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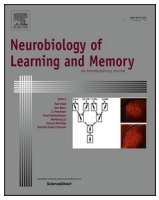

The effect of fasting on human memory consolidation

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ABSTRACT

The consolidation of long-term memory is thought to critically rely on sleep. However, first evidence from a study in *Drosophila* suggests that hunger, as another brain state, can benefit memory consolidation as well. Here, we report two human (within-subjects crossover) experiments examining the effects of fasting (versus satiated conditions) during a 10-hour post-encoding consolidation period on subsequent recall of declarative and procedural memories in healthy men. In Experiment 1, participants (n = 16), after an 18.5-hour fasting period, encoded 3 memory tasks (word paired associates, a visual version of the Deese-Roediger-McDermott task, finger tapping) and subsequently either continued to fast or received standardized meals. Recall was tested 48 h later in a satiated state. Experiment 2 (n = 16 participants) differed from Experiment 1 in that a What-Where-When episodic memory task replaced the Deese-Roediger-McDermott task and recall was tested only 24 h later in a fasted state. Compared with the satiated state, fasting enhanced cued recall of word paired associates (more correct and faster responses) and item recognition in the What-Where-When task. By contrast, fasting impaired recall of episodic context memory, i.e., spatial context in the Deese-Roediger-McDermott task, and temporal-spatial context in the What-Where-When task. Procedural memory (finger tapping) remained unaffected. This pattern suggests a differential effect of fasting selectively promoting consolidation of semantic-like representations in cortical networks whereas hippocampal representations of episodic context are weakened. We speculate that hunger strengthens cortical representations by suppressing hippocampal interference during wake consolidation. Yet, the underlying mechanism remains to be clarified.

1. Introduction

Memory consolidation refers to a process by which newly encoded representations are transformed into more persistent long-term representations (Müller & Pilzecker, 1900). It is thought to crucially depend on the brain's state, with sleep representing the state most strongly promoting the consolidation of representations into long-term memory. Consolidation during sleep has been conceptualized as an active systems consolidation process that mainly impinges on hippocampus-dependent declarative memory and supports the transformation of newly encoded episodic memories into more abstract, semantic memories (Brodt et al., 2023; Diekelmann & Born, 2010; Klinzing et al., 2019). This transformation process likely evolves via repeated replay of hippocampal neuronal representations during sleep that produces a gradual redistribution of the representations towards extrahippocampal, neocortical knowledge networks serving as long-term store (Hardt & Nadel, 2018; Sekeres et al., 2018). Notably, through the hippocampal replay mechanism, sleep also supports consolidation of non-declarative types of memory, e.g., for procedural motor skills (Sawangjit et al., 2018, 2022; Schapiro et al., 2019).

Although sleep is commonly considered an optimal brain state that is, perhaps, even critical to consolidating long-term memory, it may not

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be the only one serving this function. Indeed, some findings in humans and animal models have nurtured the idea that memory consolidation might also profit from a state of starvation. For example, in *Aplysia,* short-term fasting produced an enhancement of aversive memory, likely mediated by an increase of insulin levels in the CNS (Totani, Nakai, Dyakonova, et al., 2020a; Totani, Nakai, Hatakeyama, et al., 2020b). In rodent studies, short-term fasting facilitated fear extinction memory (Huang et al., 2016; Verma et al., 2016), whereas excessive food intake impaired hippocampus-dependent memory (Mattson, 2019; Stranahan et al., 2008). However, these experiments remained basically inconclusive because they did not separate the effects of starvation on processes of consolidation from those on memory encoding and recall.

Only recently, a study in *Drosophila* has provided clear evidence that starvation specifically supports memory consolidation (Chouhan et al., 2021). These experiments employed an appetitive conditioning task requiring flies to associate sucrose as the unconditioned stimulus with a specific odor. Successful encoding of the association requires that the flies are starved. When, after conditioning, the flies continued to starve, they showed well-preserved memory for the odor-sucrose association on a recall test one day later, whereas the association was forgotten when they were fed after encoding. Importantly, flies that were starved after encoding consolidated the memory while they were kept awake, dissociating hunger-related consolidation as a process separate from sleep-associated consolidation, and thus representing an alternative route to long-term memory formation.

Inspired by these findings in fruit flies, the present study aimed to explore the possibility of hunger-mediated consolidation of memory in humans. In two experiments, we tested effects of fasting on the consolidation of declarative memories with more or less pronounced semantic versus episodic features, using a word paired-associates task, a visual version of the Deese-Roediger-McDermott (DRM) paradigm, and an episodic "What-Where-When" task. We also tested non-declarative procedural memories for finger sequence tapping skills. In order to manipulate hunger specifically during the post-encoding consolidation period, like the flies in the study by Chouhan et al. (2021), our participants encoded the tasks being fasted and only after encoding they received standardized meals in the "Satiated" control condition but continued to fast in the experimental "Fasting" condition. Delayed recall was tested with participants being fully satiated (Experiment 1) or again fasted as during encoding (Experiment 2). We found consistent improving effects of hunger on the consolidation of semantic aspects in declarative memory whereas consolidation of episodic aspects appeared to be rather impaired by fasting. No clear effects emerged for procedural finger tapping skills.

2. Experiment 1

2.1. Material and methods

2.1.1. Participants

Sixteen healthy men (mean age ± SD: 22.56 ± 3.69 years; range: 18–29 years) participated in the experiment. Only male participants were included to reduce heterogeneity related to menstrual cycle-associated variation in endocrine and metabolic parameters (e.g., Barbieri, 2014; Benton et al., 2020), as well as memory consolidation, in this initial proof-of-principle study (e.g., Genzel et al., 2012; Ikarashi et al., 2020). The group size was calculated based on a medium-to-strong effect size of $d = 0.75$ ($1 - \beta = 0.8$, $\alpha = 0.05$), as a conservative estimate deriving from a study by Witte et al. (2009) investigating fasting and verbal memory performance in humans. In addition, we considered related studies in animals (Chouhan et al., 2017, 2021; Huang et al., 2016; Verma et al., 2016), and human studies using similar tasks to test sleep effects on memory consolidation (e.g., Gais et al., 2006; Wilhelm et al., 2011; Drosopoulos et al., 2007; Ngo et al., 2013; Weber et al., 2014; Lutz et al., 2017; Walker et al., 2002), which yielded overall large effect sizes. One participant was excluded from the analyses as he did not adhere to the fasting protocol before the encoding session. Participants had regular sleep-wake cycles, normal sleep quality (Pittsburgh Sleep Quality Index, PSQI ≤ 6), were right-handed, had a BMI of 22.21 ± 2.50 kg/m^2 (range 17.92–25.68 kg/m^2), and normal or corrected-to-normal vision. None had neurological or psychological impairments, had taken psychoactive medication during the previous 8 weeks, or was on shift work during the previous 4 weeks. Participants gave written informed consent prior to participation and were paid for participating. The experiments were approved by the Ethics Committee of the Medical Faculty of the University of Tübingen.

2.1.2. Design and procedure

The experiments were performed according to a within-subject cross-over comparison with each participant participating in two conditions (Satiated vs. Fasting) separated by at least four weeks. Participants were kept unaware about the condition until the end of the encoding phase (see below). The order of conditions was counterbalanced across participants. Each condition lasted four days (day 0 – day 3) and comprised an encoding, consolidation, and retrieval phase (Fig. 1A).

Before the beginning of each experimental condition, participants were required to keep a regular diet (breakfast, lunch, snack, dinner, for 2 days before), not to consume caffeine or alcohol (2 days before), and not to take naps (7 days before). On day 0, participants arrived at the laboratory at 12:30 h (after a regular morning breakfast). After completing initial questionnaires that tested inclusion and exclusion criteria, they received a standardized lunch at 13:00 h. Afterwards, diaries were distributed (to be filled in every morning until day 3) and participants were asked to start fasting (i.e., to abstain from any food including sweetened drinks, caffeine and alcohol). Water and fruit tea were allowed. Adherence to the fasting protocol was ensured by an evening call by the experimenter.

On day 1, participants returned to the lab at 08:00 h. Blood glucose concentration was assessed. During the following encoding phase, three memory tasks were performed (always in the same order), i.e., a Word Paired-Associates (WPA) learning task, a Finger Tapping Task (FTT), and a visual Deese-Roediger-McDermott (DRM) task. Tasks were separated by 10-min breaks during which participants played a simple computer game ('Snood'). After encoding, participants completed a Psychomotor Vigilance Test (PVT), a Digit Span test, a Verbal Fluency test (Regensburger Wortflüssigkeitstest, RWT), and the Stanford Sleepiness Scale (SSS).

