1	Slow-wave sleep and REM sleep differentially contribute to
2	memory representational transformation
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## 24 Abstract

Memory transforms over time, gradually becoming less idiosyncratic and more gist-like. 25 26 While sleep contributes to memory transformation, how different sleep stages and EEG activity influence memory transformation is far from clear. Applying representational 27 similarity analysis to electroencephalogram (EEG) recordings, we examined memory 28 representational transformation at both the idiosyncratic "item-level" and the generic 29 30 "category-level". Our findings revealed that after an overnight sleep, item-level neural representations for post-sleep remembered items were abolished. In contrast, category-31 level representations remained prominent, but they became distinctive from pre-sleep. 32 33 Across participants, more rapid eye movement (REM) sleep relative to slow-wave sleep (SWS) was associated with reduced item-level neural representational strength, 34 increased category-level representational strength, as well as the decreased item-level 35 representational similarity between pre-sleep learning and post-sleep retrieval sessions. 36 Moreover, the theta and beta EEG power during REM sleep, and delta power during 37 SWS differentially supported these representational transformations. These findings 38 suggest that post-learning REM sleep and SWS play differential roles in supporting 39 40 overnight memory transformation.

41 Keywords: REM sleep, SWS, memory transformation, representational similarity
42 analysis, episodic memory

43

#### 45 Introduction

Sleep consolidates and transforms newly acquired information, making it long-lasting for 46 47 future use (Diekelmann & Born, 2010; Rasch & Born, 2013; Stickgold, 2005). While extensive evidence has established the sleep's benefits in consolidating episodic 48 memory (for meta-analysis see Berres & Erdfelder, 2021), how sleep transforms 49 memory remains unclear. Theoretical models propose that sleep transforms 50 idiosyncratic memory episodes into generalized gist or schema (Dudai et al., 2015; 51 Inostroza & Born, 2013; Landmann et al., 2014; Nadel et al., 2012; Payne, 2011; 52 Stickgold & Walker, 2013; Xue, 2022). This sleep-mediated memory transformation is 53 largely inferred from pre- vs. post-sleep behavioral changes in memory tests implicating 54 integration, generalization, and schematization (Barry et al., 2019; Ellenbogen et al., 55 2007; Friedrich et al., 2015; Lewis & Durrant, 2011; Payne et al., 2009). Despite these 56 promising findings, behavioral measurements may fall short in characterizing the 57 complexity and fidelity of memory representations (Heinen et al., 2024; Xue, 2022). 58 Therefore, it is desirable to obtain direct neural evidence delineating the sleep-mediate 59 memory representational transformation. 60

We aim to address this question by leveraging the analytical power of 61 62 Representational similarity analysis (RSA) to examine memory representations at different levels in the human brain (Diedrichsen & Kriegeskorte, 2017). Specifically, RSA 63 can decompose neural representations of individual items into item- and category-level 64 representations (Lee et al., 2019; Ritchey et al., 2013; Wu & Fuentemilla, 2023). Item-65 level representations capture neural representations unique to specific stimuli (Kuhl & 66 Chun, 2014), while category-level representations capture neural patterns shared across 67 stimuli within semantic categories (Koutstaal et al., 2001; Naspi et al., 2021). Applying 68 the RSA to EEG recordings, we examined both item- and category-level representations 69 70 within pre-sleep learning and post-sleep retrieval sessions, respectively (i.e., within-71 session RSA), and item-/category-level representational similarity between pre- and post-sleep sessions (i.e., cross-session RSA). We hypothesize that sleep facilitates 72 memory transformation and gist-extraction among post-sleep remembered items. 73 Specifically, for within-session RSA, we expected that both item- and category-level 74

representations would be present in the pre-sleep learning session (Liu et al., 2021). 75 Following sleep, we hypothesized that the item-level representation would be diminished 76 77 and even abolished in the post-sleep retrieval session (i.e., reduced item specificity) (Feld & Born, 2017). In contrast, we anticipated that category-level representation shall 78 79 persist and remain identifiable in the post-sleep retrieval session (i.e., enduring gist-like information). Moreover, we expected that the cross-session RSA will show lower item-80 81 level and/or category-level neural representational similarities as compared to the withinsession RSA, as a result of memory representational transformation (Fig. 1A-B). 82

More critically, how different sleep stages, particularly the SWS and REM sleep, 83 interactively contribute to memory representational transformation remains controversial. 84 One perspective suggests that these two sleep stages may complement each other in 85 optimizing memory consolidation and transformation (Brodt et al., 2023; Diekelmann & 86 Born, 2010; Giuditta et al., 1995; Inostroza & Born, 2013). Specifically, during SWS, 87 repeated memory reactivation would integrate newly encoded memories into pre-88 existing memory schema, transforming hippocampal-dependent memory into more 89 neocortex-dependent gist-like representations. Subsequent REM sleep would further 90 91 stabilize these transformed representations via synaptic consolidation. Supporting this 92 hypothesis, animal studies suggest that SWS-initiated cortical plasticity for memory consolidation is reinforced by the following REM sleep episode (Miyawaki & Diba, 2016; 93 Ribeiro et al., 2007). Moreover, human studies showed that the product of the durations 94 95 of SWS and REM sleep (SWS \* REM), reflecting their complementary roles, explains 96 overnight memory consolidation (Hu et al., 2015; Mednick et al., 2003; Stickgold et al., 2000). If SWS and REM complement each other in memory transformation, then a 97 higher SWS \* REM should be associated with greater overnight memory 98 representational transformation (Fig. 1C). 99

An alternative perspective posits that SWS and REM sleep play differential roles in sleep-mediated memory transformation (MacDonald & Cote, 2021; Payne, 2011). According to this view, SWS stabilizes memory representations in their original formats, while REM sleep primarily refines and transforms them into schema-like formats. Supporting this perspective, research has shown that REM sleep duration is positively

associated with schema-conformant memory consolidation and creative problemsolving, while SWS duration showed an opposite trend (Cai et al., 2009; Durrant et al.,
2015). Consistent with this idea, a recent study showed that greater memory distortion
or modification occurs after REM-rich sleep, while stabilization of the undistorted original
memory occurs after SWS-rich sleep (Kaida et al., 2023). If this perspective holds true, a
higher REM to SWS duration ratio (i.e., REM/SWS) should be associated with greater
memory representational transformation (Fig. 1C).

Here, combining overnight sleep EEG recordings with RSA, we examined item- and 112 category-level memory representational transformation across sleep. Our results 113 114 revealed substantial memory representational transformation for post-sleep remembered items: while pre-sleep memory representations contained both item-level 115 116 and category-level content, post-sleep memory representations were predominantly categorical. More importantly, a higher REM/SWS duration ratio was associated with 117 reduced item-level representational strength, increased category-level representational 118 strength, and reduced item-level cross-session similarity. Thus, our findings support the 119 120 differential roles of SWS and REM in memory representational transformation.

