In for a pound, in for a penny: How the opportunity to gain reward influences the competition for memory resources

Deborah Talmi[a], Nathaniel D. Daw[b], Deimante Kavaliauskaite[a]

[a]Division of Neuroscience and experimental psychology, University of Manchester

[b]Princeton Neuroscience Institute and Department of Psychology, Princeton University

Address for correspondence

Deborah Talmi, Division of neuroscience and experimental psychology, School of Biological Sciences, University of Manchester, Manchester, UK, M139PL.

Telephone: 0161 2751968 Email: Deborah.Talmi@manchester.ac.uk

Abstract

When people encounter items that they believe will help them gain reward, they later remember them better than those that do not. While it is adaptive to preferentially remember experiences that will be useful later, it is unknown how the competition for memory resources is implemented in time, through the processes of encoding, consolidation, and retrieval. In two experiments we promised participants £1 for remembering some pictures, but only 10 pence for remembering others. Their ability to describe the pictures was tested after one minute and after 24 hours. Memory at immediate test showed effects of list composition, suggesting local competition at encoding and/or retrieval. These results are consistent with our recently-proposed emotional Context Maintenance and Retrieval model, supporting it as a general account of motivated memory. In contrast, relative to this baseline, more valuable memories were not preferentially retained following delay, suggesting no detectable role of competition for consolidation.

Introduction

It is paramount to remember information that can help us attain our goals and increase our subjective utility. Because memory resources are limited, it is adaptive for the brain to prioritise experiences that can be leveraged to obtain rewards and avoid punishments over less-important experiences (Gershman & Daw, 2017). This intuition was expressed by Sherlock Holmes, Arthur Conan Doyle's timeless protagonist, when (justifying his ignorance of astronomy) he remarked that "It is of the highest importance… not to have useless facts elbowing out the useful ones". Holmes' intuition agrees with rational considerations, which suggest that if memory resources are limited, it is best to hold on to the most valuable information, compared globally against all other information (Anderson & Schooler, 1991). But how such competition plays out in practice is not so simple, for at least two reasons. First, experiences are encountered sequentially rather than all at once, meaning that a rational agent must decide which memories to retain without knowing the full set of competitors. Second, Holmes' picture of the mind as a storeroom of fixed, limited capacity is grossly oversimplified: memories can compete, interfere with each other and promote each other at many stages of encoding, consolidation, and retrieval. For a rational analysis it's not clear to what extent each of these stages represents a meaningful resource bottleneck. Both of these considerations suggest that competition may occur locally, only among items that are close to each other on some contextual dimension, such as time (the preceding or following items) or space (various objects in the same scene). Our research question, therefore, concerns the scope of the competition of reward-predicting information for memory resources.

To answer this question it is useful to consider how the opportunity to maximise utility influences the cognitive mechanisms that underlie successful recall. In an experimental setting where remembering some items earn more money or ‘points’, high-value items are attended preferentially and remembered better (e.g. Ariel & Castel, 2014; Lee, Greening, & Mather, 2015; for review see Mather & Sutherland, 2011), although some only observe memory facilitation in delayed tests (e.g. Montagrin, Brosch, & Sander, 2013; Spaniol, Schain, & Bowen, 2014). It is less clear how increased attention to high-value items influences memory formation. The emotional Context Maintenance and Retrieval model (eCMR), a variant of retrieved-context models that describes the influence of emotional value on free recall (Talmi, Lohnas, & Daw, in press), suggests that the extra attention participants allocate to high-value items binds items more tightly to their encoding context. When asked to freely recall these items later this tighter binding enhances the competitive advantage of high-value items against low-value items, but makes it difficult to link them to a new context later on (Madan, Fujiwara, Gerson, & Caplan, 2012). This account assumes a global competition during encoding, but a local competition during recall.

There is evidence for local competition for recall from experiments with emotionally-arousing words, sentences, and pictures: all items that are known to capture attention preferentially, and which might heuristically be interpreted as fitness-relevant. In these experiments memory for emotional items typically increases, and memory for neutral ones decreases, when emotional and neutral items are presented and recalled together, in ‘mixed’ lists (Barnacle, Tsivilis, Schaefer, & Talmi, 2017; Hadley & MacKay, 2006; MacKay et al., 2004; Talmi, Luk, McGarry, & Moscovitch, 2007), or when the emotional item is the ‘oddball’ among

neutral ones (Hurlemann et al., 2005; Mather & Knight, 2009). The recall advantage of emotional items is less pronounced and sometimes disappears altogether when emotional and neutral items are presented and recalled separately, in ‘pure’ lists. eCMR simulates these situations successfully (Talmi, Lohnas, & Daw, in press). There is also evidence that recalling items that are not personally valued, but attract attention because they are bizarre, is enhanced because of local completion for retrieval, not because of competition for encoding resources (McDaniel, Dornburg, & Guynn, 2005). It is unknown, at present, whether these accounts generalise to information that predicts reward directly and explicitly. To whatever extent competition for memory resources is global in nature, high-value items should out-compete low-value items regardless of the local context of the list in which they were presented. Indeed, it would be irrational for a fully informed observer to allocate encoding or retrieval resources to low-value items.

