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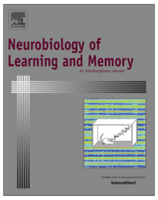

Motivated encoding selectively promotes memory for future inconsequential semantically-related events

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ABSTRACT

Neurobiological models of long-term memory explain how memory for inconsequential events fades, unless these happen before or after other relevant (i.e., rewarding or aversive) or novel events. Recently, it has been shown in humans that retrospective and prospective memories are selectively enhanced if semantically related events are paired with aversive stimuli. However, it remains unclear whether motivating stimuli, as opposed to aversive, have the same effect in humans. Here, participants performed a three phase incidental encoding task where one semantic category was rewarded during the second phase. A memory test 24 h after, but not immediately after encoding, revealed that memory for inconsequential items was selectively enhanced only if items from the same category had been previously, but not subsequently, paired with rewards. This result suggests that prospective memory enhancement of reward-related information requires, like previously reported for aversive memories, of a period of memory consolidation. The current findings provide the first empirical evidence in humans that the effects of motivated encoding are selectively and prospectively prolonged over time.

1. Introduction

It is now well established that memory formation is shaped by motivational factors such as relevance or novelty of the events (Adcock, Thangavel, Whitfield-Gabrieli, Knutson, & Gabrieli, 2006; Lisman & Grace, 2005). Those events that are credited as more important during encoding – e.g., being predictive of a reward or an aversive stimuli – are better remembered over time (Wittmann et al., 2005). The mechanisms underlying novelty or reward-driven memory enhancement have been largely explored in rodents and humans (Schultz, 2002; Shohamy & Adcock, 2010). Both novelty and reward processing are tightly interrelated since both events drive responses in the midbrain dopamine regions (Lisman & Grace, 2005). Dopamine in turn modulates hippocampal activation promoting long-term potentiation (Bethus, Tse, & Morris, 2010) and behavioral persistence of long-term memories for reward predicting cues (Schultz, 1998). In this regard, electrophysiological recordings in monkeys trained in a reward-based classical conditioning paradigm have identified single midbrain dopamine neurons firing in response to cues that predict reward (Fiorillo, Tobler, & Schultz, 2003). In humans, images that predicted (Wittmann et al., 2005) or were preceded by cues predicting rewards (Adcock et al., 2006) were more likely to be remembered. Such memory benefits were correlated with greater activity in reward related brain areas during image presentation (Wittmann et al., 2005) and higher connectivity between the ventral tegmental area and the hippocampus previous to image encoding (Adcock et al., 2006). Thus the hippocampal memory system and the mesolimbic reward system form a functional loop to enhance relevant episodic memories (Lisman & Grace, 2005).

Importantly, reward-driven memory enhancement can out-last the event that elicits the dopaminergic activity and also influence other memories encoded during different time periods: before, during and after the rewarded event. Theoretical (Lisman, Grace, & Duzel, 2011) and animal models (Ballarini, Moncada, Martinez, Alen, & Viola, 2009; Frey & Morris, 1997; Redondo & Morris, 2011; Wang, Redondo, & Morris, 2010) argued that reward-guided memory enhancement during encoding could act in fact as a memory penumbra (Lisman et al., 2011), through which memory for inconsequential events taking place close in time could also be enhanced. According to the synaptic tag and capture model (Frey & Morris, 1997), a behavioral experience that up-regulates

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the availability of plasticity related proteins (e.g. rewarding or novel events) can augment the persistence of a separated behavioral memory that occurs in a near temporal window (before or afterwards). Salvetti, Morris, and Wang (2014) showed that rats that learned a T-maze rewarding task were better at remembering locations that had been weakly encoded before in a separate spatial task. In a human study Mather and Schoeke showed enhanced memory for images presented two trials after winning trials (Mather & Schoeke, 2011).

Interestingly, in a recent behavioral study in humans (Dunsmoor, Murty, Davachi, & Phelps, 2015), retrospective and prospective memories were enhanced by fear conditioning learning. Participants incidentally encoded images of animals and objects in three consecutive phases. During phase 1 and 3 participants were asked to categorize pictures of animals and objects. During phase 2, using a classical conditioning paradigm, one picture category was associated with an electrical shock. This work showed selective memory enhancement for neutral items if other items from the same category were paired before or after with an aversive stimulus (i.e., electric shock). Testing memory at different timings, they described a critical period of consolidation where retrospective and prospective memory enhancement could be observed after 6 h and 24 h respectively, thereby suggesting that only the neural mechanisms for prospective memory enhancement were promoted during sleep.