After the encoding phase, participants were allocated to the experimental conditions. In the Satiated condition, participants received standardized meals during the experimental consolidation phase at 10:00 h (breakfast), 13:00 h (lunch), 15:00 h (snack), and at 18:00 h (dinner). In the Fasting condition, participants continued to fast until 18:00 h when they also received a standardized dinner. Participants left the lab at ~ 18:30 h. During the consolidation phase, participants engaged in standardized activities (watching documentary films, walking outdoors, playing card games).

On day 2, participants stayed at home, maintaining their regular diet (breakfast, lunch, dinner, snacks), and recorded their daily activities. On day 3, participants returned to the lab (after regular breakfast and lunch) and received a standardized dinner at 17:00 h, followed by a blood glucose test. The subsequent retrieval phase comprised testing on the three memory tasks (in the same order as encoded). Then, the control tasks (PVT, Digit Span, RWT, SSS) and a final debriefing were performed.

2.1.3. Standardizing food intake

The standardized meals were chosen to be not particularly tasty (e.g., not too sweet) to diminish positive reinforcement effects. They were scaled according to the participant's daily calorie requirement as calculated based on their height, weight, and age, corrected for exercise frequency. Breakfast, lunch, and dinner each accounted for 30 % of the daily calorie requirements, while the remaining 10 % were eaten as

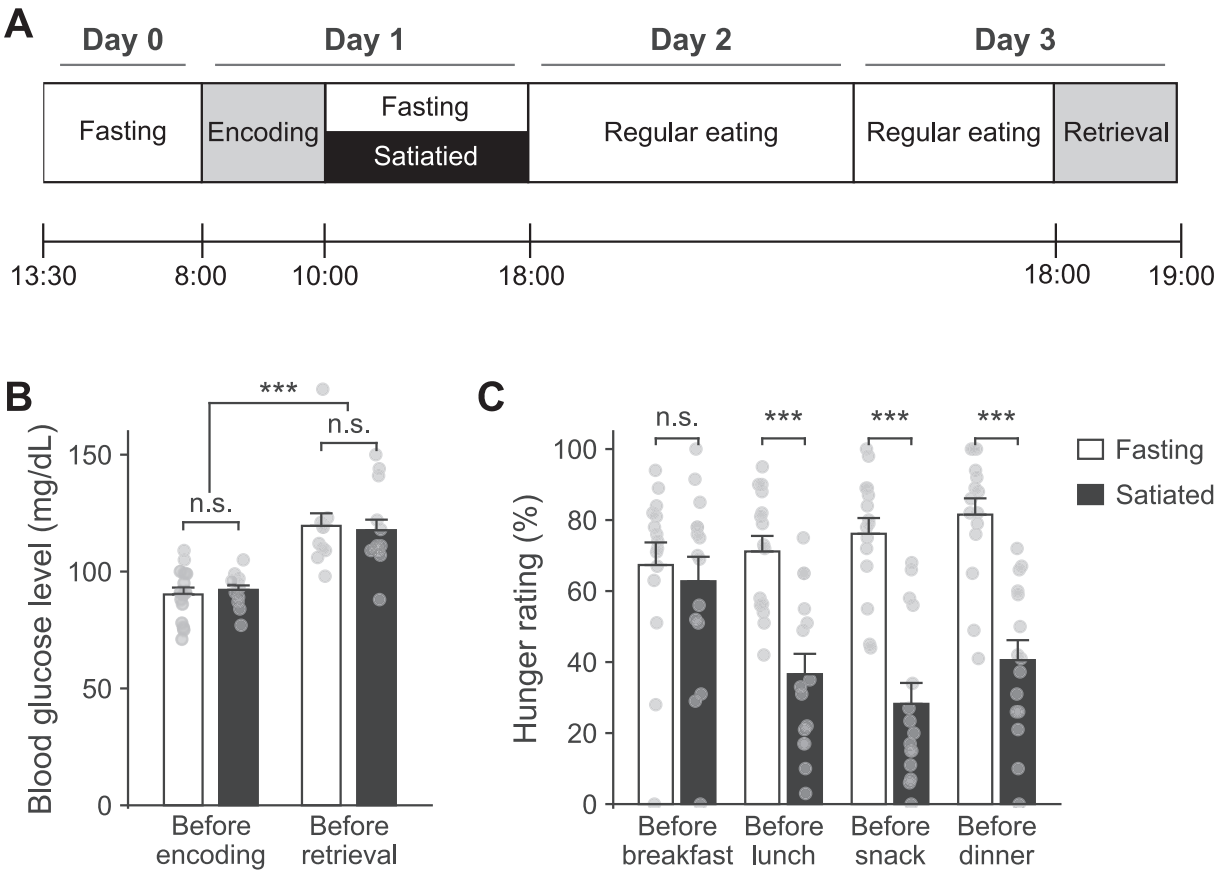

Fig. 1. Experiment 1. A) Experimental design. Participants took part in in both a Fasting condition and a Satiated condition, with the order of condition counterbalanced across participants. In both conditions, they started fasting after a standardized lunch at 13:30 h on day 0. On day 1, encoding took place at 08:00 h in the fasted state. Thereafter, participants continued fasting throughout the 8-hour experimental consolidation phase (Fasting condition) or received standardized meals (breakfast, lunch, afternoon snack; Satiated condition). In both conditions, participants received a standardized dinner at 18:00 h. On days 2 and 3, participants had regular meals at home. On day 3, they received a standardized dinner at 17:00 h before retrieval testing at 18:00 h. B) Blood glucose levels (mg/dL) before encoding and retrieval in the Fasting and Satiated conditions. C) Hunger ratings (in %) at different time points during the consolidation phase for both Fasting and Satiated conditions. Means ± SEM are shown with dot blots overlaid, ***$p < 0.001$; n.s., not significant. N = 15.

snacks. Three questionnaires were used to assess hunger, mood, and fatigue before each meal, and a food quality questionnaire was filled in after each meal.

2.1.4. Memory tasks

WPA task. The WPA task assessed declarative memory. In this task, participants learned a list of 80 semantically related (German) word-pairs (Fig. 2A). Parallel lists were used for the two conditions, with list order counterbalanced across participants. Each word-pair was presented for 4 s on a screen (inter-stimulus interval: 1 s). List presentation was followed by a 2-min distractor task (counting backward from 2000 in steps of 13). Then, half of the word-pairs (randomly selected) was used for a cued recall test, i.e., participants were presented with the first word of a pair and were asked to respond by naming the associated second word. There was no time limit for the response. Both word response and reaction time were recorded. Responses were rated as correct when the answer was identical or highly similar to the associated word in question. After each response, participants made a remember/know/guess judgement and rated their confidence in the response on a 4-point scale ranging from 1 ("I am very unsure") to 4 ("I am very sure"). No feedback was given. During the retrieval phase, cued recall of the other half of list words was tested using the same procedure.

Visual DRM paradigm. The visual DRM task tests the formation of gist memory from abstract visual shapes (Diekelmann et al., 2011; Lutz et al., 2017; Slotnick & Schacter, 2004, Fig. 3A). During encoding, participants learned 16 sets of abstract shapes. Each set consisted of 10 similar shapes (with similar outlines, filled with the same color) which were all derived from a prototype (representing the "gist" of the encoded information) that was, however, not presented during encoding. The shapes were presented sequentially on either the left or right side of a computer screen (on a black background) for 2.5 s, separated by 3-s inter-stimulus intervals. Participants were informed of the number of sets, and there was a 2.5-s break between the sets. Shapes from the same set were presented consecutively at the same location, with the locations of each set counterbalanced across participants. Participants were instructed to memorize both the shape and its location. Two parallel versions of shape sets were used, counterbalanced across the participant's two conditions. During retrieval testing, participants were presented in pseudo-random order with three kinds of shapes: studied old shapes (32; 2 from each set), non-studied new shapes (32; 2 from each set not used during the participant's encoding phase), and the non-studied prototypes (16; 1 from each set). The participants had to indicate whether they had seen each shape during encoding ("old" vs. "new") and if a shape was judged as "old", they were to indicate whether it was presented on the left vs. right side of the screen during encoding. "Old" responses to prototypes were judged as recall of gist memory, and "old" responses to old shapes were judged as correct recall of item memory. After each "old" response, participants gave a remember/know/guess judgement and rated their confidence on a 4-point scale. There was no time limit for responses.