In this paper we test this prediction by examining memory for stimuli whose later recall explicitly predicts high and low reward, encoded in pure and mixed lists. In two experiments, our participants viewed lists of neutral pictures that were presented framed or unframed. They knew that they could gain larger monetary reward by recalling framed items on later test. The critical manipulation was the arrangement of framed and unframed items in the list, such that some lists included both item types (mixed) and some only one (pure). We did not expect that the list arrangement would influence the attention participants pay to framed, compared to unframed, pictures, because the frame provides a clear signal of which stimulus type should be prioritised (Mather, Clewett, Sakaki, & Harley, 2017; Mather & Sutherland, 2011). Importantly, in the global context of the experiment – and, indeed, the participant’s day outside the laboratory – remembering framed pictures promised more reward

than average, certainly more reward than unframed pictures. If the competition for memory resources is global, rational participants should recall the framed pictures better than unframed pictures regardless of the list in which they were presented, in both mixed and pure lists; recall will mirror the priority assigned to these stimuli during encoding. By contrast, if the competition for recall is local, as predicted by eCMR, the recall advantage for high- over low-value items will be observed only in mixed lists, but eliminated when they are studied and tested in pure lists, a pattern called a 'list composition effect'. Confirming this prediction would support eCMR as a general model of motivated memory, across very different operationalisations of value.

Because the degree of competition for retrieval resources is independent of the timing of the memory test, eCMR predicts a list-composition effect both when memory is tested immediately and when it is tested after a delay. By contrast, theories of modulated consolidation ascribe enhanced memory for items that are highly emotional or that are associated with reward to competition for resources during memory storage (Lisman, Grace, & Duzel, 2011; McGaugh, 2013; Yonelinas & Ritchey, 2015). There is evidence that the consolidation of hippocampal memory traces of items that are emotionally-arousing, or that are associated with high reward, is modulated by noradrenaline or dopamine, respectively, over the course of the hours and days after encoding. Even in experiments where participants are unlikely to allocate resources strategically to high-value items, for instance when encoding is incidental, the reward associated with some items is thought to trigger dopaminergic neuromodulation, so that these items are forgotten more slowly, and are recalled more readily in a delayed test (Bunzeck, Dayan, Dolan, & Duzel, 2010; Mason, Ludwig, & Farrell, 2017; Montagrin et al., 2013; Patil, Murty, Dunsmoor,

Phelps, & Davachi, 2017; Spaniol et al., 2014). Modulated consolidation theories imply competition for resources during consolidation, where high-value items will be forgotten more slowly. Crucially, this prediction holds irrespective of the list in which items were presented. Despite decade-long interest in list composition effects, to our knowledge this effect has never been tested with a prolonged retention interval. In Experiment 2 we examine this hypothesis by testing half of the lists only after 24 hours.

Methods

Materials

Stimuli consisted of pictures retrieved from freely-available databases, adjusted in size to 280x210 pixels. In addition, the experiments used 9 printed sheets with 36 easy arithmetic subtraction and addition problems for the distractor task, with one sheet assigned randomly to each block. The experiment was implemented using Cogent200 on a MATLAB platform.

Experiment 1. Stimuli consisted of 48 pictures of clothing and 48 pictures of stationary. Pictures were retrieved from the Bank of Standardized Stimuli (Brodeur, Dionne-Dostie, Montreuil, & Lepage, 2010; Brodeur, Guérard, & Bouras, 2014) and from Food-Pics (Blechert, Meule, Busch, & Ohla, 2014; scores for pictures drawn from the Food-pic database were converted from a 1-100 scale to the BOSS 1-5 scale). Pictures from the two categories were matched for familiarity (clothing: M=4.30, SD=.32; stationary: M=4.39, SD=.35) and complexity (clothing: M=2.29, SD=.37; stationary: M=2.30, SD=.49). Each list included 8 pictures from each category. In the pure list condition they were all either framed with a grey square, or

unframed. In the mixed list condition, 4 pictures of each type were framed and 4 unframed. The assignment of pictures to conditions was randomised for every participant.

Experiment 2. Stimuli consisted of 16*9 pictures from 9 different categories: clothing, animals, cityscapes, food, household objects (non-kitchen), kitchen objects, landscapes, office items, and people. They were drawn from the same sources as in Experiment 1, as well as the Nencki Affective Picture System (Marchewka, Zurawski, Jednoróg, & Grabowska, 2014), ImageNet (image-net.org), and internet sources. None had an overt emotional tone. While categories and pictures differed on multiple attributes, they were randomly assigned to conditions for each participant, eliminating the danger of systematic error. Each list included 16 pictures, which all belonged to a single semantic category. The Clothing list was always used in the practice block; otherwise, allocation of list to condition was randomised for each participant. In the pure list condition all pictures were either framed or unframed; in the mixed list condition 8 pictures were framed and 8 unframed.

Procedure

Participants were tested individually, in a quiet room, in the presence of a single experimenter. Each experiment began with instructions and practice, delivered on PowerPoint. The experiment comprised of a number of blocks. Each block included a picture task and a distractor task (see below). The allocation of picture lists to the picture task in each block, the order of pictures in each list, and the order of blocks were randomised for each participant.

Experiment 1 included 6 blocks, 2 with pure lists of framed pictures, 2 with pure lists of unframed pictures, and 2 with mixed lists where half the pictures were framed and the other half unframed. All blocks ended with a free recall test (see below).

Experiment 2 included 8 blocks, 2 with pure lists of framed pictures, 2 with pure lists of unframed pictures, and 4 with mixed lists. Half of the blocks in each of these three conditions were assigned to the immediate memory condition, and ended with a free recall test. The other half was assigned to the delayed memory condition and did not include a free recall test. To increase engagement throughout session 1, participants were also told that one of the lists that will *not* be tested immediately will be tested at the end of session 1. To maintain credibility, session 1 always began with an additional practice block, which appeared to participants to be part of the experiment proper. The practice block always used the same Clothing list, and included only the picture and the distractor task. Session 1 always ended with a delayed free recall test (see below) of that list. To decrease rehearsal between sessions, participants were told that they will perform different tasks in session 2.