Despite the relevance of the previous work, it remains unclear whether motivated stimuli, as opposed to aversive, exert similar effects on memory. To address this issue, we investigated whether, in humans, similar retrospective and prospective memory enhancement for inconsequential material could also be driven by motivated encoding.

2. Experiment 1: Classical conditioning

2.1. Participants

All participants in the 2 experiments were undergraduate students from the Faculty of Psychology at the University of Barcelona. They all signed informed consent before the experiment and were given credit or paid for their participation. All participants had normal or corrected-to-normal vision. The study was approved by the ethics committee of the University of Barcelona. To avoid benefits driven by test expectancy (Wilhelm et al., 2011), in all experiments we only included the participants who self-rated themselves as surprised (3 or higher on a 5 point scale) when instructed about the recognition test.

Two versions of experiment 1 were performed. In one version, 23 students were administered a memory recognition test 24 h post-sleep. In the other version, 45 students were tested immediately after encoding. In the 24 h retrieval version, three students were discarded because they scored below 3 in the surprise test leaving a total sample of 20 participants that were included in the analysis (mean age = 23; SD = 3.1, 18 women). In the immediate version, 36 of them (mean age = 20.31; SD = 3.07, 37 woman), who were surprised by the incidental recognition test (i.e., scored > 2), were included in the analyses.

2.2. Material and methods

As in Dunsmoor et al. (2015), participants incidentally encoded images of animals and objects in three consecutive phases. Sixty different images of animals and objects were presented in each phase with a randomly assigned inter-trial interval within a range of 2–4 s. For phases 1 and 3, images were presented for 2.5 s and participants classified each one into ‘animal’ or ‘object’. Participants used left and right arrow keys to indicate each response and a reminder of each category side was displayed during every image presentation. Critically for phase 2, one category was partially rewarded (66.6% of times) (Fig. 1). Rewarded categories were counter-balanced across participants. In this phase, images were presented for 4.5 s and participants, instead of classifying images, would have to indicate whether they expected to receive or not a monetary reward. Participants used left and right arrow keys to indicate whether “Yes” or “No” they expected reward after each image and a reminder of each response side was displayed during every image presentation. In rewarded trials, images were followed by a 1 s coin picture that indicated a money bonus. In addition, a coin sound was presented with the last 1.5 s of the rewarded image and co-terminated with the coin picture. In non-rewarded trials images were followed by a 1 s “0€” picture that indicated no money bonus. Participants were told that answers based on their expectations did not affect compensation. They collected the money accumulated at the end of this phase.

2.2.1. Surprise recognition test

Since reward driven memory modulations operate during the process of memory consolidation and thus are observed after long-term but not immediate retrieval (Murayama & Kuhbandner, 2011), one group of participants was tested on a recognition memory test after 24 h and another immediately after encoding. In addition, since expectancy of a future test can bias the reactivation of those memories during sleep and thus improve memory recollection (Wilhelm et al., 2011), participants were not informed that they were going to be tested at any time.

In the surprise recognition memory test participants were presented with old (the 180 images from the three phases presented the day before) and new images (180 new images of animals and objects). For each image, participants were told to rate whether it was old or new and their confidence by choosing 1 of the 4 possible responses: ‘sure new’, ‘maybe new’, ‘maybe old’, or ‘sure old’. To ensure that participants would not expect a memory test of the encoded material, they were instructed that the same task would be conducted on the second day, for the 24 h retrieval group, or in a fourth block, for the immediate retrieval group. In addition, before administering the test, we assessed whether participants expected a memory test by asking: ‘Do you have any expectation of what the task for today will be: yes or no?’ After participants were told that they were going to be memory tested for the pictures that they had seen the day before, they were asked to rate how surprised they were about this test. This allowed excluding participants who expected the recognition test.