FTT. The FTT measures procedural memory and requires the participant to repeatedly enter a five-digit sequence (e.g., 4–1-3–2-4) on

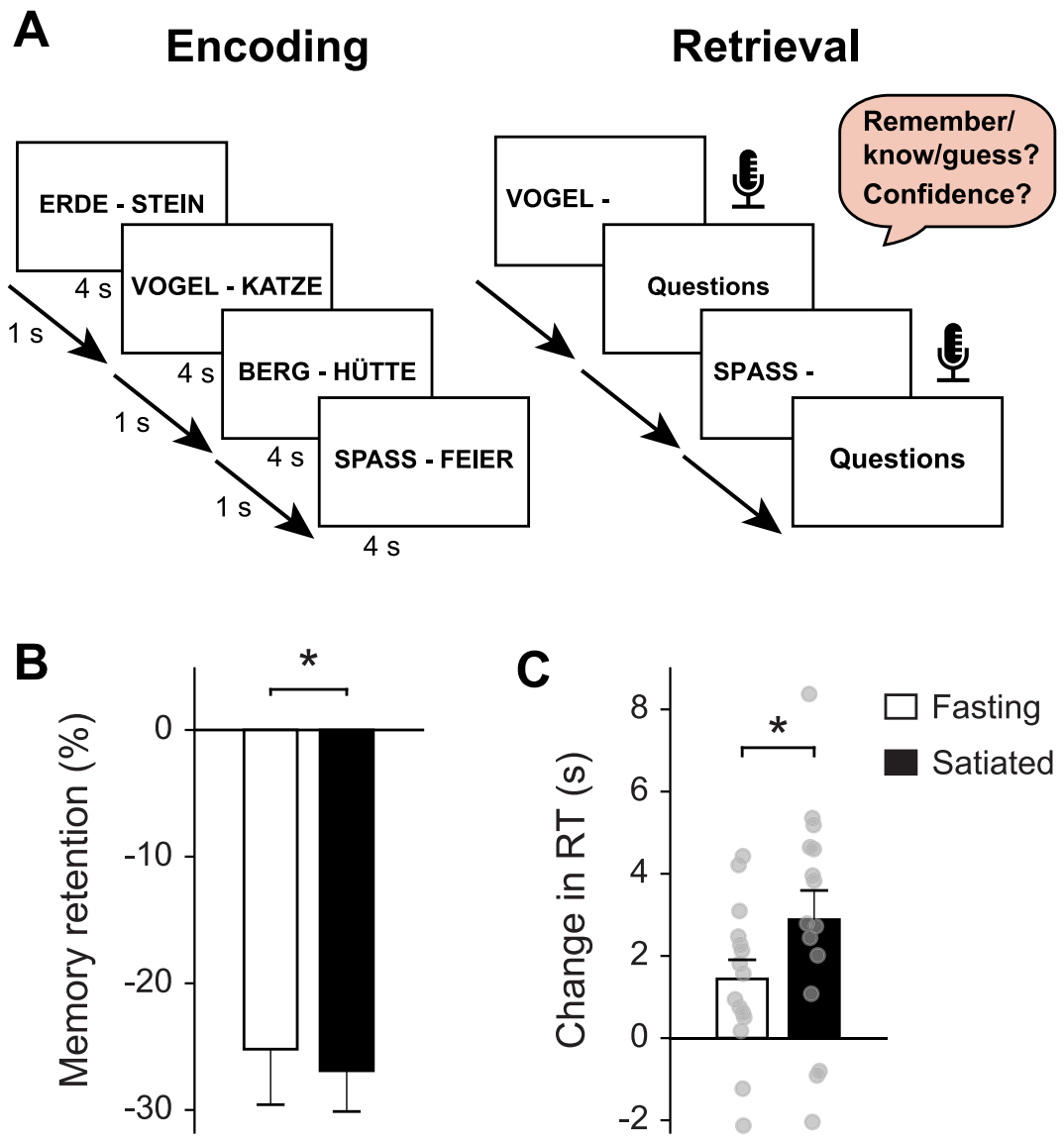

Fig. 2. Word Paired-Associates (WPA) task and results in Experiment 1. A) Participants encoded word pairs and were later tested by presenting the first word of each pair with the request to speak out the associated word. In addition, participants were asked to give remember/know/guess and confidence judgements for every recall. B) Estimated marginal means ± SEM of retention performance (change from pre- to post-intervention recalls) in both Fasting (white bar) and Satiated conditions (black bar), shown as % of the total number of word pairs. C) Mean ± SEM response times (RT) for correct answers (change from pre- to post-intervention recalls) in both Fasting (white bar) and Satiated conditions (black bar). Dot blots overlaid, *p < 0.05. N = 15.

a computer keyboard as quickly and accurately as possible in blocks of 30 s with their non-dominant (left) hand (Walker et al., 2002, Fig. 4A). The sequence to be tapped was presented on a screen throughout the task to reduce working memory demands. In addition, each key press produced an asterisk on the screen, forming a row from left to right, to indicate the current position in the sequence without providing direct accuracy feedback. After each 30-s block, feedback was given (for 2 s), including the total number of sequences tapped and the number of correct sequences. Blocks were separated by 30-s breaks. The encoding phase comprised 12 training blocks, preceded by 4 practice trials on a different sequence (1–1-2–3-4). The retrieval phase consisted of 3 test blocks (identical to training blocks) followed by a transfer test (3 blocks) on the same trained sequence but performed with the other (dominant, right) hand, and a control test (3 blocks) in which performance with the non-dominant hand on a new sequence was tested to control for unspecific effects on motor performance. Four parallel sequences were used for the participant's two conditions, counterbalanced across participants and sessions.

2.1.5. Control variables

Blood glucose. For the assessment of blood glucose levels, a finger prick test was used (Safety-Lancet, Normal, 21G, Poland). Results were read out with a blood glucose meter (ACCU-CHEK, Roche, USA).

PVT. To assess the participants' level of alertness, a vigilance task was used that required pressing a button as fast as possible whenever a bright millisecond clock presented on a dark computer screen started counting upward. After the button press, this clock displayed the reaction time.

Digit span test. To assess participants' short-term memory, they were presented with a sequence of digits at a rate of 1/s and were asked to repeat the sequence (by entering it on a keyboard). The sequence length started from 3 and was increased stepwise by 1 additional digit after presentation of two different sequences with the same length. The task was finished when a participant failed on two consecutive trials.

RWT. To test verbal fluency as an estimate of long-term memory retrieval, the participants were asked to write down as many different words as possible, starting with a particular letter, within a duration of 2