At the end of session 1 one block (in Experiment 1, only one of those blocks allocated to the immediate memory condition) was selected randomly, and participants were paid according to their free recall performance - £1 for each framed picture they recalled (if there were any in that block) and 10 pence for each unframed picture they recalled. Participants were informed of this and were explicitly told that their goal is to maximise their monetary reward.

Instructions and practice. Participants were given detailed instructions about each of the tasks. They practiced each of the tasks using a set of 16 additional pictures (3 framed). During the practice block a lower reward rate was in effect (10

pence vs. 1 penny). At the end of the practice block participants were given feedback about their performance and paid any money they earned.

Picture task. Each picture was individually presented. It was presented centrally, on a white background, for 2s followed by a blank screen for 3.5, 4 or 4.5s (randomised ISI) before the next picture presentation. Participants were asked to view the pictures and try to commit them to memory.

Distractor task. Participants were given 60s to complete as many arithmetic questions as possible. They were informed that to qualify for reward they must (1) complete at least eight questions (2) those two that are randomly selected for checking must be completed accurately.

Free recall test. Participants were given a few minutes to describe in writing each of the pictures they remembered (3 minutes in Experiment 1, 4 minutes in Experiment 2). They were prompted to keep trying if they stopped before the time. A beep signalled the start and end of the memory task. Participants were instructed that each description should include three details about the picture, separated by a comma; e.g. “A plant, spikey leaves, in round pot”.

Delayed free recall. Participants were shown the title of the category of the list from one block, and given 4 minutes to recall the pictures from that block. In session 1, only the practice block was tested in this way. In session 2, all 8 experimental blocks were tested, one after the other.

Results

The analysis reported here follows exactly on the analytic approach we have used in previous work. That work led to the prediction that we would find an interaction between list type and reward. Therefore, the four comparisons that ensue – within lists (high vs. low reward, in pure and mixed lists separately) and across lists (high and low reward in mixed vs. pure lists) are all planned contrasts. To be conservative we corrected these for familywise error by using a Bonferroni-corrected p-value threshold of $p<.0125$.

Experiment 1. The average free recall data are depicted in Figure 1. They were analysed with a 2 (list: pure, mixed) x 2 (reward: high, low) repeated-measures ANOVA. The effect of list type was not significant, but the interaction with reward was significant and large, $F(1,28)=20.09$, $p<.001$, partial $\eta 2 =.42$, qualifying the significant main effect of reward, $F(1,28)=10.71$, $p<.001$, partial $\eta 2 =.28$. These results reveal a reward-dependent list-composition effect. Planned paired t-tests showed that the effect of reward was only significant in the mixed list condition, $t(28)=4.38$, $p<.001$, where participants recalled high-rewarded items earlier than low-rewarded items (Figure 1). There was no significant difference between recall of pure lists, $t<1$. There was no statistical difference between memory for high-rewarded items in mixed and pure lists, $t(28)=1.69$, $p>.1$. Low-rewarded items were recalled less well in mixed lists, $t(28)=4.72$, $p<.001$. The average recall of mixed lists, collapsing across reward ($M=41.27$, $SD=12.48$) was numerically lower than the average recall of unrewarded pure lists ($M=43.86$, $SD=13.79$).

Experiment 2. The average free recall data were analysed with a 2 (delay: immediate, delayed) x 2 (list: pure, mixed) x 2 (reward: high, low) repeated-measures ANOVA. This analysis only includes lists that were tested once – either immediately (session 1) or only after a delay (only tested in session 2). The three-

way interaction was significant and large, $F(1,37)=19.19$, $p<.001$, partial $\eta 2 = .34$. We unpacked this interaction with two separate repeated-measures ANOVAs. The first was a list-by-reward analysis which focused on average recall in the immediate condition; these data are depicted in Figure 1. Its aim was to examine whether this experiment replicated Experiment 1. The effect of list type was not significant, $F<1$, but the interaction with reward was significant and large, $F(1,37)=27.15$, $p<.001$, partial $\eta 2 =.42$, qualifying the significant main effect of reward, $F(1,37)=39.60$, $p<.001$, partial $\eta 2 =.52$, which was also observed in Experiment 1. Planned paired t-tests showed that as in Experiment 1, the effect of reward was only significant in the mixed list condition, $t(37)=7.66$, $p<.001$, where participants again recalled high-rewarded items earlier than low-rewarded items (Figure 1). There was no difference between the recall of the two pure lists, $t<1$. As in Experiment 1, low-rewarded items were recalled less well in mixed compared to pure lists, $t(37)=4.84$, $p<.001$. However, while in Experiment 1 high reward did not increase memory, here recall of high-rewarded items was better than their recall in pure lists $t(37) = 4.96$, $p<.001$. The average recall of mixed lists, collapsing across reward ($M=26.64$, $SD=8.92$) was equivalent to the average recall of unrewarded pure lists ($M=26.32$, $SD=15.32$), $t<1$.

The list composition effect was less pronounced in the delayed test (Figure 2). Indeed, after a delay the interaction between list type and reward was small in size and not statistically significant, $F(1,37)=3.31$, $p=.077$, partial $\eta 2 =.08$, while the effect of reward was significant, $F(1,37)=26.28$, $p<.001$, partial $\eta 2 =.41$. Importantly, planned paired t-tests showed that the effect of reward was only significant in the mixed list condition, $t(37)=4.10$, $p<.001$, but not in the pure list condition, $t(37)=1.99$, $p=0.054$..

