to as little as 5 h of sleep opportunity a night did not show inferior declarative memory consolidation for words compared to those with a 9-h sleep opportunity [57]. This suggests that consolidation may be unhindered provided a minimum amount of nocturnal SWS is obtained [15, 58].

Limitations and future directions

While a recent study found comparable benefits of prior knowledge on sleep-dependent memory consolidation in children [59], our findings in adolescents should not be generalized, until

further research is extended to other age groups [60]. Moreover, only C3 and C4 electrodes were used in this study, which may have limited the detection of slow spindles with predominant topographical distribution in the frontal regions. However, C3 and C4 are sensitive to detect fast spindles that are more dominant in the centroparietal regions [61–63], and our findings are aligned with prior works using C3 and C4 electrodes to investigate spindle characteristics in adolescents [28, 64, 65]. It is also unclear if the benefit of sleep for memory consolidation is distinct from that accrued from quiet rest alone [66]; especially over a week or longer. Recent accounts suggest a bidirectional link between sleep and waking cognition [67]. Similar underlying physiology such as the recently discovered awake replay-like phenomena could be involved in this process that is interesting to be explored in future work [68].

Conclusion

A schedule combining slightly suboptimal nocturnal sleep with a daily nap can facilitate the building of robust and flexible schemas that confer significant learning benefits. Schema-driven benefits were consistently associated with higher fast spindle density during schema assimilation and restudy, indicating their likely contribution to schema-related memory integration. Overall, these findings inform current theories on underlying neural mechanisms involved in the emergence of higher-order schematic cognitive frameworks, reinforcing how sleep optimizes knowledge construction.

Supplementary Material

Supplementary material is available at *SLEEP* online.

Acknowledgments

We would like to thank Kian F. Wong, Jesisca Tandi, Shamsul Azrin Jamaluddin, TeYang Lau, for their help in coding the stimuli and running the experiments. We also thank the research staff of the Center for Sleep and Cognition for their support in data collection.

Funding

This work was supported by the National Medical Research Council, Singapore (NMRC/STaR/19may-0001) awarded to MWLC, grant NRF2016-SOL002-001 from the National Research Foundation, Singapore, awarded to MWLC as well as the Far East Organization.

Disclosure Statement

Financial Disclosure: There are no financial conflicts of interest.

Nonfinancial Disclosure: MWLC and JLO have a patent for the Z3-score framework.

Data and Material Availability

Data and analytic scripts used in this publication are available upon reasonable request.

References:

1. Gilboa A, *et al*. Neurobiology of schemas and schema-mediated memory. *Trends Cogn Sci*. 2017;**21**(8):618–631.
2. Fernandez G, *et al*. Memory, novelty and prior knowledge. *Trends Neurosci*. 2018;**41**(10):654–659.
3. Bartlett FC. *Remembering: An Experimental and Social Study*. Cambridge: Cambridge University; 1932.
4. Ghosh VE, *et al*. What is a memory schema? A historical perspective on current neuroscience literature. *Neuropsychologia*. 2014;**53**:104–114.
5. McClelland JL. Incorporating rapid neocortical learning of new schema-consistent information into complementary learning systems theory. *J Exp Psychol Gen*. 2013;**142**(4):1190–1210.
6. van Kesteren MTR, *et al*. Congruency and reactivation aid memory integration through reinstatement of prior knowledge. *Sci Rep*. 2020;**10**(1):4776.
7. Lewis PA, *et al*. Overlapping memory replay during sleep builds cognitive schemata. *Trends Cogn Sci*. 2011;**15**(8):343–351.
8. van Kesteren MTR, *et al*. How to optimize knowledge construction in the brain. *npj Sci Learn*. 2020;**5**:5.
9. Dudai Y, *et al*. The consolidation and transformation of memory. *Neuron*. 2015;**88**(1):20–32.
10. Wagner U, *et al*. Sleep inspires insight. *Nature*. 2004;**427**(6972):352–355.
11. Monaghan P, *et al*. Sleep promotes analogical transfer in problem solving. *Cognition*. 2015;**143**:25–30.
12. Ellenbogen JM, *et al*. Human relational memory requires time and sleep. *Proc Natl Acad Sci USA*. 2007;**104**(18):7723–7728.
13. Werchan DM, *et al*. Generalizing memories over time: sleep and reinforcement facilitate transitive inference. *Neurobiol Learn Mem*. 2013;**100**:70–76.
14. Lo JC, *et al*. Cognitive effects of multi-night adolescent sleep restriction: current data and future possibilities. *Curr Opin Behav Sci*. 2020;**33**:34–41.
15. Cousins JN, *et al*. Splitting sleep between the night and a daytime nap reduces homeostatic sleep pressure and enhances long-term memory. *Sci Rep*. 2021;**11**(1):5275.
16. Richter FR, *et al*. Flexible updating of dynamic knowledge structures. *Sci Rep*. 2019;**9**(1):2272.
17. Antony JW, *et al*. Sleep spindles and memory reprocessing. *Trends Neurosci*. 2019;**42**(1):1–3.
18. Fernandez LMJ, *et al*. Sleep spindles: mechanisms and functions. *Physiol Rev*. 2020;**100**(2):805–868.
19. Antony JW, *et al*. Sleep spindle refractoriness segregates periods of memory reactivation. *Curr Biol*. 2018;**28**(11):1736–1743.e4.
20. Batterink LJ, *et al*. Sleep-based memory processing facilitates grammatical generalization: evidence from targeted memory reactivation. *Brain Lang*. 2017;**167**:83–93.
21. Tamminen J, *et al*. Sleep spindle activity is associated with the integration of new memories and existing knowledge. *J Neurosci*. 2010;**30**(43):14356–14360.
22. Hennies N, *et al*. Sleep spindle density predicts the effect of prior knowledge on memory consolidation. *J Neurosci*. 2016;**36**(13):3799–3810.
23. Lo JC, *et al*. Cognitive effects of split and continuous sleep schedules in adolescents differ according to total sleep opportunity. *Sleep*. 2020;**43**(12). doi:10.1093/sleep/zsaa129.
24. Kumaran D. Schema-driven facilitation of new hierarchy learning in the transitive inference paradigm. *Learn Mem*. 2013;**20**(7):388–394.

