On the search for a selective and retroactive strengthening of memory: repeated failure to find
category-specific behavioral tagging

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We gratefully acknowledge the assistance of Friederike Baier, Leandra Feldhusen, Denise
Hartwig, Schmaila Kahn, Constantin Kuhlmann, Vincent Kühn, Moana Lamm, Fabian
Schacht, Felix Schiborn, Celine Schneller, Elizabeth Sievert and Till Thelosen during data
collection. We further thank Dr. Joseph Dunsmoor for providing the stimulus materials used
in Experiments 1B and 1C and for helpful advice on instructions and experimental procedure.

Part of the data of Experiments 1A and 1B were analyzed to address a research question
unrelated to the present manuscript and has been reported in Kalbe, F., & Schwabe, L. (in
press). Beyond arousal: Prediction error related to aversive events promotes episodic memory
formation. *Journal of Experimental Psychology. Learning, Memory, and Cognition*.

Abstract

Storing motivationally salient experiences preferentially in long-term memory is generally adaptive. While such relevant experiences are often immediately obvious, a problem arises when the relevance of initially ambiguous events becomes evident sometime after encoding. Is there a mechanism that enables the retroactive enhancement of specific memories? Recent evidence suggests the existence of such a mechanism that selectively strengthens weak memories for neutral stimuli from one category when their respective category gains motivational significance later. While such a selective retroactive memory enhancement has considerable implications for adaptive memory, evidence for this phenomenon is based on only two studies. Here, we report data from five failed attempts to produce category-specific retroactive memory enhancements in the context of aversive or reward learning. Experiments 1A, 1B, and 1C aimed to closely replicate findings of category-specific retroactive memory enhancements for neutral stimuli from a category that was later predictive of aversive electric shocks. Experiment 2 was designed to broaden the scope of these experiments by replacing electric shocks with an ecologically more valid psychosocial stress procedure. Finally, in Experiment 3, we aimed to replicate findings of category-specific retroactive memory enhancement in the context of instrumental reward learning. Although our data showed enhanced memory for the arousing stimuli themselves as well as related subsequent stimuli, none of our experiments provided any evidence for category-specific retroactive memory enhancement. Thus, our data cast doubt on the proposed selective retroactive enhancement of initially weak memory.

Keywords: episodic memory, adaptive memory, behavioral tagging, reproducibility

ON THE SEARCH FOR A SELECTIVE AND RETROACTIVE STRENGTHENING OF MEMORY: REPEATED FAILURE TO FIND CATEGORY-SPECIFIC BEHAVIORAL TAGGING

Our memories provide not only a window into the past but may also guide our future behavior. In particular, detailed memories of past experiences allow predicting future events as well as the potential consequences of actions and can therefore serve as a basis for optimized choices in complex environments (Gershman & Daw, 2017; Murty, FeldmanHall, Hunter, Phelps, & Davachi, 2016). However, out of the numerous experiences that we make every day, only few are of significant value for future decisions. According to the theory of adaptive memory, these motivationally significant experiences should be preferentially stored in episodic memory (Nairne & Pandeirada, 2008; Nairne, Thompson, & Pandeirada, 2007; Shohamy & Adcock, 2010). Phylogenetically, such an adaptive memory might have been critical to survival by allowing the identification and subsequent avoidance of potentially threatening situations, thereby improving fitness (Nairne & Pandeirada, 2008). The preferential memory processing is relevant because limited memory resources during both encoding and retrieval should optimally be reserved for motivationally relevant experiences.

Such motivationally salient experiences are usually immediately obvious to an individual. Exciting or stressful experiences elicit physiological arousal during encoding, a well-known factor that promotes episodic memory formation (Cahill & McGaugh, 1998; LaBar & Cabeza, 2006; McGaugh, 2018). However, other events appear initially neutral or mundane and their link to important consequences is only later revealed. Consider a bank customer entering her local branch as usual, when another presumed customer is leaving in a hurry. She barely notices his face. Soon it is revealed to her that the person she saw leaving had just robbed the bank and she realizes that she will soon be asked by the police to give a detailed description of the alleged robbers unmasked face. Since the initial encounter with the

