Curiosity-driven memory enhancement persists over time but does not benefit from post-learning sleep

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Abstract

Sleep-dependent memory processing is dependent on several factors at learning, including emotion, encoding strength, and knowledge of future relevance. Recent work documents the role of curiosity on learning, showing that memory associated with high-curiosity encoding states is retained better and that this effect may be driven by activity within the dopaminergic circuit. Here, we examined whether this curiosity effect was enhanced by or dependent on sleep-related consolidation. Participants learned the answers to trivia questions that they had previously rated on a curiosity scale, and they were shown faces between each question and answer presentation. Memory for these answers and faces was tested either immediately or after a 12-hour delay containing sleep or wakefulness, and polysomnography data was collected for a subset of the sleep participants. Although the curiosity effect for both the answers and incidentally-learned faces was replicated in immediate tests and after the 12-hour delay, the effect was not impacted by the presence of sleep in either case, nor did the effect show a relationship with total sleep time or time in slow-wave sleep. This study suggests that curiosity may be a learning factor that is not subsequently affected by sleep-dependent memory consolidation, but more work ought to examine the role of sleep on curiosity-driven memory in other contexts.

Introduction

The memory benefits of sleep are far reaching and have been widely examined (Rasch & Born, 2013), and the role of sleep on declarative memory consolidation has been especially well-documented. Particularly, slow-wave sleep (SWS) has been found to play an important role in the strengthening of declarative memory (Gais & Born, 2004; Yaroush, Sullivan, & Ekstrand, 1971). However, sleep's facilitation of memory consolidation does not improve retention of everything learned throughout the day, nor does it randomly bolster some memories over others. It is a selective process in which only some memories are strengthened (Stickgold & Walker, 2013), and the specific mechanisms by which the brain determines which memories to strengthen and which not remains unclear. Although we have evidence of several neurocognitive factors during learning that may serve as salience cues and mediate subsequent memory retention over sleep – such as strength of encoding (Hauptmann, Reinhart, Brandt, & Karni, 2005; Tucker & Fishbein, 2008), knowledge of future relevance (Fischer & Born, 2009; van Dongen, Thielen, Takashima, Barth, & Fernández, 2012; Wilhelm et al, 2011;), and emotion (Hu, Stylos-Allan, & Walker, 2006; Lewis, Cairney, Manning, & Critchley, 2011; Payne, Stickgold, Swanberg, & Kensinger, 2008; Wagner, Hallschmid, Rasch, & Born, 2006) – curiosity has gone unexamined as a driver of specificity in this process.

Reward is a particularly well-known cue for information saliency, and like the previously mentioned encoding factors, reward at encoding might influence later consolidation during sleep, as physiological markers of neural replay during rat sleep are most prominent for memories associated with rewards (Dupret, O'Neill, Pleydell-Bouverie, & Csicsvari, 2010; Lansink et al., 2008; Peyrache, Khamassi, Benchenane, Wiener, & Battaglia, 2009). Though research on this topic is sparse in the human literature, there is evidence that sleep enhances memory for

reinforcement-dependent transitive inference learning (Werchan & Gómez, 2013), that materials associated with high reward (but not low) are remembered better following sleep than wakefulness (Igloi, Gaggioni, & Sterpenich, 2015), and that low reward associations deteriorate more than high reward associations during sleep (Studte, Bridger, & Mecklinger, 2017).

One important neuromodulator for learning and memory – especially for memories associated with reward and novelty – is dopamine. Dopamine neurons can aid in the learning of reward associations by coding for reward prediction errors (RPEs) (Schultz, 1998), as well as via a ramping up of activity during reward anticipation (Chiew, Stanick, & Adcock, 2016; Shohamy & Adcock, 2010). Additionally, under the NOMAD model of dopamine-driven activity (NOvelty-related Motivation of Anticipation and exploration by Dopamine), exploration of novel environments can induce a steadier tonic upregulation of activity, facilitating phasic firing for specific rewarding or novel events, which in turn increases memory encoding and encourages further exploration (Düzel, Bunzeck, Guitart-Masip, & Düzel, 2010). Indeed, hippocampal LTP induction, LTP maintenance, and memory performance in rats are consistently enhanced by this tonic dopaminergic firing induced by novelty, while dopamine antagonists block these effects (Li, Cullen, Anwyl, & Rowan, 2003; Moncada & Viola, 2007). Additionally, dopamine plays a pivotal role in the synaptic tag and capture hypothesis, in which the selectivity of synapses for strengthening via LTP is facilitated by dopaminergic activity at encoding (Frey & Morris, 1998; Redondo & Morris, 2011). Finally, recent work has demonstrated reward-driven selectivity in consolidation in waking rest (Gruber & Ranganath, in preparation). This assistance in long-term memory selectivity in particular makes dopamine an interesting potential arbiter of specificity in sleep-dependent memory consolidation.