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#### 122 **Results**

A total of 35 participants (26 females, mean age  $\pm$  SD: 22  $\pm$  2.79) were included in the 123 analysis. Participants completed three major task sessions: pre-sleep learning, overnight 124 125 sleep, and post-sleep mental retrieval tests (see Fig. 1 and Methods). During pre-sleep learning, participants learned 96 unique word-picture pairs, with each repeated three 126 127 times. After a distraction task, participants were tested for their memory on half of the learning pairs. Subsequently, participants went to nocturnal sleep, during which targeted 128 memory reactivation (TMR) was performed during SWS. In the post-sleep mental 129 130 retrieval session, participants closed their eyes to mentally recall associated pictures as 131 vividly as possible, prompted by auditory cues. Similar to the pre-sleep learning, each word-picture pair was mentally retrieved three times. Immediately after the mental 132 133 retrieval task, participants were asked to write down the picture content, promoted by individual printed cue words. Participants showed an average accuracy rate of 0.40 (SD: 134

135 0.18) in this task, serving as the post-sleep memory retrieval performance. Note that the 136 TMR cued versus uncued items did not differ in post-sleep retrieval performance (t(34) =137 -1.68; p = 0.102). The TMR effect and the associated neurocognitive processing are not 138 the main focus of the study and were reported in Liu et al., 2023.



140 Fig 1. Experimental paradigm and analytic scheme of memory representational

141 transformation across sleep. (A) The experimental procedure includes pre-sleep

learning (i.e., encoding and maintenance), pre-sleep tests, overnight sleep with TMR 142 cueing during slow-wave sleep, and post-sleep retrieval tests. EEG was recorded 143 throughout the whole experiment. (B) Within-session RSA examined memory 144 145 representations within each of the pre-sleep learning (Pre-Pre similarity) and post-sleep mental retrieval (Post-Post similarity) sessions; Cross-session RSA examined the 146 memory representational similarity between these two sessions (Pre-Post similarity). 147 Both the within-session RSA and cross-session RSA were performed at two different 148 levels: item-level and category-level. Item-level representations were obtained by 149 contrasting the within-item similarity versus within-category similarity (WI-minus-WC), 150 151 while the category-level representations were obtained by contrasting the withincategory similarity versus between-category similarity (WC-minus-BC). We hypothesized 152 153 that memory representational transformation would be manifested by the following 154 indexes: decreased item-level representations, while persistently prominent category-155 level representations from pre- to post-sleep; and the low cross-session pre-post similarities. (C) If SWS and REM sleep play complementary roles in memory 156 157 representational transformation, then the product of the REM sleep amount by the SWS 158 amount (SWS\*REM) should correlated with memory representational transformation 159 indexes. Otherwise, if REM sleep and SWS play differential roles, then the REM sleep 160 amount relative to the SWS amount (REM/SWS), should be correlated with the memory representational transformation indexes. 161

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## 163 **Overnight neural representational transformation for post-sleep remembered items**

To understand how memory representation transforms across an overnight sleep while 164 remaining retrievable, we first examined the neural representations during the pre-sleep 165 166 learning session (i.e., including both encoding and maintenance periods) for post-sleep remembered items. Following previous studies (Lee et al., 2019; Liu et al., 2020; Ritchey 167 et al., 2013), we performed the RSA on the auditory cue-elicited EEG power patterns to 168 extract item- and category-level neural representations. These representations capture 169 170 fine-grained item-specific information and generalized categorical information, respectively. For item-level representations, we contrasted the EEG power pattern 171 172 similarities between trials of the same pictures (Within-item, WI similarity) versus the similarity between trials of different pictures from the same category (Within-category, 173 174 WC similarity, see Methods). For category-level representations, we contrasted the WC similarity with the similarity between trials of different pictures from different categories 175 (Between-category, BC similarity) (Fig. 1B). 176

To examine the temporal dynamics of representational transformation, we 177 computed the similarity values by correlating the EEG power pattern across frequencies 178 179 (2-40 Hz) and all clean channels between artifact-free learning trials, in 500 ms sliding time windows with a stride of 100 ms during the 5 s post-stimuli epoch. We found 180 181 significant item-level representations (i.e., WI > WC similarity) within a ~700-2500 ms cluster and a ~2000-4000 ms cluster post-stimuli onset ( $p_{scluster} < 0.032$ , corrected by 182 183 the non-parametric cluster-based permutation test, Fig. 2A). We also found significant category-level representations (i.e., WC > BC similarity) within a significant cluster (~0-184 185 1000ms and 3000-4800ms post stimuli onset, p<sub>cluster</sub> = 0.043, Fig. 2B). These results suggested that both item-level and category-level neural representations emerged 186 187 during pre-sleep learning session for those post-sleep remembered items.

As a control analysis, we performed the same RSA for post-sleep forgotten items. 188 The results only revealed two significant clusters showing significant item-level 189 190 representations ( $ps_{cluster} < 0.042$ , Fig. 2C), but no significant category-level representations ( $ps_{cluster} > 0.690$ , Fig. 2D) during pre-sleep learning. Comparisons 191 between post-sleep remembered and forgotten items revealed two clusters showing 192 193 Remember < Forget item-level representations (all  $p_{\text{scluster}} < 0.050$ , see Fig. S1) and three clusters showing Remember > Forget category-level representations (all pscluster < 194 0.027, see Fig. S1), may reflect that greater transforming from item-level to semantic 195 196 category-level representations during learning predicts better long-term memory (Liu et 197 al., 2021).

198 Next, we examined item- and category-level neural representations during the post-199 sleep mental retrieval session. For post-sleep remembered items, contrary to the presleep learning session, we did not find significant clusters showing item-level 200 representations ( $p_{cluster} > 0.455$ , Fig. 2E). However, we found significant category-level 201 representations during ~900-2900 ms time window,  $p_{cluster} = 0.045$ , Fig. 2F). Control 202 203 analyses on post-sleep forgotten items did not reveal any significant clusters for either item- or category-level representations (all *p*s<sub>cluster</sub> > 0.064, Fig. 2G-H). Direct 204 comparison between remembered vs. forgotten items only revealed a significant cluster 205

showing Remember > Forget category-level representations ( $p_{cluster} = 0.017$ ), but there was no significant difference for item-level representations ( $p_{cluster} > 0.233$ , see Fig. S1).