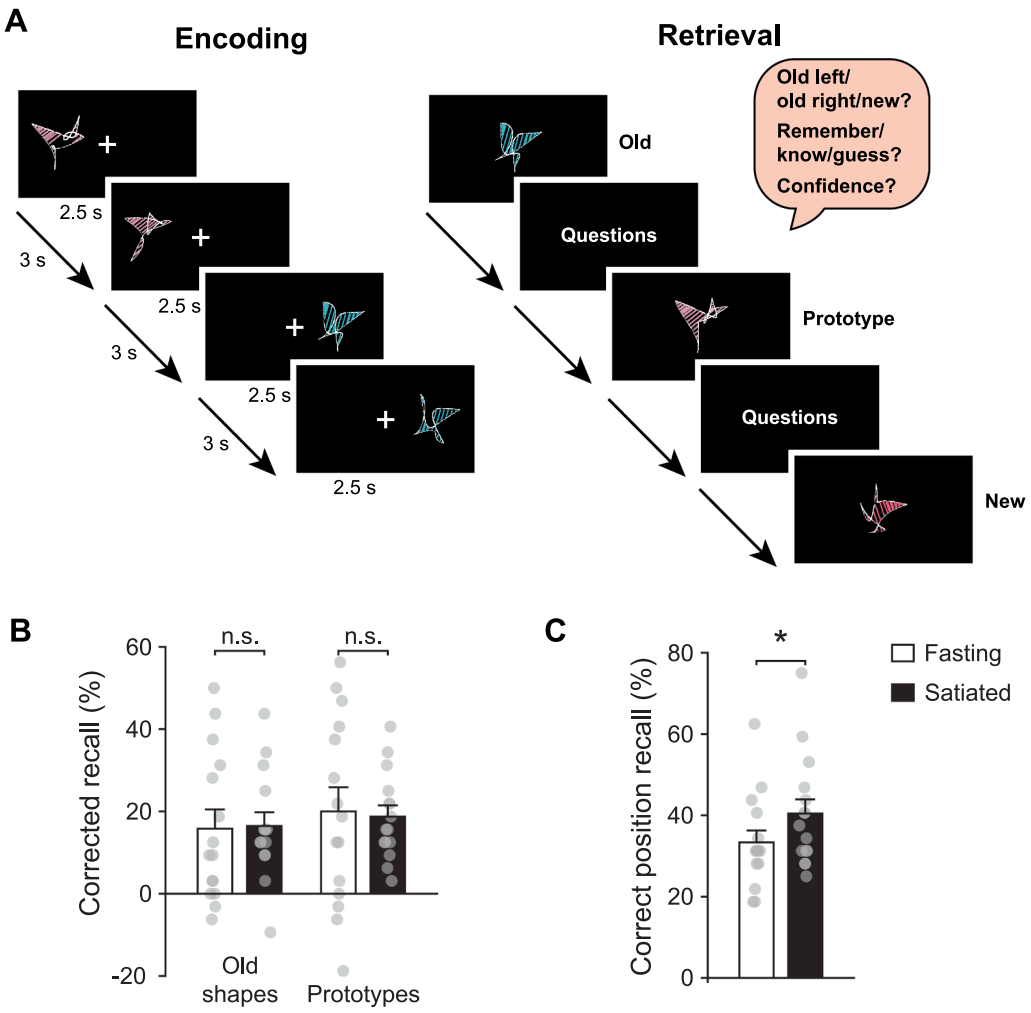

Fig. 3. Visual Deese-Roediger-McDermott (DRM) task and results in Experiment 1. A) Participants encoded 16 sets of 10 shapes each, presented on either the left or right side of the screen (only two shapes per set shown). During retrieval, they were presented with encoded old shapes as well as with unseen prototype shapes (representing the "gist" of each studied set) and new shapes. For each shape, participants were asked to indicate whether it was presented during encoding and if so, whether it had been presented on the left or right side. In addition, participants were asked to give remember/know/guess and confidence judgements for each recall. B-C) Mean ± SEM for (B) corrected recall (% hits minus % false alarms) for both old shapes and prototypes, and (C) correct position recall shown in % of the total number of trials, for both Fasting (white bars) and Satiated conditions (black bars), respectively. Dot plots overlaid, *p < 0.05; n.s., not significant. N = 15.

min (Aschenbrenner, Tucha, & Lange, 2000).

SSS. To test participants' acute subjective sleepiness, they were asked to rate their sleepiness state on this 7-point scale (Hoddes et al., 1973).

Assessment of hunger, fatigue, and mood. To assess participants' subjective hunger state, we used a questionnaire including visual analog scales to rate hunger, fullness, thirst, anxiety, happiness, stress, and tiredness. In this questionnaire, 8 questions were related to acute feelings associated with hunger, and 3 questions assessed general appetite for food, as well as for sweet and savory dishes. We further used the Brief Fatigue Questionnaire that includes 4 questions using 10-point scales to measure acute and 24-hour fatigue levels. Participants rated their fatigue in the areas of general activity, mood, daily work, relationships, and enjoyment (Mendoza et al., 1999) (see Supplementary material). Participants' mood was assessed using the Multidimensional Mood Questionnaire (short form A) which contains 3 bipolar scales (good – bad mood, alertness – tiredness, and calmness – restlessness; Steyer, Schwenkmezger, Notz, & Eid, 1997).

Sleep diaries. Diaries were used to assess participants' sleep at home during the three nights between sessions. The diary comprised 11 questions to be answered in the morning after waking up, covering, e.g., the time lights were turned off in the evening, bedtime, wake up time, awakenings during the night. Diaries also included sleep quality rating, and a short report of activities and unusual events during the day (see Supplementary material).

Food quality questionnaire. This questionnaire contained two visual analogue scales concerning how tasty the participants found the food, and how satiated they felt after a meal (see Supplementary material).

2.1.6. Statistical analysis

To examine the effects of fasting vs. being satiated on memory consolidation, we focused, for the WPA and DRM tasks, on recall performance during encoding and/or retrieval, and for the FTT on retention scores, i.e., the difference between performance in the post-intervention recall session minus the pre-intervention encoding session. We performed repeated-measures analyses of variance (ANOVAs), including the within-subject factors Fasting/Satiated (Fasting vs. Satiated condition) and Pre/Post (Encoding vs. Retrieval). Analyses of covariance (ANCOVAs) were used to exclude differences in rated sleepiness and hunger as potential confounds. ANCOVA results are reported when the covariates (sleepiness, hunger values at recall test) explained significant performance variance, thus improving the statistical model, which was only the case for the WPA task ($p = 0.025$, for sleepiness and $p = 0.012$, for hunger ratings). Repeated-measures ANOVAs are reported with Greenhouse-Geisser correction of degrees of freedom when applicable.

Two-tailed tests were chosen for all statistical analyses. The level of significance was set to $p = 0.05$. Statistical analyses were performed in jamovi (ANCOVAs and estimated marginal means; The jamovi project, 2024) and R (R Project for Statistical Computing, RRID:SCR_001905).

2.2. Results

2.2.1. Blood glucose levels and hunger ratings

Blood glucose measurements and hunger ratings confirmed the efficacy of the experimental hunger manipulation. Blood glucose concentrations tested before encoding (day 1) and before retrieval (day 3) did not differ between the Fasting and Satiated conditions (all $p > 0.3$, Fig. 1B), but glucose levels were generally higher on day 3, i.e., after the standardized dinner, than day 1, i.e., when participants were fasted ($F(1,8) = 24.45$, $p < 0.001$, $\eta_p^2 = 0.75$).

Hunger ratings did not significantly differ between Fasting and Satiated conditions before lunch (day 0; $F(1,14) = 3.61$, $p = 0.078$) or before breakfast (day 1; ($F(1,14) = 0.244$, $p = 0.629$)) but, as expected, indicated marked differences before lunch on day 1 when the participants had received a first meal in the Satiated condition but continued to fast in the Fasting condition ($F(1,14) = 20.70$, $p < 0.001$, $\eta_p^2 = 0.60$; Fig. 1C). Hunger ratings were likewise higher in the Fasting than Satiated condition at the following ratings, before the snack and before dinner on day 1 (all $p < 0.001$; Fig. 1C). Unexpectedly, hunger ratings also differed between the conditions before dinner on the day of retrieval testing (day 3) although participants in both conditions had eaten a regular breakfast and lunch on this day. Indeed, participants in the Satiated condition felt more hungry ($F(1,14) = 9.45$, $p = 0.008$, $\eta_p^2 = 0.40$) and less satiated ($F(1,14) = 8.90$, $p = 0.010$, $\eta_p^2 = 0.39$), than in the Fasting condition. In addition, the Satiated condition indicated a higher need for food in general ($F(1,14) = 6.26$, $p = 0.025$, $\eta_p^2 = 0.31$) and savory food in particular ($F(1,14) = 10.44$, $p = 0.006$, $\eta_p^2 = 0.43$) than the Fasting condition (Supplementary Fig. S1).

2.2.2. Memory performance

WPA task. Memory performance in the WPA task decreased from pre- to post-intervention recalls ($F(1,14) = 89.04$, $p < 0.001$, $\eta_p^2 = 0.86$). Importantly, this change in performance depended on whether participants were fasting or satiated: memory retention was improved in the Fasting condition compared with the Satiated condition (Satiated: -26.9 ± 3.22; Fasting: -25.2 ± 4.38, Fasting/Satiated x Pre/Post interaction, $F(1,12) = 9.55$, $p = 0.009$, $\eta_p^2 = 0.44$) (Fig. 2B). This difference also emerged in analyses restricted to responses where participants indicated to be "confident" about their response (confidence level of 3 or 4 on 4-point scale; $F(1,12) = 5.86$, $p = 0.032$, $\eta_p^2 = 0.33$).