alleged robber was not particularly remarkable and therefore not paralleled by significant arousal, the robber's face was not encoded preferentially. Is there still a mechanism to make such initially weak memories last? Adaptive memory would call for a mechanism that temporarily and non-selectively stores recent experiences and transfers them to long-term memory when a motivationally significant event follows within a certain time window. Indeed, such a mechanism was first discovered at the synaptic level and inspired the *tag and capture hypothesis* (Frey & Morris, 1997, 1998; Martin & Kosik, 2002; Rogerson et al., 2014). According to this hypothesis, at least two distinguishable steps are necessary to achieve long-term potentiation, the dominant neurophysiological model of long-term memory (Bliss & Collingridge, 1993; Malenka, 1999). First, weak stimulation of a neuron creates a local transient tag at a synapse, which decays within hours and by itself is insufficient to create long-lasting memories. To produce long-term potentiation, additional plasticity-related proteins are required that result from a stronger stimulation of the neuron. These proteins bind to the synaptic tag set earlier (i.e., the capturing step) inducing long-term physiological changes in synaptic signaling. Critically, plasticity related proteins evoked through strong stimulation of the neuron can bind to synaptic tags set earlier through unrelated weak stimulation and therefore create lasting memories for events that would by themselves be too weak to produce long-term potentiation (Moncada & Viola, 2007; Redondo & Morris, 2011). This mechanism therefore provides a neurophysiological basis for the retroactive memory enhancement of events with an initially unclear motivational significance (Moncada, Ballarini, & Viola, 2015).

Evidence that the synaptic tag and capture hypothesis can be translated to behavior has been found in both rodents (Almaguer-Melian et al., 2012; Ballarini, Moncada, Martinez, Alen, & Viola, 2009; de Carvalho Myskiw, Benetti, & Izquierdo, 2013; Moncada & Viola, 2007; Wang, Redondo, & Morris, 2010) and more recently in humans (Ballarini, Martínez,

Díaz Perez, Moncada, & Viola, 2013). In paradigms demonstrating a *behavioral tagging* mechanism, participants first superficially encode stimuli. This encoding session is then followed by either a significant event (e.g., an aversive or novel experience) or a non-significant control event. Subsequent memory tests typically show that the significant event – compared to a neutral control event – retroactively enhanced memory for the previously encoded stimuli. In these paradigms, retroactive memory enhancements are usually unspecific in the sense that an event enhances memory for any stimuli encoded within a certain time window before the significant event, even if these are not directly linked to the latter. In the case of the bank robbery, such unrelated details might include the color of the tie the bank clerk was wearing at the time of the robbery. From an adaptive memory perspective, promoting memory for such irrelevant details might be regarded as suboptimal when they lack any predictive value for the memory-promoting event.

A recent study suggests that there is – in addition to rather broad and unspecific behavioral tagging – a retroactive memory enhancement that is highly specific (Dunsmoor, Murty, Davachi, & Phelps, 2015). This study combined an incidental encoding task with a fear learning procedure. In a pre-conditioning phase, participants first encoded neutral pictures of animals and tools and were asked to indicate to which of the two categories a picture belonged to. Following this weak encoding session, in a Pavlovian fear conditioning phase, additional, previously unseen pictures from the same two categories were presented. Pictures from one of the two categories (i.e., either animals or tools; CS⁺) were followed by an aversive electric shock in two-thirds of all trials, while pictures from the remaining category (CS⁻) were never followed by a shock. Whether shocks followed pictures of animals or tools was counterbalanced across participants. A post-conditioning phase with an identical procedure as the pre-conditioning phase but novel stimuli followed the fear-conditioning phase. To test participants' memory for stimuli from the three encoding phases, a surprise