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Fig 2. Neural representations within pre-sleep learning and post-sleep mental

retrieval sessions, respectively. (A-B) During the pre-sleep learning session, 210 significant item-level representations and category-level representations were identified 211 for post-sleep remembered items in the clusters. (C-D) For post-sleep forgotten items, 212 item-level but not category-level representations were identified during the pre-sleep 213 learning session. (E-F) During the post-sleep mental retrieval session, no item-level 214 representations but significant category-level representations were identified for post-215 sleep remembered items in the cluster. (G-H) For post-sleep forgotten items, neither 216 item-level representations nor category-level representations were identified during the 217 post-sleep mental retrieval session. Significant clusters with  $p_{cluster} < 0.05$  were circled by 218 black lines. 219

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We next performed the cross-session RSA to examine the representational
similarity between pre-sleep learning and post-sleep mental retrieval sessions (i.e., PrePost Similarity, Fig. 1B). In line while extending previous study (Liu et al., 2021), we did
not find any significant Pre-Post representational similarities on either item-level (i.e., WI
vs. WC) or category-level (i.e., WC vs. BC) for post-sleep remembered items (all *p*s<sub>cluster</sub> > 0.487, Fig. 3A). However, post-sleep remembered items showed greater Pre-

Post WI and WC similarity than forgotten items (all  $p_{scluster} < 0.049$ , see Fig. S2). These results suggested that while successful memory retrieval leads to greater cross-session neural pattern similarity than forgotten items, there were no discernible item-level or category-level representations preserved from pre- to post-sleep session.

The absence of the cross-session, item-/category-level memory representational 231 similarity could reflect either weakened or changed neural representational patterns 232 across sleep. Previous studies suggested that memory representational pattern changes 233 entailed greater within-session representational similarities than cross-session 234 representational similarities (Liu et al., 2021; Spaak et al., 2017; Stokes, 2015; Xiao et 235 236 al., 2017). We thus compared within-session similarities (Pre-Pre and Post-Post similarity) with cross-session Pre-Post similarity at the item-level and category-level, 237 respectively. To enable direct comparisons, we averaged the Pre-Pre (see Fig. 2) and 238 Pre-Post similarity (see Figure 3 A) within each pre-sleep learning time window and then 239 240 contrasted them across pre-sleep learning time windows (see Methods). Similarly, we contrasted Post-Post similarity with Pre-Post similarity across post-sleep retrieval time 241 242 windows. The results revealed a significant cluster showing greater item-level Pre-Pre 243 similarity than the Pre-Post similarity ( $p_{cluster} = 0.013$ , Fig. 3B), while no significant 244 difference between item-level Post-Post and Pre-Post similarity (p > 0.275, Fig. 3C), which may reflect decayed item-level representations. In addition, for the category-level 245 representations, we found significant clusters indicating that both within-session 246 247 similarities (i.e., Pre-Pre and Post-Post) were significantly greater than the cross-session 248 Pre-Post representational similarity (Pre-Pre > Pre-Post clusters: pscluster < 0.027; Post-Post > Pre-Post clusters: pscluster < 0.032; Fig. 3D-E, see also Fig. S3). These results 249 250 suggested that despite significant category-level memory representations within both pre-sleep learning and post-sleep retrieval sessions, they were transformed into distinct 251 252 formats after an overnight sleep.

To rule out the possibility that pre-sleep testing (on half of word-picture pairs) following pre-sleep learning may influence the overnight memory transformation, we compared the memory representations between pre-sleep tested items and pre-sleep untested items. The results revealed that, among post-sleep remembered items, no

257 significant difference between tested and untested items was found at either the itemlevel or category-level during the post-sleep mental retrieval session (all *p*s<sub>cluster</sub> > 0.152, 258 259 see Fig. S4). In addition, no significant difference was found at either the item-level or category-level Pre-Post similarity (all pscluster > 0.340, see Fig. S4). Similarly, we 260 compared the TMR cued versus uncued items to examine the impact of TMR on 261 memory representations. The results revealed no significant difference at either the 262 263 item-level or category-level during post-sleep mental retrieval session (all ps<sub>cluster</sub> > 0.196, see Fig. S5) and no significant difference at either the item-level or category-level 264 265 Pre-Post similarity (all *p*s<sub>cluster</sub> > 0.195, see Fig. S5). 266



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Fig 3. Cross-session representational similarities and their contrast with the 268 within-session representational similarities. (A) No significant item-level (upper 269 panel) or category-level (lower panel) Pre-Post similarity for post-sleep remembered 270 items in the cross-session RSA. (B-C) The item-level Pre-Post similarity was lower than 271 that within the pre-sleep learning session (i.e., Pre-Pre similarity) but not significantly 272 different from that within the post-sleep retrieval session (i.e., Post-Post similarity). (D-E) 273 The category-level Pre-Post similarity was lower than both the category-level Pre-Pre 274 similarity and Post-Post similarity. Significant clusters were indicated by the shaded 275 276 rectangles. \*:  $p_{\text{cluster}} < 0.05$ .

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# REM/SWS, but not SWS\*REM, is associated with memory representational transformation for remembered items

We next investigated how SWS and REM sleep influence representational
transformation. To answer this question, we first scored the sleep EEG using the
toolbox, Yet Another Spindle Algorithm (YASA, Vallat & Walker, 2021), the results of
which were further verified by an experienced sleep researcher (see Methods; See
Table 1, Fig. S6 for sleep staging). One participant with disconnected EEG recordings
during sleep was excluded, resulting in 34 participants in the following data analysis.

286 We hypothesize that if SWS and REM sleep play complementary roles in memory representational transformation, then the production of SWS% (i.e., percentage in total 287 sleep time) and REM% (SWS\*REM) would be associated with memory transformation 288 indexes, i.e., reduced item-level representational strength and the relatively persistent 289 290 category-level representational strength, and the low Pre-Post similarity for item-level and/or category-level representations. In contrast, if SWS and REM sleep play 291 292 differential roles in memory transformation, then the REM% relative to the SWS% (i.e., REM/SWS) should be associated with memory representational transformation indexes. 293

To test these hypotheses, we computed overnight item-level (or category-level) 294 representational strength change by subtracting the mean strength of Pre-Pre item-level 295 (or category-level) representational similarity from Post-Post item-level (or category-296 level) representational similarity for each participant (i.e., Post minus Pre). We then 297 performed the correlation analysis between SWS\*REM and representational strength 298 299 change across all participants (see Fig. 1C). The results revealed no significant clusters correlating SWS\*REM with either item-level strength change or with the category-level 300 strength change (all *p*s<sub>cluster</sub> > 0.220, corrected by the non-parametric cluster-based 301 permutation test, Fig. 4A-B). In addition, no significant clusters were found correlating 302 303 SWS\*REM with either item-level Pre-Post similarity or category-level Pre-Post similarity 304 (all  $p_{\text{Scluster}} > 0.140$ , Fig. 4C-D).