A relatively little-studied encoding factor potentially implicating dopamine is curiosity, a phenomenon characterized by motivated exploratory behavior in order to resolve a perceived lack in knowledge or incongruity between experience and knowledge (Berlyne, 1966; Litman, Hutchins, & Russon, 2005; Loewenstein, 1994). This description is strikingly similar to the drives associated with reward-seeking behavior, and some have speculated that is possible that some neural correlates are alike as well (Marvin & Shohamy, 2016). Indeed, dopaminergic firing is the highest for cues associated with the highest level of uncertainty (i.e. probability of 50%) before reward presentation (Fiorillo, Tobler, & Schultz, 2003), and a key component of the NOMAD model (Düzel et al., 2010) is the sustained interest in environment exploration after reward receipt. As such, some of the first neurophysiological curiosity research in humans has approached the topic from the perspective of reward seeking and learning and examined the associated brain regions. When participants study trivia questions and make subjective ratings of their curiosity for the answers, higher curiosity ratings predict greater memory retention (Fastrich, Kerr, Castel, & Murayama, 2017; Galli et al, 2018; Gruber, Gelman, & Ranganath, 2014; Kang et al., 2009; Marvin & Shohamy, 2016; McGillivray, Murayama, & Castel, 2015). When these questions are paired with rewards, the effects of reward and curiosity are not additive (i.e. only memory from low-curiosity questions benefits from reward), indicating these effects may share similar mechanisms (Murayama & Kuhbandner, 2011). When faces are presented alongside trivia answers during encoding, those faces presented with high-curiosity questions are later remembered best, mirroring the previously discussed effects of dopamine upregulation ‘bleeding over’ into the encoding of material unrelated to the dopamine-inducing stimuli (Gruber et al., 2014). fMRI data from these studies demonstrate curiosity-induced activity in the hippocampus and parahippocampal gyrus, as well as in the ventral tegmental area

(VTA), substantia nigra, and nucleus accumbens, all dopaminergic areas also associated with reward (Gruber et al., 2014; Kang et al., 2009). Further, activation of these regions – as well as functional connectivity between them – during learning predicts memory performance, indicating a potential role of the hippocampal-VTA loop in promoting curiosity-driven memory enhancement (Lisman & Grace, 2005). Although most studies on curiosity demonstrate the maintenance of the curiosity effect over delays of days or weeks (Fastrich et al., 2017; Gruber et al., 2014; Kang et al., 2009; Marvin & Shohamy, 2016; McGillvray et al., 2015), and despite work suggesting that dopaminergic inputs specifically influence late-LTP and memory consolidation (Atherton, Dupret, & Mellor, 2015; O'Carroll et al., 2006), it has not yet been investigated whether curiosity affects consolidation processes.

Finally, individual differences in resting eye blink rate (EBR) have been found to be associated with dopaminergic functioning (for a review, see Jongkees & Colzato, 2016). Pharmacological and neuroscientific manipulations in animals have demonstrated a causal relationship between EBR and dopamine activity, and studies in those with Parkinson's disease and schizophrenia – disorders of the dopaminergic system – have revealed relationships as well. Critically, EBR predicts healthy human performance in cognitive tasks associated with dopaminergic functioning such as reinforcement learning, inhibition of novelty bias, and cognitive flexibility (Dreisbach et al., 2005; Pas, Custers, Bijleveld, & Vink, 2014; Zhang et al., 2015). As such, EBR may be a useful and easy tool for predicting the effects of dopamine on memory.

This study examines the relationship between sleep-dependent memory strengthening and curiosity, which may serve as a potential dopaminergic salience cue aiding specificity to such strengthening. By using the trivia question paradigm from Gruber, Gelman, and Ranganath

(2014) and manipulating the presence of sleep between encoding and retrieval, we assessed whether the maintenance of the curiosity effect on memory is enhanced by or dependent on sleep. We predicted that the answers and faces associated with trivia questions ranked high in curiosity would be remembered better than those associated with low-curiosity questions, and that testing after a period of sleep would demonstrate a greater memory difference than after an equivalent period of wakefulness. We also tested some subjects immediately to control for circadian rhythm and assess whether the curiosity effect was impacted by time more generally, and we hypothesized that those tested after a delay containing sleep would demonstrate the curiosity effect to a degree similar to those tested immediately but that those tested after a delay involving only wakefulness would see a deterioration of this effect.

Additionally, we used polysomnography to assess the impacts of total sleep time (TST) on this effect, as well as slow wave sleep (SWS). Given the central role of these sleep stages in explicit memory consolidation, we predicted that a greater amount of time spent in these stages would allow for a longer opportunity for sleep-dependent memory processing, resulting in a greater discrepancy between low- and high-curiosity memory. Finally, we used eye blink rate (EBR), a measure of endogenous baseline dopamine production, to indirectly examine the effect of individual differences in dopamine production on curiosity-driven memory enhancement, and we hypothesized that a higher resting EBR may be associated with an increase in dopaminergic availability and a resultant facilitation of the curiosity effect through the enhancement of high-curiosity stimuli.

Methods

Participants

Participants were recruited from the University of Arizona campus and surrounding Tucson area via fliers, advertisement on Facebook, and the inclusion of the experiment on the Introductory Psychology subject pool website. All work was conducted with the formal approval of the University of Arizona Institutional Review Board, all participants gave written informed consent prior to participation in the study, and all mandatory laboratory health and safety procedures were complied with during the course of the study.

All 93 participants (62 women, 29 men, 2 unknown) included for analyses had no history of psychiatric disorders, seizures, traumatic brain injuries, or sleep problems, and none reported current use of psychoactive medication. These participants were native English speakers (or learned English and were immersed in an English speaking culture by the age of 4), had attained at least some college education, and were between the ages of 18 and 47 ($M = 21.38$, $SD = 5.01$). At the completion of the study, participants received either course credits or cash. Though 125 participants completed the entirety of the experiment, 28 initially recruited via the subject pool website were excluded from all analyses for not meeting the above *a priori* participation criteria, and an additional four wakefulness subjects were excluded from analysis for disclosing that they had napped during the delay.