Decreases in average recall between the immediate and the delayed test are depicted in Figure 2. To understand whether reward modulated forgetting we computed proportional forgetting scores [(average immediate recall – average delayed recall)/ average immediate recall]. Proportional forgetting scores were computed for each list-by-reward condition, and therefore necessitated excluding 6 participants who did not recall any items immediately in one of these four conditions (resulting in a sample of N=32). This calculation was carried out twice. First, we examined lists that were only tested once - immediately or after a delay, i.e. in session 1 or 2, but not both. Proportional forgetting scores of high and low reward items in pure and mixed lists were remarkably similar. They were analysed with a list-by-reward repeated-measures ANOVA. While forgetting was substantial, approximating 60%, it was the same in all conditions, so none of the factors were significant, $F<1$. Next we examined proportional forgetting of the same lists. In this analysis we calculated proportional forgetting scores using the same formula, but here using the average immediate recall from session 1 and the average delayed recall of the same lists after a delay (session 2). Forgetting of items that were already recalled once in session 1 was lower than forgetting of items that were never recalled, approximating 20%, but again, none of the factors were significant, $F<1$.

Discussion

In two experiments, participants only recalled high-value items more than low-value items when they were studied and recalled together, in a mixed list, but not when they were studied and recalled separately, in pure lists. This result supports our

hypothesis that the competition for memory resources is local in nature, constrained by the context specified by the task set (here, the temporal context of the previous list). It aligns with a core prediction of eCMR, supporting it as a general model of motivated memory.

This is the first demonstration of a list-composition effect with a manipulation of reward. These results concur with previous findings where between-group manipulations of motivation failed to increase free recall, source memory, and recognition (Ngaosuvan & Mantila, 2005; Nilsson, 1987). While previous studies could only document a null effect of subjective motivation on memory, and check that the manipulation worked by collecting subjective ratings of motivation, the list-composition paradigm allowed us to document a significant interaction between list type and value, ensuring that the same manipulation of motivation that did not result in significant effects in pure lists influenced recall significantly in mixed lists. The null effect of value in pure lists does not mean that there is no effect of value on memory in that condition; the significant interaction shows that it is smaller than the effect in mixed lists.

The remarkable similarity between the list-composition effects obtained with emotional pictures in our previous work (summarised in Table 1 in Talmi et al., 2018) and high-value pictures here suggests that they result from the same mechanism. eCMR explains enhanced recall for emotional information as resulting from the interplay of encoding, storage, and retrieval processes. In eCMR, items that are encoded in the same way – through similar encoding operations - share a ‘source’ context. Emotional items trigger unique cognitive, affective and physiological changes, which distinguish their source context from that of neutral items. During encoding, preferential attention to emotional items binds them more strongly to their

source context. During retrieval, when the context is used to probe memory, increased connection strength gives emotional items an advantage over neutral ones, allowing them to win the competition for recall.

Translating eCMR to the experiments reported here is not completely straightforward. In eCMR, recalling an item with a particular source context updates the source context of the retrieval probe, thereby promoting the recall of other items with the same source context. This is evident in experiments using emotional stimuli where recall clusters around the emotional category(Long, Danoff, & Kahana, 2015; Talmi et al., 2007), but it was is less evident here. The difference may be due to the fact that in experiments with emotional and neutral stimuli the high-value “emotional” category is also a cohesive semantic category of distressing scenes, and the low-value items are either unrelated to the emotional ones and to each other, or, when semantic relatedness is controlled, related to each other but not to the emotional category. By contrast, here the semantic and value categories were orthogonal; for example, in the mixed lists half of the ‘office’ items were framed and half were unframed. It is possible that the presence of strong semantic associations between list items masked an effect of clustering based on reward.

. The comparison between high- and low-value items is particularly important here, because the opportunity to gain is thought to be associated with dopamine release, and many believe that it underlies the memory-enhancing effect of reward even in immediate tests (Rouhani, Norman, & Niv, 2018), and even more so after a delay (Adcock, Thangavel, Whitfield-Gabrieli, Knutson, & Gabrieli, 2006; Bunzeck et al., 2010; Mason, Farrell, Howard-Jones, & Ludwig, 2017; Mason, Ludwig, et al., 2017; Patil et al., 2017; Spaniol et al., 2014). Here the forgetting rate of items that participants encoded, but did not immediately recall, was equivalent regardless of

whether these items predicted high or low reward. The same was true for the forgetting rate of items that participants encoded and recalled immediately. These results suggest that to the extent that dopaminergic neuromodulation occurs in experiments that reward participants monetarily for remembering, it does not enhance delayed recall substantially, at least not when people know broadly what kind of items they are expected to recall. Note that the latter proviso likely characterises most emotional memory experiments, where participants generally can report that they've seen some "nasty" and some "normal" scenes. The non-significant effect of reward on forgetting aligns with the general finding in cognitive psychology that manipulations that increase immediate memory do not attenuate proportional forgetting rates (Loftus, 1985; Slamecka, 1985). While a variety of forgetting scores have been proposed in the literature (Wixted, 1990), it is, of course, imperative to take immediate performance into account when it differs between critical conditions, as it did here, and proportional forgetting scores achieve this goal.

Our experiments show that reward does not enhance memory globally, and does not make items more resistant to forgetting. The bias to attend reward-predicting information increases its competitive advantage only if it competes for recall with other, less-important information. Crucially, memory for reward-predicting information is not any better than memory for any other information unless the two compete for recall. This finding could have implications for the design of reward schemes in educational settings, because it suggests that motivating learners to commit a subset of material to memory by promising a prize is unlikely to enhance memory for that material – unless an assessments happens to also include material that learners did not prioritise, in which case the memory advantage for former will be at the cost of the latter. If further research supports eCMR as a model of motivated memory the

model can be used to predict how reward schemes might be best employed to support learning.