25. Preston AR, *et al*. Interplay of hippocampus and prefrontal cortex in memory. *Curr Biol*. 2013;**23**(17):R764–R773.
26. Kumaran D, *et al*. Computations underlying social hierarchy learning: distinct neural mechanisms for updating and representing self-relevant information. *Neuron*. 2016;**92**(5):1135–1147.
27. Aghayan Golkashani H, *et al*. Schema-driven memory benefits boost transitive inference in older adults. *Psychol Aging*. 2021;**36**:463–474.
28. Jegou A, *et al*. Cortical reactivations during sleep spindles following declarative learning. *Neuroimage*. 2019;**195**:104–112.
29. Patanaik A, *et al*. An end-to-end framework for real-time automatic sleep stage classification. *Sleep*. 2018;**41**(5). doi:10.1093/sleep/zsy041.
30. Ibert C, *et al*. *The AASM Manual for the Scoring of Sleep and Associated Events: Rules, Terminology and Technical Specification*. Westchester: American Academy of Sleep Medicine; 2007.
31. Molle M, *et al*. Fast and slow spindles during the sleep slow oscillation: disparate coalescence and engagement in memory processing. *Sleep*. 2011;**34**(10):1411–1421. doi:10.5665/SLEEP.1290.
32. Schabus M, *et al*. Hemodynamic cerebral correlates of sleep spindles during human non-rapid eye movement sleep. *Proc Natl Acad Sci USA*. 2007;**104**(32):13164–13169.
33. Astill RG, *et al*. Sleep spindle and slow wave frequency reflect motor skill performance in primary school-age children. *Front Hum Neurosci*. 2014;**8**:910.
34. Bodizs R, *et al*. Sleep spindling and fluid intelligence across adolescent development: sex matters. *Front Hum Neurosci*. 2014;**8**:952.
35. Leong RLF, *et al*. Memory performance following napping in habitual and non-habitual nappers. *Sleep*. 2021;**44**(6). doi:10.1093/sleep/zsaa277.
36. Goldstone A, *et al*. Sleep spindle characteristics in adolescents. *Clin Neurophysiol*. 2019;**130**(6):893–902.
37. R C, *et al*. Analyzing human sleep EEG: a methodological primer with code implementation. *Sleep Med Rev*. 2020;**54**:101353.
38. Banks S, *et al*. Neurobehavioral dynamics following chronic sleep restriction: dose-response effects of one night for recovery. *Sleep*. 2010;**33**(8):1013–1026. doi:10.1093/sleep/33.8.1013.
39. Benjamini Y, *et al*. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J R Stat Soc Ser B Methodol*. 1995;**57**(1):289–300.
40. van Kesteren MT, *et al*. Consolidation differentially modulates schema effects on memory for items and associations. *PLoS One*. 2013;**8**(2):e56155.
41. Jenkins JG, *et al*. Obliviscence during sleep and waking. *Am J Psychol*. 1924;**35**(4):605–612.
42. Tamminen J, *et al*. The role of sleep spindles and slow-wave activity in integrating new information in semantic memory. *J Neurosci*. 2013;**33**(39):15376–15381.
43. Groch S, *et al*. Prior knowledge is essential for the beneficial effect of targeted memory reactivation during sleep. *Sci Rep*. 2017;**7**:39763.
44. Latchoumane CV, *et al*. Thalamic spindles promote memory formation during sleep through triple phase-locking of cortical, thalamic, and hippocampal rhythms. *Neuron*. 2017;**95**(2):424–435.e6.
45. Zhang J, *et al*. The effect of zolpidem on memory consolidation over a night of sleep. *Sleep*. 2020;**43**(11). doi:10.1093/sleep/zsaa084.
46. Mednick SC, *et al*. The critical role of sleep spindles in hippocampal-dependent memory: a pharmacology study. *J Neurosci*. 2013;**33**(10):4494–4504.