305 For REM/SWS, we found a significant cluster showing the REM/SWS was negatively correlated with the item-level representational strength change ( $p_{cluster}$  = 306 0.028, within the cluster:  $\beta$  = -0.022, adjusted  $R^2$  = 0.196, p = 0.005, Fig. 4E-F). In 307 contrast, the REM/SWS was significantly positively correlated with the category-level 308 representational strength change ( $p_{cluster} = 0.021$ , within the cluster:  $\beta = 0.014$ , adjusted 309  $R^2$  = 0.126, p = 0.022, Fig. 4G-H). In addition, the results revealed a significant cluster 310 311 showing that REM/SWS was negatively associated with the item-level Pre-Post crosssleep similarity ( $p_{cluster} = 0.008$ , within the cluster:  $\beta = -0.014$ , adjusted  $R^2 = 0.276$ , p < 0.014312 0.001, Fig. 4I-J), while no significant clusters were observed between REM/SWS and 313 category-level Pre-Post similarity ( $p_{scluster} > 0.202$ , Fig. 4K). However, when correlating 314 315 the memory representational transformation indexes with REM% and with SWS% respectively, we only found a significant cluster showing a negative correlation between 316 317 item-level Pre-Post similarity and REM% (see Fig. S7), with the explained 25.2% of inter-participant variance lower than the REM/SWS (27.6%). Control analysis between 318 319 REM/SWS and memory representational transformation indexes among post-sleep forgotten items revealed no significant results (all  $p_{\text{Scluster}} > 0.282$ , see Fig. S8). 320

These results collectively suggest that SWS and REM sleep play differential roles, instead of complementary roles, in memory representational transformation among postsleep remembered items. The greater amount of REM sleep, in contrast to SWS, is associated with significant memory representational transformation across participants, as indexed by the reduced item-level representational strength and enhanced categorylevel representational strength, alongside the reduced item-level cross-session representational similarity.

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## 330 Fig 4. The interactive functional roles of SWS and REM sleep in memory

representational transformation. (A-B) SWS\*REM showed no significant correlation 331 with either item-level or category-level representational strength change (Post minus 332 Pre). (C-D) SWS\*REM showed no significant correlation with Pre-Post item-level or 333 334 category-level representation. (E-F) REM/SWS was negatively associated with itemlevel representational strength change. (G-H) REM/SWS was positively correlated with 335 category-level representational strength change. (I-J) REM/SWS was negatively 336 correlated with item-level Pre-Post similarity. (K) No significant clusters were found 337 between category-level Pre-Post similarity and REM/SWS. Significant clusters with 338 *p*<sub>cluster</sub> < 0.05 were circled by black lines. \*\*\*: *p* < 0.001; \*\*: *p* < 0.01; \*: *p* < 0.05. 339

340

# 341 **REM and SWS EEG power are differentially associated with the neural**

#### 342 representational transformation for remembered items

- 343 Beyond the REM and SWS duration, we next investigated what electrophysiological
- activities during REM sleep and SWS modulate this transformation. Prior studies have

suggested that during REM sleep, frontal theta and beta activities contribute to memory 345 consolidation (Harrington et al., 2021; Nishida et al., 2009; Vijayan et al., 2017). Building 346 347 on these results, we calculated the frontal (F3/4 electrodes) theta (4-7 Hz) and beta (15-25 Hz) power relative to the 1-40 Hz total EEG power (see Methods) across all REM 348 349 sleep epochs. To better examine the effect of REM sleep power across entire overnight sleep on memory representational transformation indexes identified in Fig. 4, we created 350 a comprehensive index of REM sleep power. Specifically, we multiplied the relative 351 power in each frequency band by REM duration, resulting in the total power of each 352 353 frequency band for REM sleep. The robust linear regression revealed that the total theta power during REM sleep was negatively correlated with item-level representational 354 355 strength change within the cluster as shown in Fig. 4E ( $\beta$  = -29.324, adjusted  $R^2$  = 0.142, p = 0.016, Fig. 5A), while positively correlated with category-level 356 357 representational strength change within the cluster as shown in Fig. 4G ( $\beta$  = 21.600, adjusted  $R^2 = 0.134$ , p = 0.019, Fig. 5B). In addition, the total theta power during REM 358 359 sleep was negatively correlated with item-level Pre-Post similarity within the cluster as shown in Fig. 4I ( $\beta$  = -13.693, adjusted  $R^2$  = 0.109, p = 0.032, Fig. 5C). Similarly, total 360 beta band power during REM sleep was negatively correlated with item-level 361 representational strength change ( $\beta$  = -197.000, adjusted  $R^2$  = 0.168, p = 0.009, Fig. 362 363 5D), with a positive but non-significant trend with category-level representational strength change ( $\beta$  = 101.700, adjusted  $R^2$  = 0.044, p = 0.122, Fig. 5E). In addition, the 364 total beta band power during REM sleep was negatively correlated with item-level Pre-365 Post similarity ( $\beta$  = -130.23, adjusted  $R^2$  = 0.242, p = 0.002, Fig. 5F). Note that similar 366 results were found when correlating relative REM theta or beta power with these 367 368 memory representational transformation indexes (see Fig. S9). Further exploratory analysis with other frequency bands power (i.e., delta: 1-3 Hz; alpha: 8-12 Hz; sigma: 369 11-16 Hz) during REM sleep and memory representational transformation indexes did 370 not yield significant results (all ps > 0.102). 371

We next examined, during the SWS, how the canonical frontocentral (Fz and Cz electrodes) 1-4 Hz delta and 11-16 Hz spindle-related sigma power were associated with memory representations transformation indexes. In contrast to REM theta and beta power, total SWS delta power across the overnight SWS sleep (i.e., delta power \* SWS

- amount) was negatively correlated with category-level representational strength change
- $\beta = -5.181$ , adjusted  $R^2 = 0.095$ , p = 0.042, Fig. 5H). No significant correlations were
- found for item-level representational strength change or for Pre-Post similarities (all *ps* >
- 0.195, Fig. 5G, I). In addition, no significant correlation was found between total SWS
- sigma band power and all these memory representational indexes (all ps > 0.183).
- 381 Besides, relative SWS delta power but not sigma power was negatively correlated with
- category-level representational strength change (see Fig. S10).





**Fig 5.** The relationship between sleep EEG power and memory representational

transformation. (A-C) Overall frontal theta power during REM sleep was negatively 386 associated with the item-level strength change (post minus pre) and positively 387 associated with the category-level strength change (post minus pre) and negatively 388 associated with the item-level Pre-Post similarity. (D-F) Overall frontal beta power during 389 REM sleep was negatively associated with the item-level strength change and 390 negatively associated with the item-level Pre-Post similarity. A positive but nonsignificant 391 trend was found between the beta power and category-level strength change. (G-I) 392 Overall frontal-central delta power during SWS was negatively correlated with the 393 category-level strength change. No significant correlation was found between delta 394 power and item-level strength change and Pre-Post similarity. \*\*: p < 0.01; \*: p < 0.05. 395

#### 396 Discussion

Examining neural representations across pre-sleep learning, overnight sleep, and post-397 398 sleep retrieval sessions, we demonstrated that memory representations of individual items were substantially transformed. From pre-sleep learning to post-sleep retrieval, 399 idiosyncratic item-level representation was abolished while categorical representations 400 remained prominent. In addition, the Pre-Post cross-session item-level representations 401 were lower than the Pre-Pre item-level representations, and Pre-Post category-level 402 representations were lower than both Pre-Pre and Post-Post category-level 403 representations. Most importantly, we provide compelling evidence that REM and SWS 404 405 differentially impact memory representational transformation. Specifically, a greater REM sleep to SWS ratio was associated with reduced item-level representational strength, 406 407 increased category-level representational strength across sleep, and was associated 408 with reduced cross-sleep item-level representational similarity.