Acknowledgements

DT was supported by the Royal Society [IE160027]. DK was supported by the University of Manchester Learning Through Research initiative.

References

Adcock, R. A., Thangavel, A., Whitfield-Gabrieli, S., Knutson, B., & Gabrieli, J. D. E. (2006). Reward-motivated learning: mesolimbic activation precedes memory formation. *Neuron*, *50*(3), 507–17. https://doi.org/10.1016/j.neuron.2006.03.036

Anderson, J. R., & Schooler, L. J. (1991). Reflections of the environment in memory. *Psychological Science*, *2*(6), 396–408. https://doi.org/10.1111/j.1467-9280.1991.tb00174.x

Ariel, R., & Castel, A. D. (2014). Eyes wide open: enhanced pupil dilation when selectively studying important information. *Experimental Brain Research*, *232*(1), 337–44. https://doi.org/10.1007/s00221-013-3744-5

Barnacle, G. E., Tsivilis, D., Schaefer, A., & Talmi, D. (2017). 1 Local context influences memory for emotional stimuli but not electrophysiological markers of emotion-dependent attention Gemma E. Barnacle, (0161), 1–35. https://doi.org/10.1111/psyp.13014

Blechert, J., Meule, A., Busch, N. A., & Ohla, K. (2014). Food-pics: an image database for experimental research on eating and appetite. *Frontiers in Psychology*, *5*, 617. https://doi.org/10.3389/fpsyg.2014.00617

Brodeur, M. B., Dionne-Dostie, E., Montreuil, T., & Lepage, M. (2010). The bank of standardized stimuli (BOSS), a new set of 480 normative photos of objects to be used as visual stimuli in cognitive research. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0010773

Brodeur, M. B., Guérard, K., & Bouras, M. (2014). Bank of Standardized Stimuli (BOSS) phase ii: 930 new normative photos. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0106953

Bunzeck, N., Dayan, P., Dolan, R. J., & Duzel, E. (2010). A common mechanism for adaptive scaling of reward and novelty. *Human Brain Mapping*, *31*(9), 1380–94. https://doi.org/10.1002/hbm.20939

Gershman, S. J., & Daw, N. D. (2017). Reinforcement Learning and Episodic Memory in Humans and Animals : An Integrative Framework, *68*(5), 101–128. https://doi.org/10.1146/annurev-psych-122414-033625

Hadley, C. B., & MacKay, D. G. (2006). Does emotion help or hinder immediate memory? Arousal versus priority-binding mechanisms. *Journal of Experimental Psychology: Learning Memory and Cognition*, *32*(1), 79–88. https://doi.org/10.1037/0278-7393.32.1.79

Hurlemann, R., Hawellek, B., Matusch, A., Kolsch, H., Wollersen, H., Madea, B., … Dolan, R. J. (2005). Noradrenergic Modulation of Emotion-Induced Forgetting and Remembering. *Journal of Neuroscience*, *25*(27), 6343–6349. https://doi.org/10.1523/JNEUROSCI.0228-05.2005

Lee, T.-H., Greening, S. G., & Mather, M. (2015). Encoding of goal-relevant stimuli is strengthened by emotional arousal in memory. *Frontiers in Psychology*, *6*, 1173. https://doi.org/10.3389/fpsyg.2015.01173

Lisman, J., Grace, A. A., & Duzel, E. (2011). A neoHebbian framework for episodic memory; role of dopamine-dependent late LTP. *Trends in Neurosciences*, *34*(10), 536–47. https://doi.org/10.1016/j.tins.2011.07.006

Loftus, G. R. (1985). Evaluating Forgetting Curves. *Journal of Experimental Psychology*, *11*(2), 397–406. https://doi.org/10.1007/BF02645546

Long, N. M., Danoff, M. S., & Kahana, M. J. (2015). Recall dynamics reveal the retrieval of emotional context. *Psychonomic Bulletin and Review*, *22*(5), 1328–1333. https://doi.org/10.3758/s13423-014-0791-2

MacKay, D. G., Shafto, M., Taylor, J. K., Marian, D. E., Abrams, L., & Dyer, J. R. (2004). Relations between emotion, memory, and attention: evidence from taboo stroop, lexical decision, and immediate memory tasks. *Memory & Cognition*, *32*(3), 474–488.

https://doi.org/10.3758/BF03195840

Madan, C. R., Fujiwara, E., Gerson, B. C., & Caplan, J. B. (2012). High reward makes items easier to remember , but harder to bind to a new temporal context, *6*(August), 1–15. https://doi.org/10.3389/fnint.2012.00061

Marchewka, A., Zurawski, Ł., Jednoróg, K., & Grabowska, A. (2014). The Nencki Affective Picture System (NAPS): introduction to a novel, standardized, wide-range, high-quality, realistic picture database. *Behavior Research Methods*, *46*(2), 596–610. https://doi.org/10.3758/s13428-013-0379-1

Mason, A., Farrell, S., Howard-Jones, P., & Ludwig, C. J. H. (2017). The role of reward and reward uncertainty in episodic memory. *Journal of Memory and Language*, *96*, 62–77. https://doi.org/10.1016/J.JML.2017.05.003

Mason, A., Ludwig, C., & Farrell, S. (2017). Adaptive scaling of reward in episodic memory: a replication study. *Quarterly Journal of Experimental Psychology*, *70*(11), 2306–2318. https://doi.org/10.1080/17470218.2016.1233439