47. Gais S, *et al*. Learning-dependent increases in sleep spindle density. *J Neurosci*. 2002;**22**(15):6830–6834.
48. van Kesteren MTR, *et al*. Integrating educational knowledge: reactivation of prior knowledge during educational learning enhances memory integration. *npj Sci Learn*. 2018;**3**:11.
49. Himmer L, *et al*. Rehearsal initiates systems memory consolidation, sleep makes it last. *Sci Adv*. 2019;**5**(4):eaav1695.
50. Ohki T, *et al*. Neural mechanisms of mental schema: a triplet of delta, low beta/spindle and ripple oscillations. *Eur J Neurosci*. 2018;**48**(7):2416–2430.
51. Pereira SIR, *et al*. The differing roles of NREM and REM sleep in the slow enhancement of skills and schemas. *Curr Opin Physiol*. 2020;**15**:82–88.
52. Chatburn A, *et al*. Consolidation and generalisation across sleep depend on individual EEG factors and sleep spindle density. *Neurobiol Learn Mem*. 2021;**179**:107384.
53. Cowan E, *et al*. Sleep spindles promote the restructuring of memory representations in ventromedial prefrontal cortex through enhanced hippocampal-cortical functional connectivity. *J Neurosci*. 2020;**40**(9):1909–1919.
54. Ackermann S, *et al*. No associations between interindividual differences in sleep parameters and episodic memory consolidation. *Sleep*. 2015;**38**(6):951–959. doi:10.5665/sleep.4748.
55. Cordi MJ, *et al*. How robust are sleep-mediated memory benefits? *Curr Opin Neurobiol*. 2020;**67**:1–7.
56. Cordi MJ, Rasch B. No evidence for intra-individual correlations between sleep-mediated declarative memory consolidation and slow-wave sleep. *Sleep*. 2021;**44**(8). doi:10.1093/sleep/zsab034.
57. Voderholzer U, *et al*. Sleep restriction over several days does not affect long-term recall of declarative and procedural memories in adolescents. *Sleep Med*. 2011;**12**(2):170–178.
58. Cousins JN, *et al*. The impact of sleep deprivation on declarative memory. *Prog Brain Res*. 2019;**246**:27–53.
59. Peiffer A, *et al*. The power of children's sleep-Improved declarative memory consolidation in children compared with adults. *Sci Rep*. 2020;**10**(1):9979. doi:10.1038/s41598-020-66880-3.
60. Jones BJ, *et al*. Role of napping for learning across the lifespan. *Curr Sleep Med Rep*. 2020;**6**(4):290–297.
61. R C, *et al*. Individual differences in frequency and topography of slow and fast sleep spindles. *Front Hum Neurosci*. 2017;**11**:433.
62. Jobert M, *et al*. Topographical analysis of sleep spindle activity. *Neuropsychobiology*. 1992;**26**(4):210–217.
63. Zeitlhofer J, *et al*. Topographic distribution of sleep spindles in young healthy subjects. *J Sleep Res*. 1997;**6**(3):149–155.
64. Goldschmied JR, *et al*. Spindles are highly heritable as identified by different spindle detectors. *Sleep*. 2021;**44**(4). doi:10.1093/sleep/zsaa230.
65. Reynolds CM, *et al*. Reliability of sleep spindle measurements in adolescents: how many nights are necessary? *J Sleep Res*. 2019;**28**(1):e12698.
66. Tucker MA, *et al*. Comparing the effects of sleep and rest on memory consolidation. *Nat Sci Sleep*. 2020;**12**:79–91.
67. Paller KA, *et al*. Memory and sleep: how sleep cognition can change the waking mind for the better. *Annu Rev Psychol*. 2021;**72**:123–150.
68. Findlay G, *et al*. The evolving view of replay and its functions in wake and sleep. *Sleep Adv*. 2020;**1**(1):zpab002.