In an exploratory analysis, we also examined the effects of fasting on response times (RTs) of correctly recalled word pairs. For this analysis, outliers (>3 SD from the participant's mean response time) were excluded. Our results showed that participants took less time to respond in the Fasting than Satiated condition (1440.45 ± 465 ms vs. 2882.70 ± 711 ms; Fasting/Satiated x Pre/Post interaction, $F(1,14) = 4.79$, $p = 0.046$, $\eta_p^2 = 0.26$, Fig. 2C).

Visual DRM paradigm. Corrected recall measures were calculated to account for possible recall bias, i.e., prototype hits minus false alarms as a measure of gist memory, and old hits minus false alarms as a measure of item memory. Fasting and Satiated conditions did not differ for gist memory ($F(1,14) = 0.03$, $p = 0.868$) or item memory ($F(1,14) = 0.01$, $p = 0.911$; Fig. 3B).

In addition to the recognition of the shapes, our task required participants to indicate whether a shape was presented on the left or right side of the screen during encoding. Interestingly, focusing on correctly recalled shapes, we found that participants performed worse in the Fasting than Satiated condition (34.86 ± 2.84 % versus 42.22 ± 3.70 % correct, $F(1,14) = 4.99$, $p = 0.042$, $\eta_p^2 = 0.26$; Fig. 3C).

FTT. FTT performance improved from training to test (i.e., the difference between the number of correctly typed sequences during the last three blocks during training and the three blocks during test (using the same hand and tapping sequence, $F(1,6) = 7.75$, $p = 0.032$, $\eta_p^2 = 0.56$), with this improvement not depending on whether the participants were fasting or satiated ($F(1,14) = 0.01$, $p = 0.917$; Fig. 4B). Likewise, no differences between the Fasting and Satiated conditions were found for performance on the transfer test (trained sequence tested with the untrained hand, $F(1,14) = 0.94$, $p = 0.349$) or the unspecific motor learning test (new sequence tested with the trained hand ($F(1,14) = 0.03$, $p = 0.865$).

2.2.3. Control tests and mood

Fasting and Satiated conditions did not differ in any of the control tests during the encoding session (all $p > 0.5$), except that digit span performance was better in the Fasting condition ($F(1,14) = 5.51$, $p = 0.034$, $\eta_p^2 = 0.28$, Supplementary Table S1). In the retrieval session, sleepiness was slightly lower in the Fasting than Satiated condition ($F(1,14) = 7.0$, $p = 0.019$, $\eta_p^2 = 0.33$). Performance on the other control tests was comparable between conditions (all $p > 0.4$).

The participants' mood worsened when they continued to fasten after the encoding phase (day 1), in comparison with the Satiated condition (all $p < 0.01$). However, the participants' mood did not differ between Fasting and the Satiated conditions on days 0 or 3 (all $p > 0.6$).

In summary, our results in Experiment 1 indicate that fasting, compared with the satiated state, improves cued recall accuracy and response speed of word paired-associates memory. Vice versa, fasting impaired spatial memory in the DRM task, whereas procedural memory remained unaffected by the experimental manipulation.

3. Experiment 2

In order to elaborate on the findings from Experiment 1, in Experiment 2 we introduced three major changes in the procedure: (1) Recall was tested with the participants being fasted, as during encoding, assuming that recall differences would be stronger when tested in the same internal state. (2) Recall was tested one day earlier to reduce potentially masking effects of sleep-dependent consolidation during intervening nights. (3) The DRM task was replaced by a "What-Where-When" (WWW) task allowing for a more sensitive dissociation of effects on non-hippocampus-dependent item (event) memory and hippocampus-dependent memory for the episodic (spatial and temporal) context.

3.1. Methods

3.1.1. Participants

Sixteen additional healthy men (mean age ± SD: 24.56 ± 2.87 years; range: 21–31 years; mean BMI ± SD: 21.74 ± 2.12 kg/m^2; range 18.42–25.54 kg/m^2) participated in Experiment 2. Participants' background and inclusion criteria were the same as in Experiment 1. Data from one participant was excluded from the analyses of the FTT due to a technical error.

3.1.2. Design and procedure

Like in Experiment 1, participants took part in both a Fasting and a Satiated condition in a within-subjects cross-over design (Fig. 5A). The two conditions were scheduled at least four weeks apart and were conducted in different experimental rooms by different experimenters to minimize potential carryover effects from the first to the second condition. The procedure of Experiment 2 closely resembled that of Experiment 1, with some differences as detailed in the following. On day 0, participants in both conditions underwent a blood glucose test after a standardized lunch and started fasting at 13:30 h. Afterwards, they

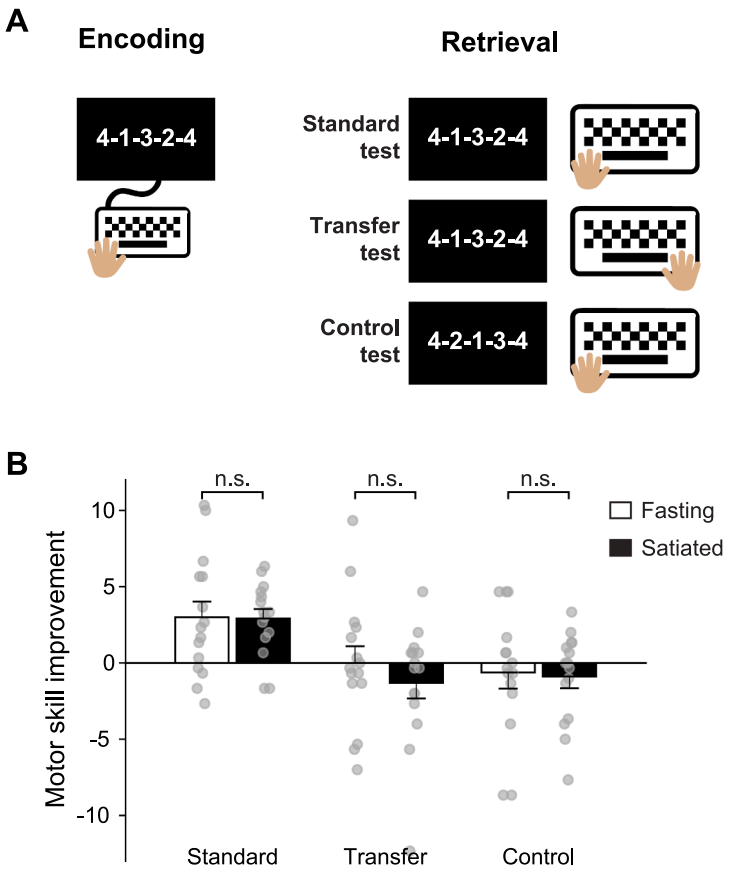

Fig. 4. Finger Tapping Task (FTT) and results in Experiment 1. A) Participants were trained by repeatedly typing the sequence with the fingers of their non-dominant left hand as fast and accurately as possible on a keyboard, in twelve 30-s blocks, separated by 30-s breaks. During retrieval, tapping skills were tested in a standard test, i.e., participants tapped the trained sequence with the trained left hand; in a transfer test where the trained sequence should be tapped with the untrained right hand, and in a control test, where the participants had to tap an novel sequence with the trained left hand. B) Mean ± SEM difference in the number of correctly tapped sequences between the three test blocks of the standard and transfer tests, respectively and the *last* three training blocks, for Fasting (white bars) and Satiated conditions (black). For the control test, the difference was calculated with reference to the *first* three training blocks. Dot blots overlaid; n.s., not significant. N = 15.

completed a familiarization phase for the WWW task (see below). Additionally, participants were provided with an actigraph (MotionWatch 8, CamNtech) that they were required to wear on their non-dominant left wrist until the end of each experimental condition to track physical activity and estimate basic sleep/wake patterns (for actigraphy results, see Supplementary material).

On day 1, participants arrived at the laboratory at 8:00 h in a fasted state. They first completed a mood questionnaire (German version of the Multidimensional Mood State Questionnaire) and blood glucose was measured. Then, encoding on three tasks followed (always in the same order): the WWW task (episode 1), the WPA task, the FTT, and the WWW task (episode 2). Encoding was followed by the experimental manipulation: in the Fasting condition, participants continued to fast, whereas in the Satiated condition, participants had standardized meals, like in Experiment 1. At 18:00 h, in both conditions, participants received a standardized dinner and, afterwards, completed an additional questionnaire to assess feelings of hunger.