Mather, M., Clewett, D., Sakaki, M., & Harley, C. W. (2017). Norepinephrine ignites local hotspots of neuronal excitation: How arousal amplifies selectivity in perception and memory. https://doi.org/10.1017/S0140525X15000667

Mather, M., & Knight, M. (2009). Reconciling findings of emotion-induced memory enhancement and impairment of preceding items. *Emotion*, *9*(6), 763–781. https://doi.org/10.1037/a0017281.Reconciling

Mather, M., & Sutherland, M. R. (2011). Arousal-Biased Competition in Perception and Memory. *Perspectives on Psychological Science : A Journal of the Association for Psychological Science*, *6*(2), 114–33. https://doi.org/10.1177/1745691611400234

McDaniel, M. A., Dornburg, C. C., & Guynn, M. J. (2005). Disentangling encoding versus retrieval explanations of the bizarreness effect: Implications for distinctiveness. *Memory & Cognition*, *33*(2), 270–279. https://doi.org/10.3758/BF03195316

McGaugh, J. L. (2013). Making lasting memories: Remembering the significant. *Proceedings of the National Academy of Sciences*, *110*(Supplement_2), 10402–10407. https://doi.org/10.1073/pnas.1301209110

Montagrin, A., Brosch, T., & Sander, D. (2013). Goal conduciveness as a key determinant of memory facilitation. *Emotion*, *13*(4), 622–628. https://doi.org/10.1037/a0033066

Ngaosuvan, L., & Mantila, T. (2005). Rewarded remembering: Dissociations between self-rated motivation and memory performance. *Scandinavian Journal of Psychology*, *46*(4), 323–330. https://doi.org/10.1111/j.1467-9450.2005.00462.x

Nilsson, L.-G. (1987). Motivated memory: Dissociation between performance data and subjective reports. *Psychological Research*, *49*(2–3), 183–188. https://doi.org/10.1007/BF00308685

Patil, A., Murty, V. P., Dunsmoor, J. E., Phelps, E. A., & Davachi, L. (2017). Reward retroactively enhances memory consolidation for related items. *Learning & Memory (Cold Spring Harbor, N.Y.)*, *24*(1), 65–69. https://doi.org/10.1101/lm.042978.116

Rouhani, N., Norman, K. A., & Niv, Y. (2018). Learning, Memory, and Cognition: Dissociable Effects of Surprising Rewards on Learning and Memory Dissociable Effects of Surprising Rewards on Learning and Memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *44*(9), 1430–1443. https://doi.org/10.1037/xlm0000518

Slamecka, N. J. (1985). On Comparing Rates of Forgetting. Comment on Loftus (1985). *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *11*(4), 812–816. https://doi.org/10.1037/0278-7393.11.1-4.812

Spaniol, J., Schain, C., & Bowen, H. J. (2014). Reward-Enhanced Memory in Younger and Older Adults. *The Journals of Gerontology Series B: Psychological Sciences and Social Sciences*, *69*(5), 730–740. https://doi.org/10.1093/geronb/gbt044

Talmi, D., Lohnas, L. J., & Daw, N. D. (2018). A retrieved context model of the emotional modulation of memory. *Psychological Review*.

Talmi, D., Luk, B. T. C., McGarry, L. M., & Moscovitch, M. (2007). The contribution of relatedness and distinctiveness to emotionally-enhanced memory. *Journal of Memory and Language*, *56*(4), 555–574. https://doi.org/10.1016/j.jml.2007.01.002

Wixted, J. T. (1990). Analyzing the empirical course of forgetting. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *16*(5), 927–935. https://doi.org/10.1037/0278-7393.16.5.927

Yonelinas, A. P., & Ritchey, M. (2015). The slow forgetting of emotional episodic memories: An emotional binding account. *Trends in Cognitive Sciences*, *19*(5), 259–267. https://doi.org/10.1016/j.tics.2015.02.009

Figure captions

Figure 1. Average immediate free recall as a function of reward and list composition. High and low reward are presented in dark and light grey, respectively.

Top: immediate memory test in Experiments 1.

Middle: immediate memory test in Experiment 2.

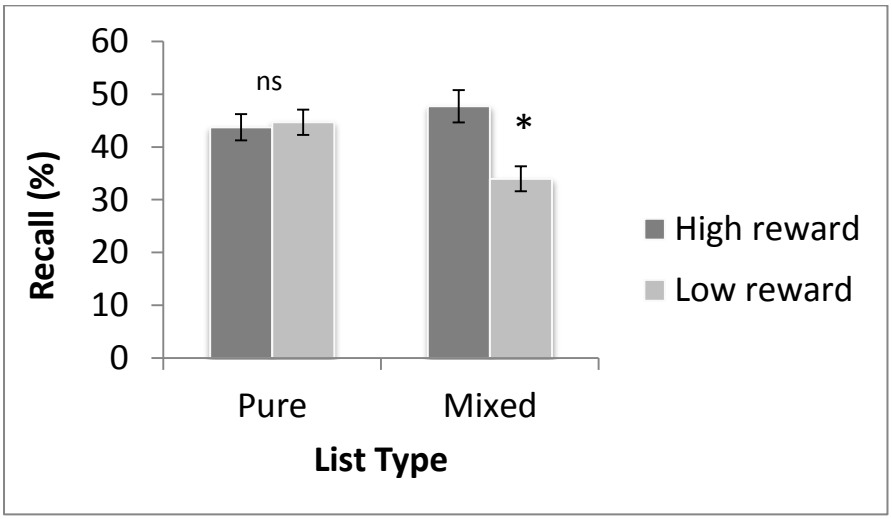
Bottom: Recall probability as a function of output order in Experiment 1(left) and 2 (right). * $p<.001$. ns $p>0.05$.