Stimuli

All stimuli were taken from the experiment performed by Gruber, Gelman, & Ranganath (2014). The first set of stimuli was a list of 375 trivia questions drawn from online trivia websites. Difficult questions were intentionally selected for inclusion in the list to reduce the effects of prior knowledge on learning. The questions spanned several themes such as science, sports, pop

culture, and history to increase the likelihood that each participant would be able to curate a learning list that catered to their genuine interests.

The second set of stimuli was a series of 168 face photographs to be presented with the trivia answers, taken from a database previously used in the literature (Bialleck et al., 2011; Gruber et al., 2014). All faces featured emotionally neutral expressions, were Caucasian, and were taken against nondescript backgrounds. These faces were split into three subsets of 56 to be associated with high curiosity trivia questions, low curiosity trivia questions, or used as foils in the recognition task. The use of each subset was counterbalanced across participants.

Apparatus

All task stimuli were presented on a desktop computer monitor using the Cogent toolbox (http://www.vislab.ucl.ac.uk/cogent.php) for MATLAB.

Overnight PSG data and blink rate EOG data were collected using a Grass-Telefactor Aurora EEG/PSG Amplifier System relaying output to a desktop computer running TWin Recording & Analysis Software. Grass gold cup electrodes and Ten20 Conductive Paste were used for all scalp and face electrodes in the PSG setup, whereas foam 3M Red Dot sticky gel electrodes were used for EKG, leg, and blink rate EOG measurement. Additional EBR measurement was done via recordings with a video camera on an Apple iTouch.

Design

The experiment consisted of three primary phases: a screening phase, in which participants rated their curiosity for trivia questions; a learning phase, in which participants viewed a series of

trivia questions, their answers, and random faces; and a testing phase, in which participants were tested on their recall for trivia question answers and recognition memory for faces.

Participants were split into one of four groups prior to participation: wakefulness, sleep, and two circadian control conditions (Figure 1). Group placement was based on the times of day that participants elected to take part in the study, and participants had no knowledge of the tasks of the experiment. Those in the wakefulness group (n = 22) participated in the learning and screening phase at roughly 9:00AM and completed the testing phase twelve hours later at roughly 9:00PM, whereas those in the sleep group (n = 34) did the reverse and completed the learning and screening phases at 9:00PM and the testing phase twelve hours later at 9:00AM. This design allowed for similar timeframes of memory consolidation while controlling for sleep or wakefulness in the interim between phases without disrupting normal circadian sleeping habits. Participants in the wakefulness group were asked to avoid sleeping between learning and test, and four were excluded from analysis for napping during this period. Those in the sleep group were asked to try to sleep for at least six hours, and all but one subject (who slept 5.2 hours) met this goal ($M = 7.09$, $SD = 0.62$).

The downfall of such a design is that learning and testing occur at different times of the day for both groups, so circadian influences on performance cannot be ruled out. Thus, we also created two control groups to account for this. The morning control group (n = 19) completed the screening and learning phases at roughly 9:00AM and underwent the testing phase immediately afterwards, and those in the evening control group (n = 18) did the same after coming in at 9:00PM. If any potential differences in the wakefulness and sleep group were to be due to circadian effects, they should also have been apparent when comparing these immediate test control conditions.

Procedure

Screening phase

On the first session of the study, participants arrived in the lab at roughly 9:00AM or 9:00PM, and signed consent was obtained by an approved researcher. After providing consent, participants began the screening portion of the experiment. During this phase, participants made a series of ratings to (unknowingly) create their own personalized learning list of 112 trivia questions, 56 of which they were not curious about and 56 they were curious about. Trivia questions pulled from the set of 375 appeared on the computer screen one at a time in a randomized order (Figure 2). After each question, the participant was instructed to rate how likely it was that they knew the answer on a 1 to 6 scale, with 1 meaning 'I am confident I do not know the answer' and 6 meaning 'I am confident I know the answer'. After making this rating, participants were asked to make a second rating on a 1 to 6 scale, this time indicating how curious they were about learning the answer, with 1 meaning 'I am not at all interested in learning the answer' and 6 meaning 'I am very much interested in learning the answer.' Participants were asked to use the whole range of 1-6 keys to give as accurate responses as possible for each rating. (Some have suggested interest and curiosity are dissociable (Hidi & Renninger, 2006), but here we use these terms interchangeably despite exclusively examining what others may refer to as curiosity.)

This task continued until the participant had rated 56 questions as evoking high curiosity (ratings of 4, 5, or 6) and 56 as evoking low curiosity (ratings of 1, 2, or 3), none of which received a rating of 6 on the confidence rating of prior knowledge. These 112 questions went on to serve as an individualized learning list for that participant. If the participant exhausted our list

of 375 questions before 50 were categorized into each group (i.e. if a participant was biased toward one end of the curiosity rating scale and/or rated a large number of questions as 6 on the scale of confidence in prior knowledge), as happened with seven participants, the experiment halted, the participant was debriefed and dismissed, and no data was used for further analysis.

Learning phase

Once each participant completed the screening phase of the experiment, they immediately began the learning task. In this procedure, each of the 112 questions in a participant's learning list were presented on the screen individually and in random order for four seconds each. The presentation of each question was followed by a fixation point for one second, the presentation of a random face for two seconds, a fixation point for seven seconds, and then the answer to the question for one second. (The timing of this paradigm differs from that of the original Gruber et al. (2014) study, in which 4 seconds of fixation were presented before and after each face. This change was made on recommendation by that group due to preliminary, unpublished findings with this timing suggesting stronger effects.) Participants were instructed to read each question, view each face, determine whether that person could help them answer the question, and make a yes or no rating before viewing the answer. These ratings were not recorded, as these instructions served only to ensure participant engagement and attention to the stimuli. This task was complete once all 112 questions and their associated faces and answers were presented.