409 First, our study advances the understanding of overnight memory representational 410 transformation, extending prior research on neural representational transformation 411 observed within minutes or a few hours during wakefulness (Cichy et al., 2014; Favila et al., 2018; Liu et al., 2021; Xiao et al., 2017). Previous research has shown that item-412 413 level memory representations are evident during both encoding and retrieval sessions 414 that occurred within 1-2 hours of wakefulness (Favila et al., 2018). Our findings extend 415 these studies by showing that, after overnight sleep, item-level memory representations were no longer significant, while category-level memory representations were 416 417 persistently prominent from pre-sleep learning to post-sleep retrieval sessions. Our results can be well explained by the functional roles of sleep in transforming memory. 418 Specifically, memory reactivation during the sleep-based consolidation process may 419 facilitate the abstract of the gist information (e.g., the concept of animal) from individual 420 items within the same category (e.g., different animal pictures) (Lau et al., 2011; Lewis & 421 Durrant, 2011). These gist-like semantic category representations were then more likely 422 to survive the global synaptic downscaling and to be extracted during the post-sleep 423 424 wake retrieval (Feld & Born, 2017). Furthermore, we found that cross-session categorylevel representations were lower than the Pre-Pre and Post-Post category-level 425

representations, suggesting distinct category-level representations between these two 426 sessions (Liu et al., 2021; Spaak et al., 2017; Xue, 2022). These results support the 427 428 transformative nature of episodic memory over time (Dudai, 2012; Xue, 2022). In addition, previous research has shown that, after overnight sleep, cortical neural pattern 429 430 similarity between different memory items is enhanced accompanied by increased hippocampal-cortical network connectivity (Cowan et al., 2020). Further study could 431 432 combine the fMRI and sleep EEG to test whether different brain networks were engaged during sleep-mediated memory representational transformation at the item- and 433 434 category-level.

Most critically, our study addressed an under-investigated question: how SWS and 435 REM sleep contribute to the sleep-based memory transformation (Diekelmann & Born, 436 2010; Inostroza & Born, 2013; Landmann et al., 2014; MacDonald & Cote, 2021; Payne, 437 2011). Despite some studies suggesting the interactive functional role of SWS and REM 438 sleep in memory enhancement (Batterink et al., 2017; Mednick et al., 2003; Stickgold et 439 al., 2000), most sleep research focused on the relationship between a single sleep stage 440 441 (e.g., either SWS or REM) and behavioral changes, leading to mixed results (Cai et al., 442 2009; Durrant et al., 2015; Hennies et al., 2017; Ketz et al., 2018; Lau et al., 2010; Pereira et al., 2023; Tamminen et al., 2013). In our study, we systematically examined 443 the complementary and differential roles of SWS and REM sleep in memory 444 representational transformation. Our findings provided novel evidence that a greater 445 amount of REM sleep is associated with greater memory representational 446 447 transformation, while a reversed pattern was observed for SWS. These results support Payne's hypothesis (2011) and sleep reinforcement and refinement hypothesis 448 449 (MacDonald & Cote, 2021), both of which emphasize the critical role of REM sleep in memory representational transformation and the role of SWS in stabilizing memory in its 450 451 original format. Note that the differential roles of REM sleep and SWS may also vary depending on the tasks, such as the emotional memory task (Cairney et al., 2015), rule 452 453 abstract task (Pereira & Lewis, 2020), creative problem-solving task (Lewis et al., 2018), as well as being affected by the amount of information being learned pre-sleep (Feld & 454 455 Born, 2017), which warrants future research.

Regarding the electrophysiological mechanisms, our results showed that both the 456 REM sleep duration and REM sleep theta and beta power contribute to memory 457 458 representational transformation. Corroborating our findings, previous research showed that both REM sleep duration and REM sleep EEG theta power were positively 459 460 correlated with the consolidation of schema-conformant memory items (Durrant et al., 2015). In addition, REM sleep amount was positively associated with facilitated semantic 461 462 processing (Carr & Nielsen, 2015; Stickgold et al., 1999). Together with these studies, our results suggested that REM sleep facilitates memory reorganization within pre-463 464 existing semantic networks or schema. Therefore, it results in more gist-like memory representations which may resist interference (Payne, 2011; Tamaki et al., 2020). Our 465 466 findings also align well with animal studies, which emphasize the REM sleep theta oscillation in memory consolidation. Specifically, the coherence of amygdalocortical 467 theta oscillations during REM sleep predicts the behavioral changes in fear-conditioned 468 cued memory recall (Popa et al., 2010). Selectively suppressing the theta oscillation 469 470 during REM sleep leads to impaired fear-conditioned contextual memory. In addition to the theta oscillation, a recent human intracranial EEG study has observed beta 471 oscillations during REM sleep (Vijayan et al., 2017), which couple with theta activity 472 (Cox et al., 2019). In line with these studies, our findings showed similar functional roles 473 of REM sleep theta and beta activities in memory representational transformation. 474

475 Notably, sleep-mediated memory representational transformation was specifically documented among post-sleep remembered items, whereas no such effect was found 476 477 among post-sleep forgotten items. Thus, the documented transformation is an adaptive process supporting long-term memory (Xue, 2022). Previous studies suggested that 478 479 SWS duration as well as the sigma and delta power during SWS were associated with overall better memory retention, as indicated by behavioral performance changes across 480 481 all post-sleep remembered and forgotten items (Holz et al., 2012; Scullin, 2013). Although we focused on memory representations rather than overall memory 482 483 performance, our supplementary analysis did reveal individual differences in the duration of SWS were positively correlated with better memory retention across all pre-484 485 sleep tested items (see Fig. S11). However, among post-sleep remembered items, we found the greater delta power during the SWS was associated with lower post-sleep 486

category-level representational strength compared to pre-sleep. While the active
systems consolidation model proposes that memory representations are repeatedly
reactivated during SWS, possibly facilitating the memory transformation into more gistlike representations (Born & Wilhelm, 2012), our study suggests that this SWS-mediated
process alone may not necessarily facilitate the gist-like representational formation.