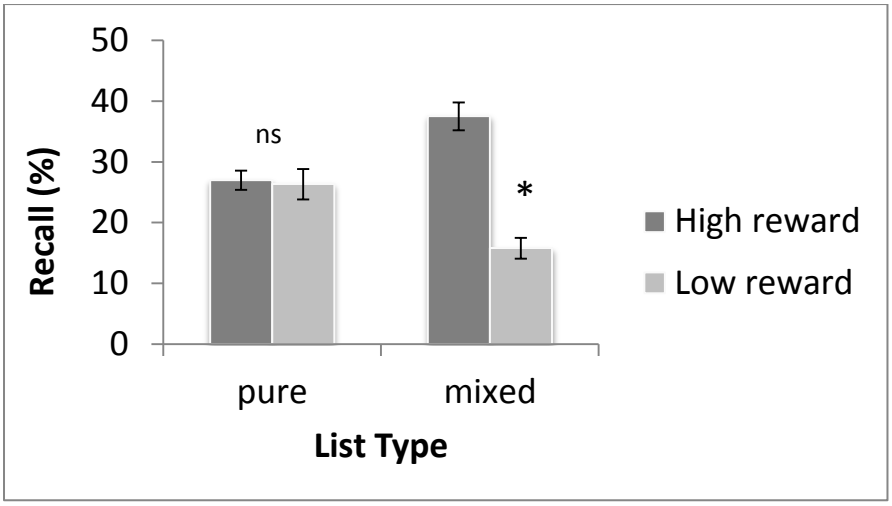
Figure 2. Forgetting of high and low-reward items over 24 hours.

Top and middle plots. These depict average immediate and delayed free recall in Experiment 2 for items presented in mixed and pure lists. The immediate memory results are the same in both plots, but the delayed memory results are shown for items only tested once, after 24 hours (**top**) or twice, both immediately and after a delay (**middle**).

Bottom. Proportional forgetting scores in these two cases.

Figure 1.