After the learning phase, participants filled out a screening/demographics form as well as a Stanford Sleepiness Scale (SSS), a survey asking for a subjective rating of sleepiness on a 1-7 scale. Participants in the wakefulness group were then dismissed and asked to continue to avoid caffeine throughout the day and avoid taking any naps. Participants in the sleep group were

dismissed at this point as well. If they were staying in the lab for recording, they got ready for bed and immediately began PSG hookup, and went to bed at roughly 12:00AM. Those who did not stay in the lab were instructed to try to get at least six hours of sleep and avoid caffeine before coming back in. All participants in the circadian control condition began the testing phase immediately after filling out the forms.

Testing phase

Participants in the wakefulness and sleep groups returned to the lab 12 hours later for the testing phase, and before completing this portion of the experiment, these participants filled out another SSS. Wakefulness participants were asked if they had napped at all in the interim between sessions, and those in the sleep group were asked roughly how many hours they slept overnight.

The first part of the testing phase was the self-paced face recognition task, in which 168 faces were presented on the screen individually and the participant was asked to determine whether they had seen the face in the learning phase. Of these 168 faces, 56 had been previously presented with trivia questions rated high for curiosity, 56 had been shown with questions rated low for curiosity, and 56 were novel lures. All faces were presented in random order for the face recognition task. Participants were instructed to make a rating on a 1 to 4 memory confidence scale for each face (1 = 'I am confident I have not seen them before,' 2 = 'I think I have not seen them before,' 3 = 'I think I have seen them before,' and 4 = 'I am confident that I have seen them before.'). To ensure participants understood these instructions, participants were asked to recall and state what each number on the scale meant before initiating the task. Upon the participant making each rating, the program would automatically and immediately move on to the next face. Due to technical errors in the program or participant failure to comply with instructions, data

from five participants (1 sleep, 1 wakefulness, 2 morning, 1 evening) were not collected on this measure. All mentioned analyses of facial recognition were performed on all remaining data (n = 88).

Once the face recognition task was complete, the trivia answer recall test began. The researcher presented the participant with a Microsoft Excel spreadsheet containing the 112 questions they saw in the learning phase, and instructed the participant to type the answers to as many questions as possible in the adjacent column without guessing. If the participant did not finish within 20 minutes, the researcher ended this part of the experiment and the completed answers were graded.

Immediately after completing the recall task, the participant was debriefed, compensated, and dismissed from the lab.

Analysis

For an early batch of analyzed participants (n = 22), trivia answers were subjectively scored by two experimenters, with rare conflicts broken by a third. Due to time and labor constraints, the remaining participants (n = 71) were scored by one experimenter who was blind to participant group and whether each question fell into the high- or low-curiosity category. Questions were judged on reasonable closeness to the correct answer without being unfairly stringent regarding minor errors such as misspellings.

Measurement of eye-blink rate

59 participants (22 sleep, 15 wakefulness, 11 morning, and 11 evening) underwent a measurement of resting eye blink rate during the same visit to the lab as the screening and

learning phase. We used two methods to assess eye blink rate: electrooculography (EOG) and video camera recordings. The EOG reading was recorded on a single channel in which a single electrode above the left eye was referenced against a single electrode below the same eye (resulting in large, obvious spikes in the reading when blinks occurred). Participants sat on the edge of a bed in the lab and were asked to simply keep their eye fixated on a camera that was placed roughly three feet in front of them. The researchers told the participant they could relax, but instructed them to try to avoid looking around, fidgeting, or touching the electrodes, and no reference was made towards blinking unless the participant explicitly asked if they were allowed to do so. Participants were then left alone, and a five-minute recording was taken of their resting blink rate.

Most participants' EBR was recorded immediately after signing their consent form, though due to space and time constraints in the lab (only one participant could be run on the EOG at a time), several participants underwent this procedure immediately following the learning task (in the wakefulness and sleep group) or following the test phase (in the circadian control groups). Thus, all participants still completed the EBR procedure on the same visit as (and within two hours of) the learning phase, the point at which we believe dopamine has the most influence on the curiosity effect, as this is when curiosity induced and resultant encoding effects would take place under the synaptic tag and capture hypothesis (Redondo & Morris, 2011). Given the lack of a circadian effect of EBR across time of day seen in the results, it is unlikely that the difference of a couple of hours altered the results of this assessment of individual differences.

Polysomnography

23 participants in the sleep group remained in the lab for overnight polysomnography (PSG) recordings. Immediately following the learning phase and the completion of the SSS and demographics/screening form, the participant prepared for bed, and once ready, underwent PSG measurement and application at about 10:30PM. Scalp electrodes for electroencephalography (EEG) were placed according to the International 10-20 system at sites Fp1, Fp2, F1, Fz, F2, C3, Cz, C4, Pz, O1, and O2, with a ground electrode at Fpz and reference electrodes on each mastoid and CPz. Two additional electrodes for overnight EOG were placed on the periphery of the eyes, and two electrodes were placed on the chin for electromyography (EMG), as were one on each tibialis anterior (just outside the shins). Electrocardiogram (EKG) electrodes were placed under the right clavicle and above the left hip, and several respiratory measures were applied: a nasal cannula measuring airway pressure, a nasal thermistor, two respiratory belts around the abdomen and upper chest, and a pulse oximeter worn on the index finger of the non-dominant hand.