2.3. Results

In both the 24 h retrieval and immediate testing groups participants successfully learned contingencies during this phase 2. Participants’ expectations of reward during encoding in phase 2 (i.e., percentage of correct responses) had a mean accuracy rate of 73.33% (SD = 17.66) for the group tested after 24 h and 68.33% (SD = 17.22) for the group tested immediately, showing no significant differences between groups (unpaired *t*-test, $t_{54} = 0.88$; $p = .38$, $d = .25$).

2.3.1. 24 h retrieval

We ran a repeated measures 3 (Phase) × 2 (Reward) analysis of variance (ANOVA) on participants’ corrected hit rates during the memory recognition test, with memory responses collapsed across confidence. We performed our analysis on the corrected hit rates (i.e., number of hits minus the number of false alarms for each category) to control any possible differences in response bias across

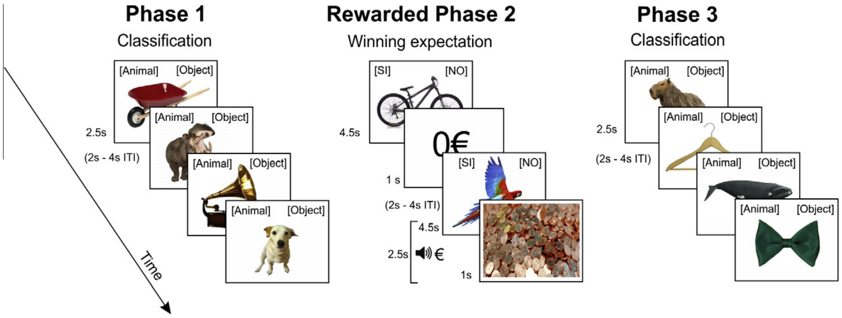

Fig. 1. Experimental design for experiment 1. Participants incidentally encoded 180 images of animals and objects in 3 consecutive phases separated by 3 min, while classifying images into animals or objects. During phase 2, at each image presentation, participants indicated winning expectations and were rewarded 66.6% of the time from one of the categories. In rewarded trials, images were followed by a 1 s coin picture that indicated money bonus. In addition, a coin sound was presented with the last 1.5 s of the rewarded image and co-terminated with the coin picture. In non-rewarded trials images were followed by a 1 s "0€" picture that indicated no money bonus.

participants (see Table S1 for information of hits, false alarms and bias).

We found a main effect of phase ($F_{2,38} = 10.42$; $p < .001$; $\eta^2_p = .35$), and a main effect of reward ($F_{1,19} = 4.99$; $p = .04$; $\eta^2_p = .2$), characterized by a phase × reward interaction ($F_{1,19} = 4.18$; $p = .02$; $\eta^2_p = .18$). Items encoded during phase 2 from the rewarded category were remembered better than those from the non-rewarded category ($t_{19} = 2.54$; $p = .02$; $d = .46$; $r = .22$; 95% CI [.01, .15]) (Fig. 2A, see individual data in Fig. S1A). In addition, we found prospective memory enhancement that was selective for items that were encoded during phase 3 (paired t-test; $t_{19} = 2.3$; $p = .03$; $d = .62$; $r = .29$; 95% CI [.00, .15]) that belonged to the previously rewarded category. We found no retrospective enhancement for items encoded during phase 1 from the rewarded category ($t_{19} = -.45$; $p = .69$; $d = -.07$; $r = -.04$; 95% CI [−.06, .04]). Direct comparisons between the different phases (averaging participants' correct hit rates for pictures of the two categories) revealed that items encoded during phase 2 showed the highest accuracy overall, those encoded during phase 1 had a lower accuracy, and those encoded during phase 3 had the lowest accuracy (paired t-tests; Phase 1 vs Phase 2: $t_{19} = -2.4$, $p = .03$, $d = -.7$, 95% CI [−.18, .01]; Phase 2 vs Phase 3: $t_{19} = 3.96$, $p = .001$, $d = 1.24$, 95% CI [.08, .26]; Phase 1 vs Phase 3: $t_{19} = 2.79$, $p = .012$, $d = .66$, 95% CI [.02, .12]). These results show an overall memory enhancement for items encoded during the conditioning phase (i.e., phase 2) and an overall decrease in memory for those encoded during phase 3, which is more pronounced for items from the non-rewarded condition.