492 While participants were capable of retrieving the individual pictures associated with 493 their corresponding auditory cues in the post-sleep written report, we did not find 494 significant item-level neural representations during post-sleep mental retrieval for remembered items. Diminished item-level memory representations could be due to 495 496 global synaptic down-scaling during sleep (Tononi & Cirelli, 2014). As a result, these 497 neural representations may be less likely to be detected using scalp EEG. In addition, the current study included TMR during the SWS (Liu et al., 2023). However, the 498 functional roles of SWS and REM sleep in modulating memory representational 499 transformation are unlikely to be driven by TMR, given the non-significant cued vs. 500 uncued differences at item-/category-level representations from both the Post-Post and 501 the Pre-Post RSA (see Fig. S5). Nevertheless, we acknowledge that our study cannot 502 rule out the possibility that TMR that occurs during SWS may trigger memory 503 504 representations into labile states which allows memory representations to be transformed during subsequent REM sleep (Batterink et al., 2017; Tamminen et al., 505 506 2017). Future studies should further examine the interactive functional roles of REM and 507 SWS in memory representational transformation during spontaneous overnight sleep.

508 Overall, our study demonstrates overnight memory transformation: while memory representations containing both item- and category-level representations during pre-509 510 sleep learning, only category-level representations were dominant post-sleep. More importantly, REM sleep and SWS played differential roles in the representational 511 512 transformation: the greater amount of REM sleep, relative to the SWS, was associated with greater memory representational transformation. These findings advance our 513 514 understanding of the interactive functional roles of human SWS and REM sleep in memory consolidation and transformation. 515

516

#### 517 Methods

#### 518 **Participants**

519 Thirty-five healthy, right-handed participants were included in the study (females, mean 520 age  $\pm$  SD: 22  $\pm$  2.79 years). Two additional participants who exhibited significant body movements during pre-sleep learning/ post-sleep mental retrieval sessions were 521 522 excluded during initial data visual inspection and screening. Behavioral and wakefulness 523 EEG data analysis were performed on all the 35 included participants. However, for the 524 sleep EEG data analysis, one participant was excluded due to disconnected EEG recordings in the middle of overnight sleep, resulting in a final sample size of 34 525 526 participants in sleep analyses. Prior to participation, all participants underwent prescreening for sleep quality using the Pittsburgh Sleep Quality Index (PSQI) and the 527 528 Insomnia Severity Index (ISI), ensuring overall good sleep quality. They had not taken any sleep-aid medicines in the past month prior to the experiment. All participants were 529 not diagnosed with any neurological or psychiatric disorders and had normal or 530 corrected-to-normal vision. The study was approved by the Research Ethics Committee 531 532 of the University of Hong Kong. All participants gave written informed consent prior to participation. 533

## 534 **Experimental design**

The experiment encompassed three primary sessions: (1) a pre-sleep session, including a word-picture associative learning task and pre-sleep memory tests, (2) an overnight sleep session with targeted memory reactivation (TMR) administered during NREM sleep for the initial 3-4 sleeping hours, and (3) a post-sleep session, including a postsleep mental retrieval task and memory tests. All the behavioral tasks were administered using PsychoPy (version: 2020.2.10; https://www.psychopy.org/).

541 During the pre-sleep word-picture associative learning task, participants were instructed 542 to memorize a total of 96 distinct word-picture pairs. The 96 words were two-character 543 Chinese verbs, while the corresponding pictures were naturalistic images. Each picture 544 fell into one of four categories, namely animals, electronic devices, plants, and 545 transportation tools, with 24 pictures in each category. Each word was randomly paired

with a picture for each participant. Each learning trial consisted of three phases: 546 encoding, maintenance, and vividness rating. During encoding, participants were 547 548 presented with a fixation cross for 0.3 s, followed by a black screen with jittering durations between 0.9 to 1.5 s. Subsequently, a picture was displayed at the center of 549 550 the screen for 2 s, accompanied by the auditory presentation of the corresponding spoken verb. Participants were explicitly instructed to focus their attention on the picture 551 552 and memorize the associations between the verbs and the pictures. In the immediately following maintenance period, the presented picture disappeared, and participants were 553 554 instructed to vividly mentally maintain the picture for a duration of 3 s while hearing the spoken verb again. In the vividness rating phase, participants were required to evaluate 555 556 the subjective vividness of the mental image they held during the maintenance period on a scale from 1 (not vivid at all) to 4 (very vivid) within 2 s. The entire pre-sleep learning 557 task consisted of three blocks, with each block consisting of 32 distinct verb-picture pairs 558 559 and each pair repeated three times within a block. To minimize the potential influence of 560 the recency effect, participants engaged in a ~5-minute math task immediately after completing the learning task. 561

562 After the distractor math task and a short break (~5 minutes), half of the pairs (i.e., 48 563 pairs) were tested via the cued category-report task and the cued recognition task presleep. In the cued category-report task, each trial started with a 0.3 s fixation, followed 564 by a blank screen (0.9-1.5 s). The spoken verb was played, prompting participants to 565 report whether they "remember" or "forget" the corresponding picture. This stage was 566 567 self-paced so that participants had enough time to recall. Following the "remember" or "forget" response, participants were asked to report the category of the picture by 568 569 pressing one of four buttons, with each button representing one of the four categories. In the cued recognition task, the same half of the pairs were tested. Each recognition trial 570 571 began with a fixation (0.3 s) and was followed by a blank screen (0.9-1.5 s). Participants were then presented with the picture (either a pre-learned picture or a similar lure 572 573 picture) in the center of the screen while simultaneously hearing the corresponding spoken verb. They were asked to indicate if the picture was the same picture paired with 574 575 the verb during the previous learning task by pressing the "Yes" or "No" button. After the pre-sleep test, participants went to sleep from approximately 12 am to 8 am. Targeted 576

577 memory reactivation cueing was delivered during SWS in the first 3-4 hours after 578 participants fell asleep (see Liu et al., 2023 for more details).

579 Approximately 30 minutes after awakening in next morning, participants were tested on all 96 pairs. The post-sleep test included the same cued recall and cued recognition 580 tasks, with an additional mental retrieval task in between. The mental retrieval task was 581 particularly designed to examine the neural representations during the post-sleep 582 retrieval task. Specifically, participants were asked to keep their eyes closed throughout 583 the entire testing block, during which they were asked to mentally retrieve the 584 associated picture as vividly as possible while hearing the auditory verbs, without any 585 586 explicit behavioral responses. These auditory verbs were randomly played via the speaker with an interstimulus interval (ISI) of  $5 \pm 0.2$  s, comparable to the trial length 587 during pre-sleep learning. Each auditory cue was repeated three times. After the 588 completion of the mental retrieval task, participants were provided with a printed form 589 590 containing all the cue verbs presented during the mental retrieval task. They were then asked to write down the specific content they retrieved during the mental retrieval task 591 592 for each cue verb. We then code the participants' retrieval performance as follows: if the 593 written content accurately represented the central elements of the corresponding picture, it was labeled as "remember"; if the written content described was incorrect or 594 left blank, it was labeled as "forget". TMR cued and uncued items (t(34) = -1.68; p =595 0.102) showed no significant difference in the post-sleep retrieval performance, we 596 597 thereby performed all the analyses after combining cued and uncued items in individual 598 participants.