PSG measurement and application typically took approximately 90 minutes, and the average time for lights out was at 12:15AM (SD = 21.46 minutes) (range 11:45PM - 12:59AM). Before lights out, impedances were checked and biocalibrations were performed. All participants received 8 hours of sleep opportunity before lights on, and with the exception of one participant who could not fall back asleep after just under seven hours, all participants remained in bed until the completion of the eight hours. (In one case, polysomnography data collection was halted for a period of 30 minutes due to the acquisition computer exceeding storage capacity, and all analyses of that participant treat those 30 minutes as a period of wakefulness.) The testing phase for overnight participants began no earlier than 8:45AM, regardless of rise time.

Results

Trivia Answer Memory

Analysis of group and curiosity

To evaluate our primary question of whether sleep influenced the curiosity effect on memory for trivia answers, we used the data from the sleep and wakefulness groups to run a 2x4 mixed ANOVA with curiosity (high or low) as the within-subjects variable and group (sleep, wakefulness, AM, or PM) as a between-subjects variable (Table 1) (Figure 3). No interaction was found between the two variables, $F(3,89) = 1.05$, $p = .38$, indicating that there was no difference in the curiosity effect between groups. Likewise, there was no main effect of group, $F(3,89) = 0.48$, $p = .70$, indicating no difference between the sleep, wakefulness, AM, and PM groups on trivia answer recall. However, there was a main effect of curiosity, $F(1,89) = 126.73$, $p < .001$, $\eta_p^2 = .59$, indicating much better recall for answers to high curiosity questions (M = 52.52%, SD = 18.61%) than answers to low curiosity questions (M = 37.76%, SD = 17.48%).

Post hoc analysis of delay

Due to the absence of an interaction between the curiosity effect and sleep, we performed an exploratory analysis on whether there was any interaction between this effect and overall consolidation over a delay, as recent work has shown selective enhancement of rewarded memories over waking delays (Gruber & Ranganath, in preparation). One final ANOVA was calculated, this time with delay as the between-subjects variable (immediate or delay) and curiosity as the within subjects factor (high or low). For trivia answers, no significant interaction was seen between immediate and delayed tests, $F(1,91) = 2.63$, $p = .11$, nor was there a main

effect of delay, $F(1,91) = 0.16$, $p = 0.69$, though this test confirmed that there was a curiosity effect, $F(1,91) = 132.99$, $p < .001$, $\eta_p^2 = .59$.

Recognition Memory for Incidental Faces

Analysis of group and curiosity

We applied the same analyses to the corrected recognition scores (hits – false alarms) for faces, collapsed across memory confidence ratings (Figure 4). We found no interaction between curiosity and group, $F(3, 84) = 1.11$, $p = .35$ or main effect of group, $F(3,84) = 1.10$, $p = .36$. We did observe a main effect of curiosity, $F(1,84) = 6.81$, $p = .01$, $\eta_p^2 = .08$, indicating a significant but small memory benefit for faces associated with high curiosity questions (M = 42.65%, SD = 16.70%) compared with those associated with low curiosity questions (M = 39.71%, SD = 19.28%). Although Gruber et al. (2014) found that this effect in the delayed test was only seen in high confidence responses, our analyses of high confidence ratings yielded similar results as our analysis of collapsed scores: there was no interaction between group and curiosity, $F(3,84) = 0.62$, $p = .61$, and there was a main effect of curiosity, $F(1,84) = 8.08$, $p = .01$, $\eta_p^2 = .09$. Although there was also a main effect of group, $F(3,84) = 2.78$, $p = .046$, $\eta_p^2 = .09$, post hoc tests using Hochberg's GT2 procedure revealed no significant individual contrasts.

Post hoc analysis of delay

As with the answer results, the lack of a group effect led us to perform exploratory analyses asking whether there were any effects over a delay. Results produced by a curiosity (high or low) by delay (immediate or delay) ANOVA of face recognition data were similar to those calculated using trivia answer scores: no interaction was seen between delay and curiosity, $F(1,86) = 1.01$,

p = .32, and no main effect of delay was found, $F(1,86) = 2.26$, p = .14, though the curiosity effect was again shown, $F(1,86) = 6.40$, p = .01, η_p^2 = .07.

Effects of Prior Knowledge

To examine whether participants' confidence in prior knowledge influenced curiosity ratings, we calculated the mean confidence rating for low-curiosity and high-curiosity questions for each participant. There was a significant difference between the prior knowledge rating means for low-curiosity (M = 1.40, SD = .36) and high-curiosity (M = 2.11, SD = .48) questions, $t(92) = -16.28$, $p < .001$, d = 1.65, indicating that participants were more confident they knew the answers to their high-curiosity questions. However, it should be noted that the difference in these means is relatively small, with the average high- and low-curiosity question still only differing by less than one point on this six-point scale, indicating that participants still had generally limited confidence in their knowledge of most answers.

To investigate the relationship between prior knowledge ratings and memory, we binned the number of trivia answers recalled for questions rated low ("1", "2", or "3") or high ("4" or "5", as questions rated "6" were not included for test) for confidence in prior knowledge. Analyses revealed that memory was better for questions rated high in prior knowledge (M = 56.84%, SD = 24.66%) than questions rated low on this metric (M = 37.80%, SD = 15.30%), $t(92) = -8.48$, $p < .001$, d = .88. Additionally, we conducted a mixed 4x2 (group x knowledge) ANOVA with these variables and observed results similar to our curiosity analyses: there was a main effect of prior knowledge, $F(1,89) = 65.36$, $p < .001$, ηp^2 = .42, but no interaction between group and knowledge, $F(3,89) = .84$, p = .47, or main effect of group, $F(3,89) = .84$, p = .47.