On day 2, participants in both conditions were instructed to start fasting again at 10:00 h, after having eaten a regular breakfast. At 13:00 h, they were called by the experimenter to confirm that they had adhered to the fasting protocol. In contrast to Experiment 1, recall was tested already on day 2, when participants returned to the lab at 17:45 h.

3.1.3. Memory tasks and control variables

To assess episodic memory, in Experiment 2 we used a WWW task (Wang et al., 2018; Weber et al., 2014) consisting of three parts: familiarization, encoding, and retrieval (Fig. 6A). Two different versions, a "party version" containing 24 cartoon drawings of humans and a "zoo version" containing 24 cartoon drawings of zoo animals, were used for the two experimental conditions, with the order of versions being counter-balanced across participants. During familiarization, 16 stimuli were presented, one at a time, at one of nine locations of a 3 x 3 grid, on a white background for 8 s (with an inter-stimulus-interval of 2 s). Each stimulus was presented 5 times, once in each of 5 blocks, with the blocks separated by 30-s breaks. Participants were instructed to attend to the presented stimuli. The encoding phase consisted of two episodes (1 and 2) separated by ~ 1 h. Participants were reminded of the episode number at the beginning of each episode. Each episode contained 4 stimuli which had been presented during the familiarization phase. These were presented sequentially at one of nine locations (3 x 3 grid) for 33 s, with an interstimulus-interval of 2 s. During encoding, the locations resembled the windows of a house, and the house was either painted in blue (party version) or red (zoo version). During the retrieval phase, 24 stimuli were presented, one at a time, in random order, including 16 familiar stimuli (8 from the encoding episodes and 8 from the familiarization phase) and 8 novel stimuli. Participants were instructed to indicate whether each stimulus was familiar or new ("what" memory). If it was familiar, they were asked to indicate whether it had appeared in episode 1, episode 2, or at another time (i.e., during familiarization), thus indicating temporal "what-and-when" memory. For familiar stimuli, participants were further asked to indicate where the stimulus was presented in the 3 x 3 grid (spatial "what-and-where" memory). Each response was followed by a remember/know/guess rating and a confidence rating on a 4-point scale. There was no

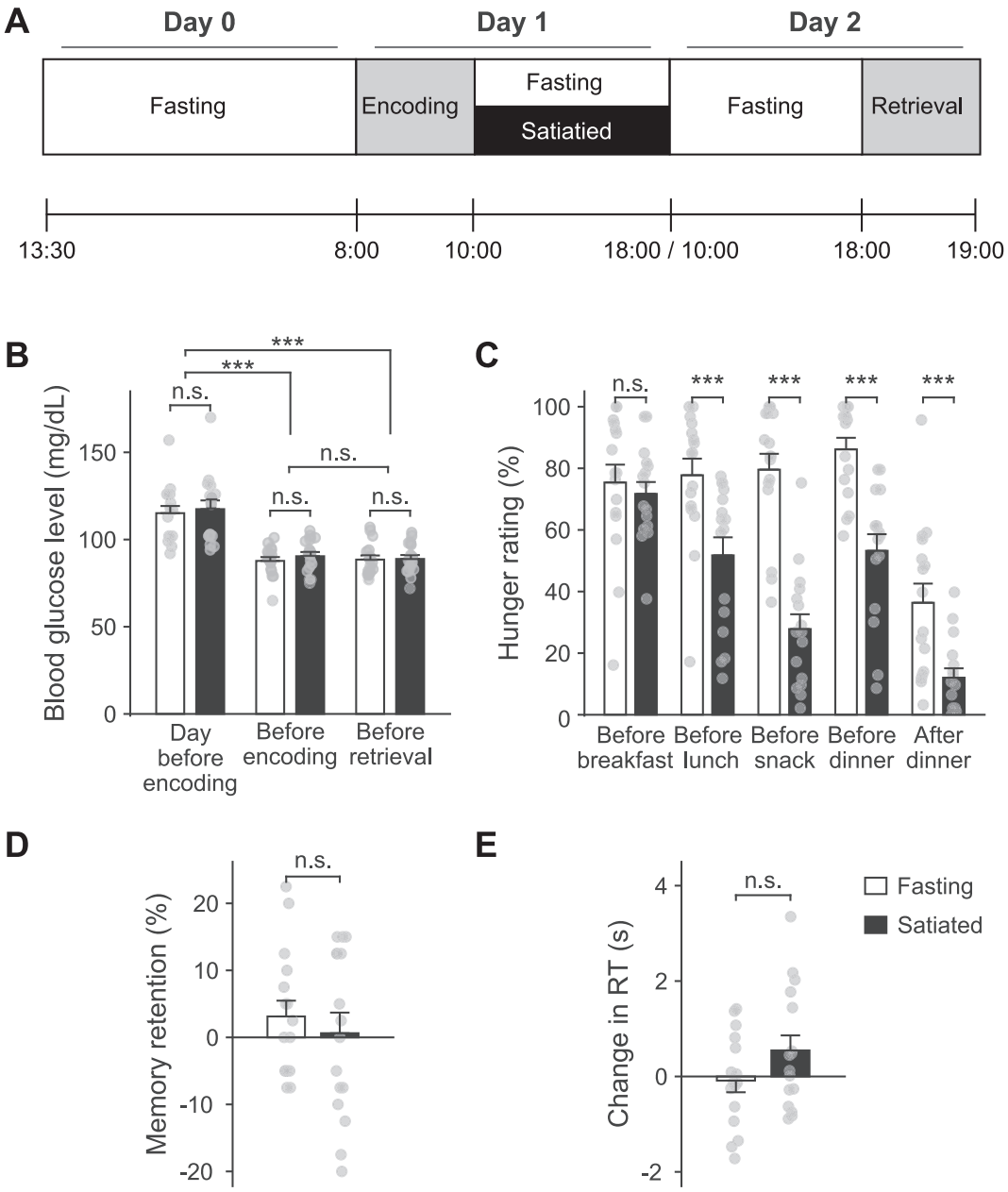

Fig. 5. Experiment 2. A) The experimental design was identical to that of Experiment 1, except that retrieval was tested in the fasted state and already on day 2. B) Blood glucose levels (mg/dL) on the day before encoding, right before encoding, and before retrieval. C) Hunger ratings (in %) at different time points during the experimental consolidation phase. D-E) Memory performance in the Word Paired-Associates (WPA) task. D) Retention performance (change from pre- to post-intervention recall) in % of total number of word pairs. E) Response times (RT) for correct answers (change from pre- to post-intervention recall). Means ± SEM are shown for the Fasting and Satiated conditions, with dot plots overlaid. ***$p < 0.001$; n.s., not significant. N = 16.

time limit for the responses.

The WPA task was identical to that used in Experiment 1 except that a set of 40 (instead of 80) pairs was to be memorized. This change was made to achieve more robust effects, based on literature showing stronger effects of sleep on memory consolidation for shorter word lists (e.g., Gais et al., 2006; Wilhelm et al., 2011; Drosopoulos et al., 2007). In addition, during the immediate recall following encoding, the correct word pair was presented for 4 s after each response, independently of whether the participant's response was correct or not. The FTT as well as the control tasks were the same as in Experiment 1.

3.1.4. Statistical analysis

Statistical analyses in Experiment 2 were analogous to those in Experiment 1 except for the WWW task. Due to the complexity of the WWW task in terms of binomial distributions of the outcome variables and the variation in trial numbers for the different aspects of "what", "where" and "when" memory, for this analysis we changed to a generalized linear mixed-effects model (GLMM) approach using the "lme4" and "lmerTest" packages in R (Bates, Mächler, Bolker, & Walker, 2015; Kuznetsova et al., 2015). The models contained fixed effects for the condition factor Fasting/Satiated, and a random intercept for variability across participants.