2.3.2. Immediate recognition

The repeated measures 3 (Phase) × 2 (Reward) ANOVA on the corrected hit rates, with memory responses collapsed across confidence, exhibited a significant main effect of phase ($F_{2,70} = 35.59$; $p < .001$; $\eta^2_p = .5$), no significant effect of reward ($F_{1,35} = 1.78$; $p = .19$; $\eta^2_p = .05$), and a significant phase × reward interaction ($F_{2,26} = 3.09$; $p < .01$; $\eta^2_p = .13$) (Fig. 2B, see individual data in Fig. S1B). As expected, follow-up paired t-tests within phases revealed no significant differences between rewarded and non-reward category pictures encoded during phases 1 and 3 (paired t-tests; Phase 1 $t_{35} = .5$, $p = .62$, $d = .09$, 95% CI [−.05, .09]; Phase 3 $t_{35} = .55$; $p = .58$; $d = .11$, 95% CI [−.05, .09]) but significantly better memory for category rewarded items encoded during phase 2 ($t_{35} = 2.51$, $p = .01$, $d = .51$, 95% CI [.01, .16]). Direct comparisons between the phases (averaging correct hits between categories) revealed that memory for items shown during phase 2 was highest (paired t-tests; Phase 2 vs Phase 1: $t_{35} = 8.05$, $p < .001$, $d = 1.18$, 95% CI [.13, .22]; Phase 2 vs Phase 3: $t_{35} = 4.5$; $p < .001$; $d = .7$, 95% CI [.05, .14]) and images encoded during phase 3 were better remembered than those presented during phase 1 (Phase 1 vs Phase 3: $t_{35} = -4.05$; $p < .001$; $d = -.51$, 95% CI [−.11, −.038]).

As expected, for both groups, we found a selective memory boost for items encoded during conditioning, specifically those items from the rewarded category.

Interestingly, we found semantic-driven memory enhancement upon future-encoded inconsequential events only for the group that was tested after 24 h but not if the test was conducted immediately after encoding. These results support the idea that the selective-prospective memory benefits observed were dependent on consolidation mechanisms.

Previous animal studies showed that reward-based learning could drive a tag-and-capture mechanism acting as a memory-modulating event upon previously and future encoded items in a non-selective manner (Salvetti et al., 2014). Therefore, given the lack of retrospective memory enhancement in experiment 1 (24 h retrieval group), we reasoned an alternative possibility would be that such enhancement was non-specific to reward-related information but observed in a more general manner across picture categories. To test this possibility, we ran a second experiment in which the encoding of items in phase 2 was never rewarded. We hypothesized that if there was a retrospective, and/or prospective, non-selective memory enhancement due to reward, we would expect a greater forgetting rate for all items encoded in phase 1 and phase 3 for participants in experiment 2 compared to those from experiment 1 (24 h retrieval group).

3. Experiment 2: Control group

3.1. Participants

Fifty-two students were recruited for this experiment (mean age = 27.89; SD = 7.8). Thirteen participants that scored low (i.e. scored < 3) in the surprise test and two other participants, whose overall memory performance was extremely low (overall < 20%) and extremely high (overall > 90%) respectively (both detected as outliers in the sample ±3 SD) were not included in the analysis. Thus, the total sample group included thirty-seven participants.

3.2. Material and methods

The same material and procedure used in experiment 1 (i.e., phase 1, phase 3 and a delayed 24 h surprise memory test) was used in this experiment except that participants never received a reward during phase 2. Instead of indicating whether they expected to receive or not a monetary reward, participants only classified items into each category (as in phase 1 and 3).