We further investigated to what extent prior knowledge may have influenced the curiosity effect by running an ANCOVA with the prior knowledge effect (high prior knowledge memory - low prior knowledge memory) as a covariate. There was an interaction between curiosity and the prior knowledge effect, $F(1,88) = 7.42$, $p = .008$, $\eta p^2 = .08$, suggesting that the greater the prior knowledge effect, the greater the difference between low and high curiosity memory. Despite the removal of this variance, the curiosity effect remained significant, $F(1,88) = 50.10$, $p < .001$, $\eta p^2 = .36$. A correlation between the curiosity effect and the prior knowledge effect was significant, $r = .28$, $p = .007$, showing that only 7.84% of variance caused by the curiosity effect can be accounted for by the prior knowledge effect. Taken together, these results suggest that prior knowledge may have influenced memory performance and accounts for some, but not all, of the difference in curiosity conditions.

Sleep Variables

To assess each sleep variable's relationship with memory outcomes, we analyzed the relationship each had with memory in the high curiosity and low curiosity conditions separately, as well as with the difference between the two scores, representing the curiosity effect. We defined these as three families for purposes of analysis for each sleep variable. We used the Bonferroni corrections for multiple comparisons, alpha = .05/3 = .0125.

Slow wave sleep

Because we predicted a role of SWS on the curiosity memory effect, we performed Pearson's correlations between the time spent in SWS (Stage N3) and memory scores for subjects who underwent PSG measurement (n = 23 for answer recall; n = 22 for face recognition). For trivia

answers, there was no significant correlation between SWS time and memory for high curiosity answers, $r = .24$, $p = .27$, memory for low curiosity answers, $r = .22$, $p = .31$, or the curiosity effect, $r = -.01$, $p = .97$. Analysis of recognition memory for faces likewise revealed no relationships to SWS, as there was no correlation between time spent in N3 and memory for high curiosity faces, $r = -.33$, $p = .13$, low curiosity faces, $r = -.16$, $p = .49$, or the curiosity effect, $r = -.19$, $p = .39$.

Total sleep time

We hypothesized that the overall presence of sleep would enhance the curiosity effect, and polysomnography offers the best objective measure of participant sleep. We predicted that greater observed total sleep time (TST) would be related to greater demonstration of the curiosity effect, but additional correlations between (TST) and memory performance yielded results similar to the SWS test: there was no effect of TST on memory for low curiosity answers, $r = .05$, $p = .81$, high curiosity answers, $r = .14$, $p = .52$, or the curiosity effect, $r = .09$, $p = .69$. Likewise, no relationship was found between TST and recognition for high curiosity faces, $r = .29$, $p = .19$, low curiosity faces, $r = .21$, $p = .35$, or the curiosity effect, $r = .03$, $p = .90$. These results corroborate the lack of a difference found between wakefulness and sleep groups by further suggesting no general role of sleep on memory for this material or the preservation of the curiosity effect.

N2 and REM

Exploratory post hoc analyses were also performed on stages N2 and REM to examine their relationship to memory performance. Time spent in stage N2 failed to correlate with memory for

high curiosity faces, $r = .43$, $p = .049$ under a Bonferroni-corrected alpha of .0125 to control for family-wise error rate. Nor did we observe correlations between N2 and low curiosity faces $r = .29$, $p = .19$, or the curiosity effect, $r = .07$, $p = .76$. This nonsignificant relationship between N2 and high curiosity faces did not translate to a relationship between N2 and high curiosity trivia answers, $r = .15$, $p = .51$, low curiosity answers, $r = .06$, $p = .79$, or the curiosity effect, $r = .09$, $p = .68$.

REM duration showed no significant relationship with high curiosity trivia answers, $r = -.37$, $p = .08$, with the curiosity effect, $r = .11$, $p = .62$, or with low curiosity answers, $r = -.42$, $p = .047$, as the correlation did not survive Bonferroni corrections. There was no relationship between REM and recognition for high curiosity faces, $r = .22$, $p = .33$, low curiosity faces, $r = .03$, $p = .89$, or the curiosity effect, $r = .26$, $p = .24$. Though neither the positive association between N2 and high curiosity faces nor the negative relationship between REM and high curiosity answers were included in our a priori predictions, nor do they withstand corrections for multiple comparisons, they are worth noting and considering for further investigation in light of literature implicating N2 in memory consolidation (Ruch et al., 2012) and REM in synaptic and dendritic pruning to promote forgetting of inconsequential material and prevent oversaturation of networks (Li, Ma, Yang, & Gan, 2017; Poe, 2017).

Eye Blink Rate

As prior literature has shown circadian differences in resting EBR (Barbato et al., 2000), we first examined whether such differences existed in our sample. To do so, we compared EBR means between subjects whose EBR was assessed in the morning (i.e. those in the wakefulness delay group and morning controls) and subjects for whom EBR was observed in the evening (i.e. the sleep delay group and evening controls). We observed no difference between groups, $t(57) = -$

.14, p = .89, indicating that any relationships found with EBR would be unlikely to stem from circadian confounds.

Memory

We conducted additional correlations for EBR and memory performance for the subset of subjects who underwent the EBR procedure (n = 59 for answers; n = 56 for faces), as we had predicted that increased resting EBR would indicate higher levels of dopamine production and thus a greater facilitation specifically of dopamine-enhanced LTP induction and memory consolidation.