3.2. Results

3.2.1. Blood glucose and hunger ratings

Blood glucose concentrations tested before the onset of fasting (day 0), encoding (day 1), and retrieval (day 2) did not differ between the

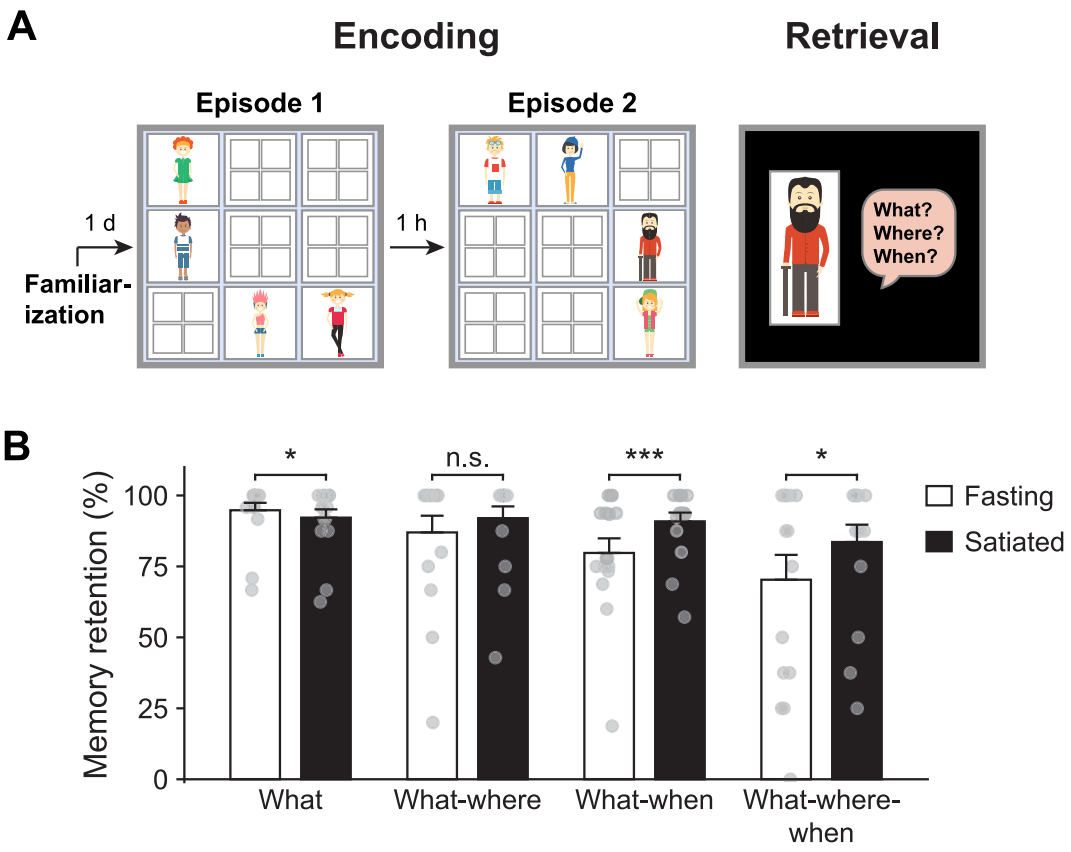

Fig. 6. What-Where-When (WWW) task. A) Participants were first familiarized with the stimuli, i.e., images of persons and animals (not shown here), respectively, presented at random locations on a white screen on the day before encoding. During encoding, half of these stimuli were presented again in two distinct episodes that were separated by 1 h. Each episode contained 4 stimuli presented one after the other, each at a different location. During retrieval, either old stimuli (shown during familiarization, episode 1 or episode 2) or novel stimuli were presented, and the participant was asked to indicate if the stimulus was familiar or new ("what" memory), if it appeared in episode 1, episode 2, or (only) during familiarization (temporal "what-and-when" memory), as well as its location (spatial "what-and-where" memory). Each response was followed by remember/know/guess and confidence ratings. B) Mean ± SEM recall in % of the total number of stimuli for the Fasting (white bars) and Satiated conditions (black bars), for the "what", "what-and-where", "what-and-when", and the "what-where-when" memory components. Dot plots overlaid, ***$p < 0.001$, *$p < 0.05$; n.s., not significant. N = 16.

Fasting and Satiated conditions (all $p > 0.3$) but, as expected, were generally higher on day 0, i.e., after the standardized lunch, than on days 1 and 2, i.e., when participants were fasted (all $p < 0.001$, Fig. 5B).

Hunger ratings did not differ between Fasting and Satiated conditions before lunch (day 0), before breakfast (day 1), after arrival (day 2, all $p > 0.1$), but as expected, showed marked differences before lunch on day 1, when participants had received a first meal in the Satiated condition but continued to fast in the Fasting condition ($F(1,14) = 14.33$, $p < 0.001$, $\eta_p^2 = 0.49$; Fig. 5C). Hunger ratings also showed greater hunger in the Fasting condition than in the Satiated condition on subsequent ratings, before the snack and before dinner, and even after dinner on day 1 (all $p < 0.01$).

3.2.2. *Memory performance*

WPA task. Retention of memory did not depend on whether participants were fasting or satiated (no Fasting/Satiated x Pre/Post interaction, $F(1,15) = 0.446$, $p = 0.514$; Fig. 5D). Also, no difference between the Fasting and Satiated conditions was found for RTs (545.69 ± 315.94 vs. −86.77 ± 244.16; no Fasting/Satiated x Pre/Post interaction, $F(1,15) = 2.44$, $p = 0.14$; Fig. 5E).

WWW task. This task included four measures: (i) recognition memory ("what"), (ii) spatial "what-and-where" memory, (iii) temporal "what-and-when" memory, and (iv) a combined "what-where-when" memory (Fig. 6A).

"What" recognition, i.e., the correct recognition of stimuli that were shown during episode 1, episode 2, or familiarization, was significantly improved following fasting compared to the Satiated condition (3.94 ± 0.47 vs. 3.17 ± 0.42; $b = 0.78$, $z = 2.18$, $p = 0.029$; Fig. 6B). In the Fasting condition, participants were also faster in correctly recognizing the stimuli than in the Satiated condition (2472.58 ± 92.20 ms vs. 2913.21 ± 134.87 ms; $b = 447.63$, $t = 3.08$, $p = 0.002$). "What-and-where" memory was comparable between conditions (Fasting: 3.18 ± 0.84, Satiated: 3.71 ± 0.88; $b = 0.53$, $z = 1.00$, $p = 0.317$), whereas "what-and-when" memory (Fasting: 1.64 ± 0.31 vs. Satiated: 2.60 ± 0.35; $b = 0.96$, $z = 3.33$, $p < 0.001$) as well as "what-where-when" memory, were significantly improved in the Satiated than Fasting condition (Fasting: 1.91 ± 0.59 vs. Satiated: 2.99 ± 0.65; $b = 1.09$, $z = 2.50$, $p = 0.012$).

FTT. Performance on the FTT again did not differ between Fasting and Satiated conditions for the trained sequence ($F(1,14) = 0.41$, $p = 0.534$), the transfer test ($F(1,14) = 0.00$, $p = 1.00$) or the test on the untrained sequence ($F(1,14) = 1.13$, $p = 0.306$, Supplementary Fig. S2).

3.2.3. *Control tests and mood*

Performance on control tests, i.e., Digit Span, RWT, and SSS did not differ between Fasting and Satiated conditions after encoding (all $p > 0.05$, Supplementary Table S2). After retrieval, performance on control tests was also comparable between the conditions (all $p > 0.1$). We found that verbal fluency was generally (across encoding and retrieval) slightly lower in the Fasting than Satiated condition ($F(1,15) = 5.17$, $p = 0.038$, $\eta_p^2 = 0.26$). To control for potentially confounding effects, we introduced verbal fluency as an additional covariate in the mixed-model

analyses. Accordingly, results reported above refer to analyses including this covariate if it was significant, which was only the case in the "what"-component of the WWW task. Participants' mood again worsened when continuing to fast compared to being satiated following the encoding phase ($p < 0.01$), but did not differ between Fasting and Satiated conditions on days 0 and 2 (all $p > 0.2$).

4. Discussion

Based on findings in *Drosophila* (Chouhan et al., 2021) we aimed at testing the effects of fasting specifically on the consolidation of different kinds of memory in healthy humans. Our findings show that fasting can enhance consolidation also in humans. However, the effect differs depending on the kind of memory. Central findings were that fasting, compared to the satiated state, produced signs of an enhanced cued recall of word pairs on the Word Paired-Associates (WPA) task in Experiment 1 (which could, however, not be replicated in Experiment 2). Moreover, fasting selectively benefitted item recognition memory on the episodic What-Where-When (WWW) task. By contrast, fasting impaired memory on the same task when genuinely episodic aspects had to be recalled, i.e., when the item had to be recalled in conjunction with the temporal-spatial context in which it had been encoded. Finally, in both experiments, consolidation of procedural motor skill memory (on the Finger Tapping Task, FTT) was not affected by fasting.