#### 599 **EEG recording and preprocessing**

EEG data were continuously collected from pre-sleep learning to post-sleep tests,
including the overnight sleep, using the amplifier from the eego system (ANT neuro,
Netherlands, <u>https://www.ant-neuro.com</u>). Data were sampled at 500 Hz using 64channel waveguard EEG caps, among which 61 channels were mounted in the
international 10-20 system, while two electrodes were placed on the left and right
mastoids, and one electrode was positioned above the left eye for EOG measurements.
During the sleep EEG recordings, two additional electrodes were placed on both sides

of the chin to measure the electromyogram (EMG) using a bipolar reference

- 608 configuration. Prior to EEG recordings, impedance levels for all channels were
- maintained below 20 KΩ. During online EEG recordings, the default reference channel
- 610 (CPz) was used. Offline preprocessing of the EEG data was conducted using the
- 611 EEGLAB (https://sccn.ucsd.edu/eeglab/) and Fieldtrip (<u>https://www.fieldtriptoolbox.org/</u>)
- toolboxes, as well as custom MATLAB code.
- Specifically, EEG data were first notch filtered at  $50 \pm 2$  Hz, and then bandpass filtered 613 between 0.5 and 40 Hz. The continuous EEG data during the pre-sleep learning task 614 were segmented into epochs spanning from 3000 ms before until 8000 ms after stimulus 615 616 onset. This long epoch was used to eliminate the edge effect in the subsequent timefrequency analysis. Our main interesting time windows for the pre-sleep learning data 617 are from 0 to 5 seconds relative to the stimulus onset. Similarly, for the post-sleep 618 619 mental retrieval data, the continuous EEG data were segmented into epochs spanning 620 from 3000ms before until 8000ms after the auditory word onset, with our interesting time windows from 0 to 5000ms post auditory word onset. Epochs affected by the muscle 621 622 movements were visually inspected and excluded from further analysis. Eye blinks and movements were corrected using the independent component analysis. Any identified 623 624 bad channels were interpolated using spherical interpolation in EEGLAB. Subsequently, the EEG data were re-referenced to the average of the artifact-free data across all 625 channels. For both the pre-sleep learning and the post-sleep retrieval data, EEG epochs 626 627 were categorized into post-sleep remembered or forgotten trials based on the accuracy 628 of the written reporting immediately following the post-sleep mental retrieval.

## 629 Sleep scoring

Sleep scoring was conducted on non-overlapping 30-second epochs using the Yet
Another Spindle Algorithm (YASA), an open-source, machine learning-based toolbox
known for its high performance in sleep analysis (Vallat & Walker, 2021). Prior to sleep
scoring, bad channels in the EEG data were marked and interpolated. To align with the
recommendations of the YASA toolbox, EEG data were re-referenced to FPz. For sleep
scoring, the C4 electrode, as well as the EOG and EMG channels, were used as inputs

to the YASA algorithm. The scoring results were then double-checked and corrected byan experienced sleep researcher to ensure accuracy and reliability.

#### 638 **Time-frequency analysis**

639 For both the pre-sleep learning and post-sleep mental retrieval stages, the epoched EEG data underwent time-frequency analysis using complex Morlet wavelets (six 640 641 cycles). The frequency range of interest was from 2 to 40 Hz, with a step size of 1 Hz. The time window of interest was from -1 to 5 seconds relative to the stimulus onset. To 642 obtain the spectral power, the magnitudes of the complex wavelet transform were 643 squared. The power data were then normalized by subtracting the mean power in the 644 645 baseline time windows and then dividing by its mean power within each frequency bin 646 and each channel. For both the pre-sleep learning and post-sleep mental retrieval EEG 647 data, the baseline time window was defined as -0.7 to -0.4 seconds relative to the stimulus onset. All spectral power data were subsequently downsampled to 100 Hz and 648 re-segmented into 5-second epochs, specifically [0 to 5 s] relative to the stimulus onset. 649 The spectral power within this broad frequency range [2 to 40 Hz] and epoch duration 650 651 were used as features for subsequent representational similarity analyses.

## 652 Oscillatory power estimation during SWS and REM sleep

For sleep EEG data, we first epoched the continuous sleep EEG into 30-second epochs. 653 To separate the oscillatory power from the 1/f power-law effect (i.e., fractal component), 654 we employed Irregular-Resampling Auto-Spectral Analysis (IRASA, Wen & Liu, 2016)). 655 656 Specifically, for each raw sleep epoch data, IRASA first segmented them into ten equally sized, partially overlapped segments, with each covering 90% of the epoch. It then 657 658 computed the power spectral density (PSD) of these segments of the raw data using the fast Fourier transform (FFT) with the function of a Hanning window. Afterward, it 659 irregularly resamples each segment by factors of h (ranging from 1.1 to 1.9 in 660 increments of 0.05) and 1/h. It uses cubic spline interpolation for irregular upsampling 661 662 and anti-aliasing low-pass filtering followed by cubic spline interpolation for irregular downsampling. Then the PSD of the resampled data was computed using the same 663 664 FFT. It then calculated the geometric mean of the auto-power spectra for each h value across upsampled and downsampled signals for each segment. The median of the 665

power spectral with all h-values for each frequency was obtained to estimate the power 666 spectrum of the 1/f power-law effect (i.e., fractal component). We then average the 667 668 estimated power spectrum of the fractal component and the original signal's power spectrum across all time segments for each sleep EEG epoch. The oscillatory power of 669 670 the PSD for individual epochs was then estimated by subtracting the average power spectrum of the fractal component from the PSD of the raw data. Oscillatory power 671 672 between 1 to 40 Hz for SWS and for REM sleep was obtained by averaging the oscillatory component across epochs labeled as 'N3' (SWS) and 'REM', respectively. 673 674 Canonical sleep oscillations were defined as follows: delta band (1-3 Hz), theta band (4-675 7 Hz), sigma band (11-16 Hz), and beta band (15-25 Hz). For REM sleep, frontal theta 676 and beta band power were calculated by averaging the oscillatory power from F3 and F4 channels (Marquis et al., 2017; Nishida et al., 2009; ten Brink et al., 2023). For SWS, 677 delta and sigma band power were calculated by averaging the oscillatory power from Fz 678 and Cz channels (Mander et al., 2015; Marshall et al., 2003). 679

#### 680 Representational similarity analysis (RSA)

681 To analyze the neural representations over time, the RSA was performed between the artifact-free trials by correlating the spectral power across frequencies (i.e., 2-40 Hz) and 682 683 across all scalp channels in sliding time windows. For both the pre-sleep learning and 684 post-sleep retrieval sessions, the length of sliding time windows was 500 ms, with an 685 incremental step size of 100 ms. To increase the signal-to-noise ratio, the spectral power was averaged across time points within each time window, as in previous studies 686 687 (Liu et al., 2021). This resulted in a set of features consisting of 39 (frequency) by 61 (channel) values for each time window. Then, for each time window, we calculated the 688 similarity between vectorized features of every two trials that were using Spearman's 689 corrections. All the correlation values were Fisher Z-transformed before further statistical 690 analysis. 691