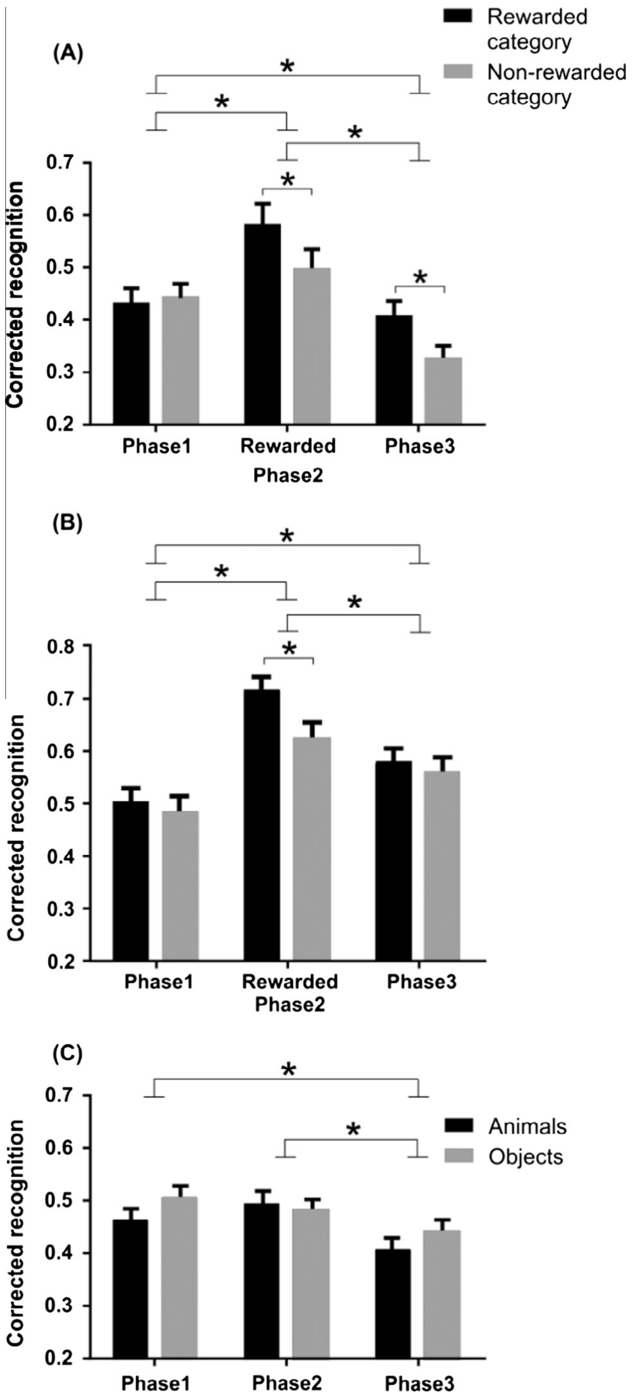

Fig. 2. Behavioral results. (A) Experiment 1, 24 h retrieval. (B) Experiment 1, immediate retrieval. (C) Experiment 2: Control group. Corrected recognition (i.e. hits minus false alarms) for old and new images for rewarded and non-rewarded category (A) and (B) or for each category in (C). Error bars in (A), (B) and (C) denote Standard Error of the Mean. $^*p < .05$.

3.3. Results

First, a 3 (Phase) × 2 (Category) repeated measures ANOVA on the corrected hit rates (see Table S1 for information of hits, false alarms and bias), with memory responses collapsed across confidence, was performed to test for performance differences between the 3 pictures encoded in each phase and picture categories. We found a main effect of phase ($F_{2,72} = 9.57$; $p < .001$; $\eta^2_p = .21$), and as expected, no effect of category ($F_{1,36} = 1.6$; $p = .21$; $\eta^2_p = .04$), and no phase × category interaction ($F_{2,72} = 2.38$; $p = .1$; $\eta^2_p = .06$) (Fig. 2C, see individual data in Fig. S1C). There was no difference in accuracy between items encoded during phase 1 and 2 (t-test Phase 1 vs Phase 2 $t_{36} = -.17$; $p = .86$; $d = -.02$, 95% CI [−.04, .03]). However, similar to the results from experiment 1 (24 h retrieval), we found an overall decrease in memory accuracy for items encoded during phase 3 (Phase 2 vs Phase 3 $t_{36} = 4.22$, $p < .001$; $d = .52$, 95% CI [.03, .09]; Phase 1 vs Phase 3 $t_{36} = 3.9$, $p < .001$; $d = .49$, 95% CI [.02, .09]).