This pattern of results suggests that fasting in humans preferentially supports the consolidation of semantic-like memory representations, involving neocortical rather than hippocampal networks. The consolidation of memory elements strongly involving hippocampal function, like contextual episodic memory, even appears to be impaired in the fasted state. Interestingly, these hippocampus-dependent memory aspects are known to particularly benefit from consolidation processes during sleep (Brodt et al., 2023; Klinzing et al., 2019). The state of hunger may thus provide an alternative route of consolidation that saves salient information to be stored for the longer term during the wake state.

In comparison with the Satiated condition, we observed distinct enhancing effects of fasting on item recognition memory in the WWW task and word-pair memory (in the WPA task), whereas fasting even impaired memory for episodic context, with this impairment most clearly reflected by the diminished recall of "what-where-when" memories in the WWW task. Unlike the recall of contextual episodic memories, item recognition can be achieved in the absence of contextual information. Accordingly, whereas recall of contextual episodic memory requires the hippocampus, recognition memory for individual items can occur in the absence a functioning hippocampus (Brown & Aggleton, 2001; Horner & Doeller, 2017; Manns et al., 2003; Sharon et al., 2011). Thus, recognition memory taps into hippocampus-independent representations that may be directly encoded and integrated into neocortical semantic networks, comparable with the fast mapping of novel associations known to occur in hippocampus-lesioned patients as well as in healthy toddlers while rapidly extending their vocabulary (e.g., Bion et al., 2013; Merhav et al., 2014, 2015). Against this backdrop, our findings of enhanced item recognition memory in the Fasting conditions supports the conclusion that fasting mainly enhances the consolidation of neocortical semantic-like representations. Indeed, this view might also explain the pattern of fasting effects we observed in WPA task performance in Experiment 1, i.e., a significant hunger-associated improvement in cued word recall and a hunger-associated shortening of response times. The shortened reaction times may reflect that in the Fasting condition, participants were able to more rapidly access and rely on these neocortical representations to generate the recognition response (Yang et al., 2023a, 2023b). The failure to replicate the fasting-induced improvement in word-pair memory and response times in Experiment 2 might be related to the shorter word-pair list employed in this experiment, which contained only half as many word-pairs as in Experiment 1. Beyond ceiling effects, this reduced set size of word-pairs probably reduced internal interference among the word-pairs and, thereby, strengthened hippocampal episodic encoding. If so, weaker consolidation of hippocampal representations during fasting may have countered enhancing effects on the consolidation of semantic-like neocortical representations (Harkotte et al., 2022; Hemmer & Steyvers, 2009).

In parallel with the enhancement of such semantic-like representations, fasting hampered the consolidation of hippocampus-dependent contextual episodic memory. This was evident not only in the WWW task (in Experiment 2) but also in the visual DRM task administered in Experiment 1. In addition to the recognition of abstract (old and prototype) shapes, the DRM task required participants to memorize the (screen) location where a specific shape was presented at encoding. In the Fasting condition, participants were significantly worse in recalling this spatial context of the shapes. In combination, these findings indicate an impairing effect of fasting on the consolidation of hippocampal contextual features of episodic memory.

In light of the parallel emergence of impairing effects (on putatively hippocampal representations of episodic context) and enhancing effects (on semantic-like neocortical representations) after fasting, it could be hypothesized that the enhancing effects of fasting on semantic-like neocortical representations are a consequence of a suppression of hippocampal episodic memory consolidation during fasting. Indeed, experiments in rats comparing consolidation processes during wakefulness and sleep have demonstrated that hippocampal activity during wakefulness interferes with the consolidation of cortical recognition memories (Sawangjit et al., 2022). In those experiments, rats encoded objects before 2-hour consolidation periods of wakefulness and sleep, with retrieval tested one week later. Inactivating the hippocampus during the post-encoding wake retention period distinctly enhanced later recognition performance to levels superior even to those seen after sleep consolidation. A superior recognition performance after consolidation during wakefulness was likewise observed in those experiments when object recognition was tested in a context differing from that during encoding, indicating that wake consolidation pertains to context-independent, semantic-like representations in cortical networks. In light of those findings, it is tempting to speculate that in the present study, fasting enhanced consolidation of semantic-like neocortical representations only indirectly, that is, by suppressing hippocampal activity that would otherwise interfere with the neocortical consolidation of these representations (see also Schwarting and Busse 2017). This view is also in line with our failure to find any effect of fasting on the consolidation of procedural motor skill memory. Training on such tasks induces strong representations in cortical and striatal networks (including the primary motor cortex; Classen et al., 1998; Karni et al., 1998), with the consolidation of these representations during subsequent wakefulness probably remaining unaffected by any interfering (contextual) inputs from the hippocampus (but see Schapiro et al., 2019).

Our two experiments differed in that participants were fasted during encoding as well as recall testing only in Experiment 2 whereas in Experiment 1, all participants were satiated at the recall test. The concept of state-dependent learning assumes that the internal state (hunger) forms part of the encoded representations, thereby facilitating recall when it occurs in the same internal state (Radulovic et al., 2017; Shulz et al., 2000). Based on this concept, the globally similar changes after fasting in both our experiments do not provide any hint that the effects of fasting might pertain to the consolidation of internal states as part of the memory representation. However, our two experiments differed in several other aspects, particularly with regard to the tasks showing the most pronounced effects of fasting (i.e., the WPA and WWW tasks), rendering our approach overall less sensitive to detecting potential effects of fasting on memory for the internal bodily state. At the same time, given that effects of fasting in animals (*Drosophila*) have so far only been shown for hunger-related tasks, the learning of which required the animal to be starved (Chouhan et al., 2021), our study in humans shows, for the first time, that hunger can strengthen aspects of

memory in motivationally neutral tasks that are not *per se* related to the hunger state (Hirano et al., 2013).

Whereas a number of studies in humans have investigated effects of hunger and satiety on memory (e.g., Shi et al., 2018; Witte et al., 2009), the present study is the first to dissociate effects of hunger specifically on post-encoding consolidation processes. Although we successfully demonstrated differential effects of fasting on semantic-like, putatively neocortical memories on the one hand and episodic contextual, putatively hippocampal representations on the other, our study has clear limitations. Since we did not include any brain imaging of recall, the conclusions as to the brain networks affected (neocortical vs hippocampal) remain preliminary. Moreover, as a first study in humans, building solely on findings in fruit flies, our study was necessarily exploratory in nature, lacking specific hypotheses particularly as to possible differential effects dependent on the type of representation. Finally, based on our approach in humans, we can only speculate about the mechanisms underlying the effects of hunger on memory consolidation. As a mediating signal, experiments in *Drosophila* identified neuropeptide F (NPF), a homologue of neuropeptide Y (NPY) which is known to invoke hunger responses in humans and is released upon fasting in food-intake regulating regions like the hypothalamic nucleus arcuatus (Chatree et al., 2023; Chouhan et al., 2021; Horio & Liberles, 2021; Kornhuber & Zoicas, 2020). However, contributions of other hypothalamic signals, like orexin, as well as peripheral signals of hunger, like ghrelin, leptin, and glucagon-like peptide 1, likewise need to be considered (e.g., Chen et al., 2019; Farr et al., 2006; Mcclean et al., 2011). There is also evidence that decreases in peripheral glucose levels associated with fasting might play a role (e.g., García et al., 2021; Smith et al., 2011). Thus, while our study provides first evidence in humans for an enhancing effect of fasting specifically on the consolidation of semantic-like memory, going along with a weakening effect on contextual aspects of episodic memory, future studies need to clarify the neuronal underpinnings of this effect.

CRediT authorship contribution statement

Xuefeng Yang: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis. **Xiu Miao:** Writing – review & editing, Methodology, Investigation. **Franziska Schweiggart:** Writing – review & editing, Investigation. **Sophia Großmann:** Writing – review & editing, Investigation. **Karsten Rauss:** Writing – review & editing, Supervision, Methodology. **Manfred Hallschmid:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Jan Born:** Writing – original draft, Supervision, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Nicolas D. Lutz:** Writing – original draft, Visualization, Supervision, Methodology, Formal analysis, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.nlm.2025.108034.

Data availability

Data will be made available on request.

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