Analyses of trivia answer memory revealed no relationship between EBR and high curiosity answers, r = .04, p = .76, low curiosity answers, r = -.04, p = .74, or this curiosity effect, r = .12, p = .37. In another finding (that does not ultimately remain significant after family-wise error correction), there was a positive relationship between EBR and memory for low curiosity faces, r = .28, p = .04, whereas there was no such relationship with high curiosity face memory, r = .15, p = .26, or the curiosity effect, r = -.25, p = .06. However, a comparison between these low curiosity and high curiosity correlations with EBR confirms they are not significantly different relationships, $t(53)$ = -1.84, p = .07.

Subjective sleepiness.

Though comparisons between the circadian control groups indicated no overall difference in scores between times of day, we wanted to ensure that there was no impact of self-reported sleepiness (as measured by the SSS) on memory. We analyzed the SSS scores according to when

the scales were completed: at learning (SSSL) or at test (SSST). (For the immediate control conditions, only one SSS was completed, so these two variables are equal).

Encoding

Across all groups, SSSL negatively predicted low curiosity trivia answer recall later, $r = -.28$, $p = .008$, though this was not the case for high curiosity answers, $r = -.17$, $p = .10$. Memory for low curiosity faces was not impacted by SSSL, $r = -.19$, $p = .09$, nor for high curiosity faces (under a Bonferroni-adjusted alpha of .025), $r = -.24$, $p = .026$, indicating that higher sleepiness at learning was unrelated to memory for all of these stimuli but low-curiosity answers.

An ANOVA comparing SSSL scores of our four groups revealed a significant difference between groups, $F(3, 87) = 6.40$, $p = .001$, $\eta_p^2 = .18$, and *post hoc* tests showed that only the sleep group differed from the others and exhibited significantly higher SSSL (M = 4.59, SD = 1.18) than each the wakefulness group (M = 3.29, SD = 1.19), $t(53) = 3.96$, $p < .001$, $d = 1.10$, the morning group (M = 3.63, SD = 1.30), $t(51) = 2.72$, $p = .009$, $d = .77$, and the evening group (M = 3.41, SD = 1.33), $t(49) = 3.22$, $p = .002$, $d = .94$, indicating that differences in subjective sleepiness at learning may have influenced differences between our test groups (or lack thereof), particularly for retention of low curiosity trivia answers for the sleep group.

Test

Across groups, there was also a significant negative correlation between SSST and memory for both high curiosity trivia answers, $r = -.32$, $p = .003$, and low curiosity answers, $r = -.26$, $p = .01$, meaning that sleepiness at test impacted answer recall scores across conditions. This was not

true, however, for the relationship between SSST and low curiosity face memory, $r = .02$, $p = .88$, or high curiosity face memory, $r = -.10$, $p = .39$. An ANOVA assessing SST showed a difference between groups, $F(3, 84) = 4.22$, $p = .008$, $\eta_p^2 = .13$, but *post hoc* tests only revealed a difference between the sleep group (M = 2.39, SD = .92) and evening group (M = 3.63, SD = 1.30), $t(48) = 3.96$, $p < .001$, $d = 1.11$, indicating that sleepiness at test may have influenced our between-groups comparison of trivia answer recall.

Discussion

Our results are consistent with earlier findings on curiosity-related memory enhancements, replicating consistent curiosity effects for trivia answer recall (Fastrich et al., 2017; Galli et al, 2018; Gruber et al., 2014; Kang et al., 2009; Marvin & Shohamy, 2016; McGillivray et al., 2015). Critically, the curiosity effect on recognition of incidental faces was replicated as well (Galli et al, 2018; Gruber et al., 2014), demonstrating that such a curiosity effect is not confined to or solely resultant from the content of the questions, but rather is defined by an underlying substrate that bleeds over into incidentally learned materials. Moreover, the curiosity effect on trivia answers and incidental faces was found in both immediate and delayed testing conditions, indicating that memory benefits for high curiosity information are shown at encoding and are retained over a 12-hour delay (cf., Gruber et al., 2014; McGillivray et al., 2015). These results support the previous results of the delayed memory test from Gruber et al (2014) with a controlled comparison between groups in similar conditions, while additionally finding an even more reliable persistence of the effect for faces than the previous work.

However, the primary novel prediction of this study – that sleep, and in particular SWS, would interact with the curiosity effect by selectively strengthening high curiosity information –

was not supported by the results. This was true for both recollection of trivia question answers and recognition of incidental faces encountered during curiosity states, despite the replication of an overall main effect of curiosity on both trivia answer and face memory. Because the curiosity effect on answers was so strong across groups, it is possible that this measure was not sensitive enough to be impacted by sleep's memory benefits. Surprisingly, between-groups comparisons showed that sleep had no main effect on memory either, running counter to much prior research on sleep and memory. We may expect this of the high-curiosity answers, as high encoding may have caused a ceiling effect, but this lack of a sleep effect is surprising for the relatively poorly remembered faces and low-curiosity answers. One potential explanation may be that, given the curiosity-inducing nature of the study and introduction of interesting information, wake subjects were more apt to ruminate about the study in general throughout the day compared to more rote paradigms used in the sleep and memory literature. This potential for daytime rumination may have strengthened neural networks enough to eliminate a detectable difference from the sleep group once the testing session began. Additionally, though all sleep subjects who went home between sessions reported sleeping for over six hours, it also cannot be ruled out that this sleep was not under ideal conditions, that subjects suffered from unknown sleep problems, or that this sleep was otherwise misreported. Similarly, in-lab subjects never underwent an adaptation night in the lab, perhaps affecting the quality of their sleep. Although these explanations are speculation, future work on curiosity and sleep should ensure sleeping conditions are more carefully controlled to detect any subtle effects that may exist.