An ANOVA with phase (phase 1, phase 2 and phase 3) and reward (rewarded and non-rewarded category) as repeated measures, and groups (post-sleep classical conditioning and non-rewarded learning groups) as the between subject factor, was performed. We found a main effect of phase ($F_{2,110} = 22.13$; $p < .001$; $\eta^2_p = .28$), as well as a significant phase × group ($F_{2,110} = 5.73$; $p < .005$; $\eta^2_p = .09$) and phase × reward ($F_{2,110} = 5.49$; $p = .005$; $\eta^2_p = .09$) interaction. Follow-up ANOVAs were conducted separately for the three phases. This analysis revealed a trend to significance and a significant reward × group interaction in phase 2 (group × reward $F_{1,55} = 3.14$; $p = .08$; $\eta^2_p = .05$) and in phase 3 (group × reward $F_{1,55} = 6.61$; $p = .01$; $\eta^2_p = .1$) respectively. Pairwise comparisons for phase 3 revealed significantly better memory for non-rewarded category items in the control group ($t_{55} = -3.07$, $p < .005$, $d = -.08$, 95% CI [−.19, −.04]). In contrast, the ANOVA for phase 1 revealed no significant interaction between reward and group ($F_{1,55} = 1.1$, $p = .3$, $\eta^2_p = .02$). Nevertheless, we cannot discard that the lack of a retrospective memory effect could be affected by the rather low statistical power (0.26) achieved in this sample, as revealed by post hoc analyses for the ANOVA restricted to phase 1. Overall, these findings support the idea that the effects of conditioning on subsequent memory for unrelated events may principally operate selectively and prospectively.

4. Discussion

The aim of the present study was to investigate the effects upon incidentally encoded neutral memories, before or after the learning of rewarded items sharing the same category. It has been described that emotionally relevant events (e.g. novel, reward related or aversive events) that promote stabilization into long-term memory (Lisman & Grace, 2005; McGaugh, 2000) can boost the consolidation of separated neutral events encoded close in time (Frey & Morris, 1997) as well as those that are semantically related (Dunsmoor et al., 2015). We used a three phase incidental encoding paradigm where one category was rewarded during the second phase. The surprise recognition test 24 h later, but not when memories were tested immediately after encoding, revealed that memory for inconsequential images was selectively modulated only if items from the same category had been previously, but not subsequently, paired with rewards. To further test for possible behavioral tag and capture mechanisms that would have an unspecific effect on all the material encoded before and after reward learning, we performed an additional experiment in which pictures were never rewarded in phase 2 (control group).

Our data showed consistently – across the two rewarded experimental groups – an overall memory enhancement for images presented during the reward session (phase 2) in comparison with those presented during the classification tasks. Such effect may be explained by a specific memory boost for pictures from the rewarded category. These results replicate a wealth of studies showing early (Wolosin, Zeithamova, & Preston, 2012) (i.e., in the immediate retrieval group) and late (Adcock et al., 2006; Murayama & Kuhbandner, 2011; Wittmann et al., 2005) memory enhancement (i.e., in the 24 h retrieval and instrumental learning group) for information encoded during events that promote dopamine release (Shohamy & Adcock, 2010) and arousal (McGaugh, 2000).

Furthermore, we observed prospective memory enhancement for images from the rewarded semantic category, which were never paired with a reward during encoding in phase 3. Importantly, selective memory enhancement was only observed when participants were tested 24 h after the encoding but not when the surprise test immediately followed encoding. The prospective memory effect was thus mediated by a process of memory consolidation most likely occurring during sleep (Dunsmoor et al., 2015). In fact, it has been described that memories that are expected to be of future relevance (as may be the case when associated to a reward) are more likely to be strengthened during sleep (Oudiette, Antony, Creery, & Paller, 2013; Wilhelm et al., 2011). Using optogenetics to control dopaminergic activity during memory encoding McNamara et al. showed that experiences tagged by dopamine were more biased to be replayed during sleep and thus better remembered, than those that were not dopamine tagged (McNamara, Tejero-Cantero, Trouche, Campo-Urriza, & Dupret, 2014). In our experiment, it is possible that a similar phenomenon occurred, but in our case tagging was specific for images from the rewarded semantic category. In fact, using a target memory reactivation paradigm, Oudiette et al. showed that inducing memory reactivation of a subset of items could also trigger memory enhancement for other items that were semantically related (Oudiette et al., 2013).