60
50
40
30
20
10
0
Recall (%)
ns
*
Pure
Mixed
List Type
High reward
Low reward


50
40
30
20
10
0
Recall (%)
ns
*
pure
mixed
List Type
High reward
Low reward

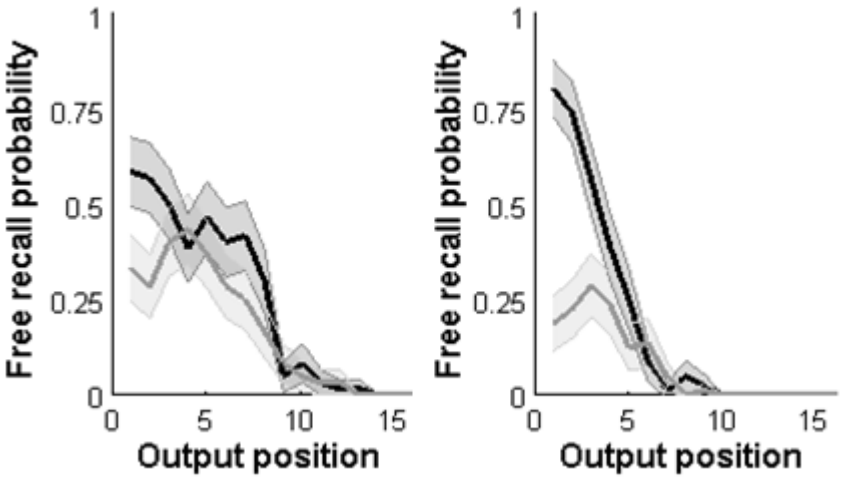
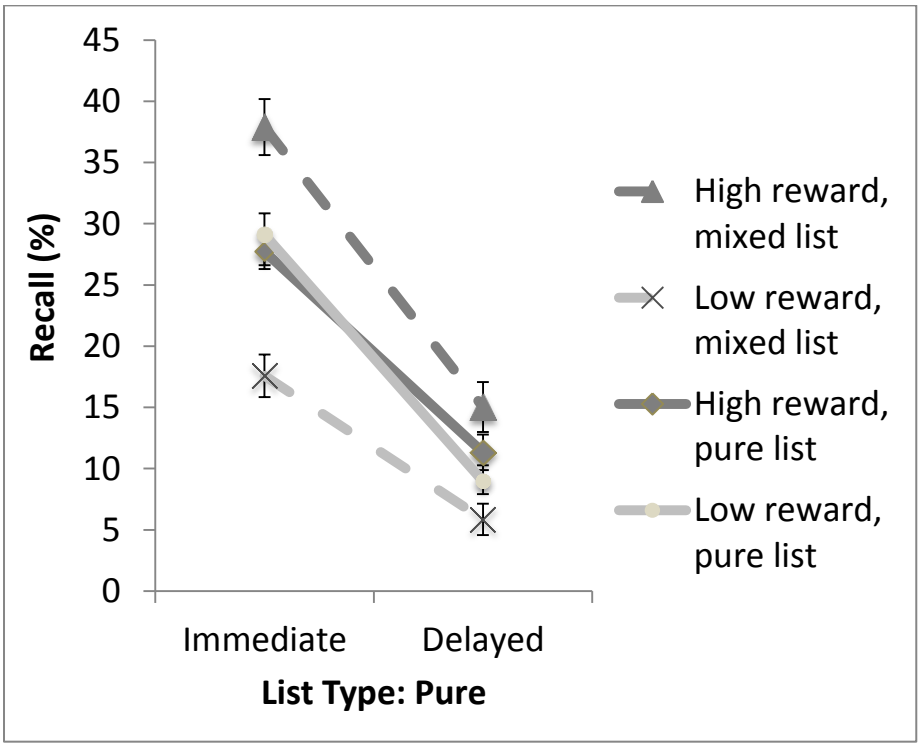
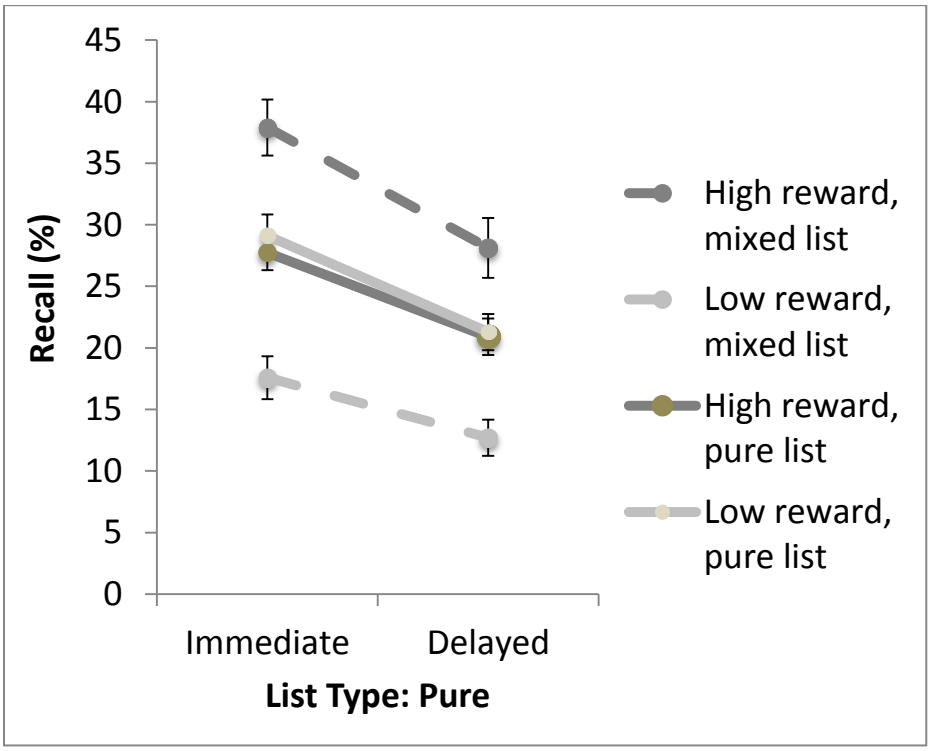
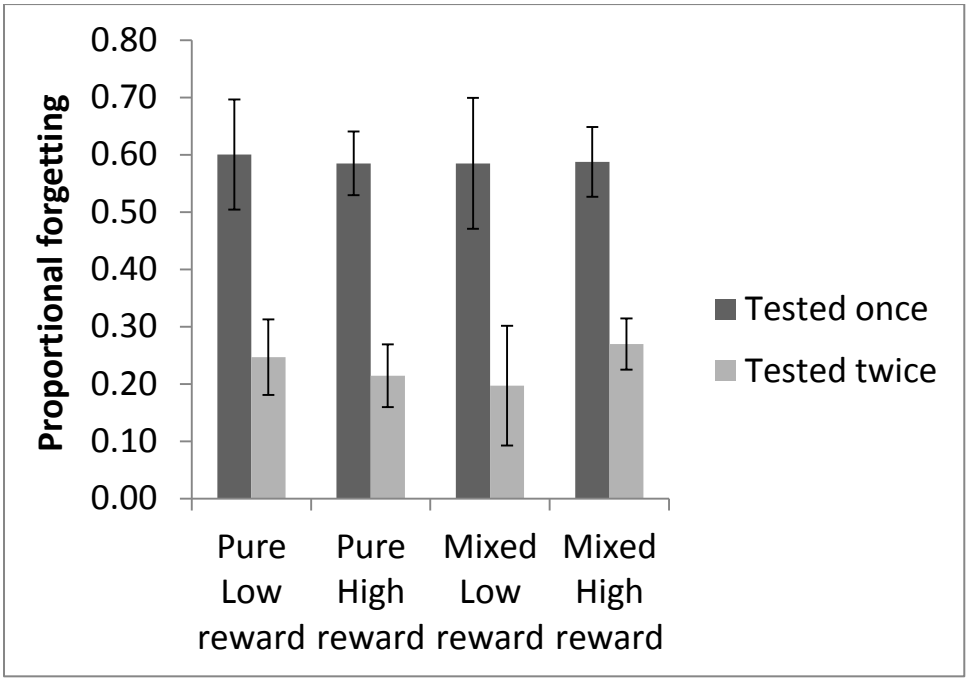

Free recall probability
1
0.75
0.5
0.25
0
0
5
10
15
Output position
Free recall probability
1
0.75
0.5
0.25
0
0
5
10
15
Output position

Figure 2.


45
40
35
30
25
20
15
10
5
0
Recall (%)
Immediate
Delayed
List Type: Pure
High reward, mixed list
Low reward, mixed list
High reward, pure list
Low reward, pure list


45
40
35
30
25
20
15
10
5
0
Recall (%)
Immediate
Delayed
List Type: Pure
High reward, mixed list
Low reward, mixed list
High reward, pure list
Low reward, pure list


0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
Proportional forgetting
Pure Low reward
Pure High reward
Mixed Low reward
Mixed High reward
Tested once
Tested twice