Our investigation of the relationship between ratings of curiosity, ratings of confidence in prior knowledge, and memory reveals that these two ratings may be partially tied together (Kang et al., 2009; Loewenstein, 1994). Participants were more curious about questions for which they

already felt more confident in their knowledge, and there was an overall main effect of knowledge confidence ratings on memory performance. It cannot be ruled out that this association may be driven by participants deriving more curiosity from a topic about which they are interested, increasing the odds that they have come across the information before. However, it may also be a demonstration of the "tip of the tongue" phenomenon driving curiosity (Maril, Wagner, & Schacter, 2001), in which a simple feeling of confidence or "nearly knowing" (irrespective of actual prior knowledge) boosts the desire to find the correct answer. Importantly, part of the reasoning for the inclusion of the incidentally presented faces was to account for potential effects of the questions' contents. The curiosity effect present in facial recognition scores indicates that this effect is not simply due to prior knowledge, but rather is resultant from a broader underlying mechanism driven by states of curiosity, one which can extend its effects to incidentally encoded information. Finally, it is important to note that the mean knowledge rating even for high-curiosity questions was only 2.11 on a 1-6 scale (and 1.40 for low-curiosity questions, only a .71 difference), indicating that these effects are driven by a minority of high-confidence, high-curiosity questions. Regardless, this is an important consideration for future curiosity research, especially in use of paradigms similar to this one. If the effects of a subjective substrate like curiosity are to be studied accurately, extra care must be taken to avoid confounding this measure with others.

Analyses of physiological sleep variables reflected the findings of our between-groups comparisons. Neither SWS nor TST accurately predicted high or low curiosity memory, a finding that is surprising given the literature on SWS and hippocampal memory consolidation (Antony & Paller, 2017; Rasch & Born, 2013). This result is consistent with the between groups comparison of sleep and wakefulness participants, and the relationship between these sleep

variables and memory may suffer for the same reasons. The curiosity effect for trivia answers is consistently strong, and a lack of an additional benefit from sleep may be due to the already large memory boost incurred at encoding. This notion is supported by our post-hoc analysis using delay as a factor, which showed the lack of a sleep effect was due to an overall absence of significant improvements over delay rather than equivalent improvements across sleep and wakefulness groups. Though many studies report that information that is initially encoded more strongly benefits more from sleep (Hauptmann et al., 2005; Tucker & Fishbein, 2008), these studies are often done on rather rote or boring tasks, memory for which may be more sensitive to additional change. In contrast, the nature of our task means that the highly encoded (high curiosity) information is inherently interesting. Because of this, it is possible that participants intentionally attempted to remember the information for future use, ruminated upon the information after the session, or otherwise processed the information at encoding to the extent that further modulation by sleep was limited. Additionally, no attempt was made on our part to assess participants' expectation of a later test, which is another factor that may have influenced encoding strength. In order to attain a more nuanced understanding of how these memories change between encoding and delayed test, within-subjects designs that are more sensitive to changes over time should be used to examine what may be the more difficult to detect influences of SWS and sleep in general on these types of memory.

Finally, we observed significant effects of subjective sleepiness (as measured by the Stanford Sleepiness Scale) on memory scores, with sleepiness at encoding impacting low-curiosity face memory and sleepiness at test impacting recall of all answer stimuli. Only our sleep group differed from the others in sleepiness at encoding, and though this increased sleepiness may have hurt low-curiosity face scores and exacerbated the curiosity effect in that

group, this would have impacted our results more had we observed significant differences in the curiosity effect between groups. However, this increased sleepiness in the sleep group is interesting itself, especially since those in the evening group completed this scale at the same time of day. One potential reason for this discrepancy is that knowledge of either a forthcoming overnight in the lab or an early morning return to the lab caused fatigue, a possibility that should be accounted for in similar sleep research designs in the future. Similarly, only the sleep and evening groups displayed differences in sleepiness at test, an effect that may have had more import had we seen significant differences between groups on answer recall. Regardless, future research should be cognizant of this significant impact of individual differences in sleepiness on testing of recall measures.

Our results indicate that the memory boost afforded by curiosity, though retained into long-term memory, is not further impacted by sleep. This finding adds to memory effects documented to have no additional benefit from sleep, including the lack of a sleep effect on retrieval-induced forgetting (Abel & Bäuml, 2012), intentional memory suppression (Fischer, Deikelmann, & Born, 2010), and the testing effect, which was equivalent to the effect of sleep on the solitary improvement of memory for studied, non-tested material (Bäuml, Holterman, & Abel, 2014). Our lack of an effect on curiosity demonstrates that saliency *per se* may not be a sufficient indicator of what memories will be enhanced by sleep. However, future studies should examine the potential interplay between the curiosity effect and sleep, as this experiment only examined explicit memory for trivia answers and the learning of incidental materials. Associative memory, motor memory, and spatial memory could be differently influenced by curiosity-driven saliency than the materials in this trivia answer paradigm, and thus paradigms

assessing these types of memory may be helpful in further investigations of the curiosity effect and its relationship with sleep-driven consolidation.

Disclosure of Interest

The authors report no conflict of interest.

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