An alternative mechanism operating during sleep is the one posited by Tononi and Cirelli (2006) in their synaptic homeostasis hypothesis. Rather than a memory strengthening, this model proposes that slow wave sleep would promote a generalized downscaling of synaptic strength that would ultimately lead to the loss of weak traces (Tononi & Cirelli, 2006). Hence, it could well be the case that the acquisition of a reward assignment to a specific semantic category during phase 2 would have promoted the strengthening of memory traces for items from this category but not for non-rewarded category items, an imbalanced effect that would be critical during off-line consolidation. In this case, the generalized downscaling during slow wave sleep would promote higher forgetting of weak memory traces associated to the non-rewarded category items while preserving memory traces for the rewarded category items. This model can better explain the decline in memory observed for non-rewarded items during phase 3.

Contrary to the recent findings employing a fear conditioning paradigm (Dunsmoor et al., 2015), here, we did not observe selective memory enhancement for images encoded before reward learning. However, given our lack of statistical power we call for caution in interpreting this absence of results and advise further studies to corroborate these findings. On the other hand, noticeable differences in ITI during encoding between our (i.e., 2–4 s) and the previous study (i.e., up to 10 s) may also be considered as a possible source of the divergent results. However, because recognition memory performance was similar between studies, the lack of retrospective memory effect cannot be simply attributed to a general decrease in memory performance in our study. One possibility is that longer ITIs favored post-encoding memory consolidation of the just encoded item (Tambini & Davachi, 2013), which may therefore result in a greater impact of reward-related effects of phase 2 on items from the same category stored during the previous phase. However, the clearest difference between both paradigms is our use of reward learning instead of aversive learning. Since reward and aversive learning rely on different systems it is likely that they have developed different mechanisms of memory consolidation. An alternative explanation would be that reward is more likely to cause phasic bursts of dopaminergic activity (Schultz, 1998), as opposed to aversive or novel stimuli which may lead to more tonic dopaminergic activity (Lisman et al., 2011). Such differences in dopaminergic activity dynamics could therefore be critical in determining whether and how the synaptic tagging and capture mechanism modulates memory performance at the behavioral level.

It could still be argued that the lack of retrospective memory enhancement using a classical conditioning task was due to a failure to motivate/engage the participants with the encoding task (and therefore, decreasing the dopaminergic release during it). In fact, other studies employing monetary reward tasks – using a [^{11}C]raclopride tracer to detect dopamine activity during a PET scan – have reported a lack of dopamine increment during reward encoding (Hakyemez, Dagher, Smith, & Zald, 2008). Given the strong connection between DA release and hippocampus-driven memory performance, we encourage future studies to use stronger motivational tasks (e.g. novelty event encoding) that could perhaps facilitate retrospective memory modulations.

In our second experiment we tested the idea that reward learning could lead to a non-specific memory boost upon all the events encoded before and afterwards (Salvetti et al., 2014). Comparisons between the 24 h and the control group – that were never rewarded during phase 2 – did not show an overall memory enhancement for phase 1 items or for phase 3 items, due to the reward learning task. This suggests that the generalization of reward learning only operated at a conceptual level. One possible explanation, is that reward during phase 2 specifically modulated category-selective regions from the extrastiate visual cortex that processed rewarded-category items, as has been shown in previous studies using fear conditioning (Dunsmoor, Kragel, Martin, & LaBar, 2013). In this manner, items that were subsequently encoded in the same rewarded category-regions would benefit from the neuroplasticity boost triggered during phase 2.

The current findings provide the first empirical evidence in humans that the effects of motivated encoding are selective and extend over time prospectively. We show that reward value can spill-over from relevant events to neutral ones through a generalization process that operates along a higher order conceptual relationship. Whether prospective memory enhancement is operating through a tag-and-capture or other mechanisms of transfer of learned reward value (for a review, Miendlarzewska, Bavelier, & Schwartz, 2016) still requires future investigation. Coherent with previous studies, we show that reward outlasting memory effects upon neutral albeit semantically related information was dependent on post-encoding long-term consolidation mechanisms (Murayama & Kuhbandner, 2011; Wittmann et al., 2005). We emphasize the role of sleep as the ultimate player in the consolidation process that would protect emotionally relevant information from future forgetting (Oudiette et al., 2013; Tononi & Cirelli, 2006). In line with the idea of an adaptive memory system, reward learning selectively influences memory stabilization for events that are credited to be of future relevance to ultimately bias future decisions (Shohamy & Adcock, 2010; Wimmer & Shohamy, 2012).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.nlm.2016.05.005.

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