692 We categorized representational similarity values into three types: within-item (WI)

similarity, within-category (WC) similarity, and between-category (BC) similarity. These

694 categories were based on the corresponding pictures used in the trial pairs for

calculating similarity values. WI similarity refers to the similarity between two trials that

share the same pictures. WC similarity refers to the similarity between two trials that

- involve different pictures from the same category. BC similarity refers to the similarity
- 698 between two trials that involve pictures from different categories. Comparing WI
- similarity to WC similarity enables us to examine the item-level neural representations
- while comparing WC similarity to BC similarity enables us to examine the category-level
- representations (Lee et al., 2019; Ritchey et al., 2013).
- 702 The representational similarity was computed either across repetitions within each task 703 session (i.e., within-session RSA) or between two different sessions (i.e., cross-session RSA). Within the pre-sleep learning session, RSA was conducted on distinct learning 704 705 trials, yielding the Pre-Pre similarity (see Fig. 1). Within the post-sleep mental retrieval 706 session, the RSA was performed between different post-sleep mental retrieval trials, resulting in the Post-Post similarity. Cross-session RSA was conducted between trial 707 pairs, with one trial originating from the pre-sleep learning session and the other from 708 709 the post-sleep retrieval session. This analysis yielded the Pre-Post similarity. Given that 710 both within-session RSA and cross-session RSA allowed us to compute WI, WC, and 711 BC similarities, we could examine item-level and category-level representations for Pre-712 Pre similarity, Post-Post similarity and Pre-Post similarity.
- 713 To enable the comparisons of the within-session representational similarity with cross-714 session representational similarity, we compared the Pre-Pre similarity versus Pre-Post 715 similarity across pre-sleep learning time windows and compared the Post-Post similarity versus Pre-Post similarity across post-sleep mental retrieval time windows. Specifically, 716 717 for a Pre-Pre two-dimensional similarity matrix C (either item-level or category-level representations, see Fig. 2), we first averaged the matrix along its first dimension *j*, 718 719 resulting in the averaged similarity values for each pre-sleep learning time window in the 720 second dimension *i*:

$$\bar{C}_i = \frac{1}{N} \sum_{j=1}^{N} C_{ij}$$

721

Similarly, we averaged the similarity matrix *C* along the second dimension *i*, resulting in the averaged similarity values in the first dimension *j*:

$$\bar{C}_j = \frac{1}{N} \sum_{i=1}^N C_{ij}$$

We then obtained the Pre-Pre similarity values for individual pre-sleep learning time 725 windows by further averaging the  $\bar{C}_i$  and  $\bar{C}_i$ . For the Post-Post similarity, we used the 726 same computation to obtain the item-level and category-level similarity values for 727 individual post-sleep retrieval time windows. For the Pre-Post similarity matrix, we 728 729 averaged it within each pre-sleep learning time window, enabling us to compare it with the Pre-Pre similarity across pre-sleep learning time windows. We averaged the Pre-730 731 Post similarity matrix within each post-sleep retrieval time window, enabling us to compare it with the Post-Post similarity across post-sleep retrieval time windows. 732

733 For the statistical analysis of representational similarity values across consecutive time 734 windows, multiple comparison corrections were applied using cluster-based nonparametric tests in MATLAB (Maris & Oostenveld, 2007). Specifically, we first 735 conducted statistical tests, such as paired *t*-tests, between conditions (e.g., WI vs. WC 736 or WC vs. BC) within individual time windows. Adjacent time points with significant 737 738 statistical values (p < 0.05) were grouped to form clusters, and cluster-level statistics 739 were calculated by summing t-values within clusters. To determine cluster significance, 740 a null distribution of cluster-level statistics was generated by randomly permuting condition labels 1000 times. For each permutation, the maximum cluster-level statistic 741 was identified. In cases where no significant cluster was observed in a permutation, a 742 743 value of 0 was assigned. The proportion of cluster-level statistics in the null distribution 744 exceeding the empirical cluster-level statistic determined nonparametric significance.

# Correlation analysis between REM/SWS (or SWS\*REM) and representational transformation indexes

We obtained the REM/SWS by dividing the REM amount (i.e., the percentage of REM sleep in total sleep time) by the SWS amount (i.e., the percentage of SWS in total sleep time). Similarly, the SWS\*REM was obtained by multiplying the SWS amount by the REM sleep amount. There are four pre-defined representational transformation indexes in the study: item-level representational strength change (post minus pre), category-level representational strength change (post minus pre), item-level Pre-Post similarity, and

753 category-level Pre-Post similarity. To calculate item-level and category-level representational strength changes, we first obtained averaged Pre-Pre similarity 754 755 matrices across trial pairs for each participant during pre-sleep learning, separately for item-level and category-level representations. Each similarity matrix was then further 756 757 averaged across all 5-second time windows, resulting in a mean value representing either the pre-sleep item-level or the category-level representational strength for each 758 759 participant. For each participant, we also obtained averaged item-level and categorylevel Post-Post similarity matrices across trial pairs. The mean strength of the pre-sleep 760 761 item-level or category-level representational similarity was then subtracted from the corresponding Post-Post similarity matrices, resulting in item-level and category-level 762 763 representational strength change matrices. For each time window, we computed Spearman's correlations between representational strength changes and REM/SWS (or 764 SWS\*REM) across participants (see Fig. 1C). Similarly, for each window of the Pre-Post 765 similarity matrices, we performed the Spearman's correlation between the item-level (or 766 767 category-level) similarity values with the REM/SWS (or SWS\*REM) across participants. These analyses resulted in correlation coefficient matrices, which were then Fisher Z-768 769 transformed. The correlation analysis across time windows was corrected for using 770 cluster-based nonparametric tests as mentioned above. Briefly, the empirical cluster-771 level statistics were obtained by summing the transformed correlation coefficients across adjacent time windows with significant correlation (i.e., p < 0.05). The null distribution of 772 cluster-level statistics was obtained by shuffling the order of participants for REM/SWS 773 774 (or SWS\*REM) 1000 times while keeping the order of participants for the representational transformation index matrix unchanged. For each shuffling, the same 775 776 correlation analysis was conducted, and the maximum cluster-level statistic was identified. The nonparametric significance of a cluster was determined by calculating the 777 proportion of cluster-level statistics in the null distribution exceeding the empirical 778 cluster-level statistic. 779

780

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# 790 Author contributions

- 791 Conceptualization, J.L. and X.H.; methodology, J.L.; investigation, J.L.; formal analysis,
- J.L.; writing original draft, J.L. and X.H.; writing review & editing, J.L., D.C., T.X.,
- S.Z., G.X. and X.H.; resources, J.L. and X.H.; visualization, J.L. and D.C.; supervision,
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- 795

# 796 **Declaration of interests**

- The authors declare that they have no competing interests.
- 798

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