recognition test followed either immediately, 6h, or 24h later (manipulated between subjects). In this recognition test, participants saw all previously presented pictures of animals and tools together with the same number of previously unseen ('new') pictures from both categories and classified each picture as either 'old' or 'new'. Results showed an enhanced recognition performance for CS⁺ pictures encoded during fear-conditioning compared to CS⁻ pictures encoded in the same phase in all three delay groups. In the 24-h delay group, this CS⁺ memory carried over to pictures presented after the fear-conditioning phase, although these items were never paired with a shock themselves. Most importantly, however, the authors found category-specific retroactive memory enhancements in both the 6-h and 24-h delay groups, as indicated by better recognition of CS⁺ pictures encoded before the fear-conditioning compared to CS⁻ pictures encoded in the same phase. This finding is particularly remarkable as participants had no information about shock contingencies being linked to one of the two categories when these pictures were encoded. When the recognition test followed immediately after the encoding, no category-specific retroactive memory enhancement was observable, suggesting the critical involvement of consolidation processes. Interestingly, there also was a negative linear relationship between the size of the retroactive memory effect and the temporal proximity of pre-conditioning items to the fear-conditioning procedure, suggesting that pictures from the CS⁺ category that were encoded first (i.e., furthest from the following fear-conditioning) received the strongest memory enhancement. Furthermore, another group of participants encoded stimuli from the pre-conditioning phase more strongly through repeated presentation of each picture. These participants showed no signs of category-specific retroactive memory enhancement after 24h, indicating that only initially weak memories are susceptible to this effect, a finding that is congruent with the literature on synaptic tagging (Frey & Morris, 1997, 1998; Martin & Kosik, 2002; Rogerson et al., 2014).

Another study from the same group of authors showed that selective, category-specific retroactive memory enhancements cannot only be triggered through aversive events, but also through rewards (Patil, Murty, Dunsmoor, Phelps, & Davachi, 2017). Following a similar design as the study by Dunsmoor et al. (2015), the authors showed that memory for initially neutral pictures of animals and tools could be enhanced for the category that was later associated with high compared to low reward opportunities in a delayed matching-to-sample task. Notably, in this task, participants were rewarded for correct responses, while shocks were independent of participants actions in the study by Dunsmoor et al. (2015). In contrast to these findings, another study from an independent lab using a similar classical conditioning procedure as Dunsmoor et al. (2015) featuring monetary rewards instead of aversive shocks obtained no evidence for category-specific retroactive memory enhancement (Oyarzún, Packard, de Diego-Balaguer, & Fuentemilla, 2016). To our knowledge, no other studies so far have investigated category-specific retroactive memory enhancement, neither in the aversive, nor in the appetitive domain.

The findings showing a selective, retroactive memory enhancement are exciting; they provide novel insights into how our memory works and may have considerable practical implications for clinical or legal settings. A selective behavioral tagging mechanism may also inspire new tools for boosting memory retrospectively. Given the far-reaching implications of selective, retroactive memory enhancements, we initially aimed to shed light on the cognitive mechanisms underlying this effect. However, what started as an attempt to unravel the fundamental mechanisms underlying selective behavioral tagging, turned out to be a search for the phenomenon itself. We present here evidence from five experiments designed to probe category-specific retroactive memory enhancements: three of these experiments aimed to closely replicate findings of category-specific retroactive memory enhancement through aversive electric shocks (Dunsmoor et al., 2015), which represented the first finding that this

effect can be category-specific instead of general and unspecific. One experiment aimed to generalize these findings to more ecologically valid conditions by using social stress instead of electric shocks as memory-modulating event. The last experiment aimed to closely replicate the so far only findings of category-specific retroactive memory enhancement in the appetitive domain (Patil et al., 2017).

Experiment 1: Testing the fear-related category-specific retroactive memory enhancement

Experiment 1A

Experiment 1A was designed to replicate findings of category-specific retroactive memory enhancement in the context of an aversive learning task (Dunsmoor et al., 2015). Because the experiment of Dunsmoor et al. (2015) showed that observed retroactive memory effects were most pronounced in a recognition test 24h after encoding, we used here a 24h interval between encoding and recognition test. Our stimulus material included pictures that were conceptually very similar to the stimulus set used by Dunsmoor and colleagues (2015), that is, also pictures from the categories ‘animals’ and ‘tools’. All other aspects of the procedure and analysis strategy were kept as close as possible to the original study.

Method.

Participants. Forty-four healthy men and women between 19 and 33 years of age took part in this experiment ($M = 25.05$, $SD = 3.75$). This sample size was based on an a priori sample size calculation with G*Power 3 (Faul, Erdfelder, Lang, & Buchner, 2007). Dunsmoor et al. (2015) reported retroactive memory improvements from a paired t -test for items conceptually related to the CS^+ compared to items related to the CS^- in the 24-h retrieval group with weak encoding ($n = 30$) and obtained a t -value of 2.48 with an effect size of $d_{av} = 0.41$. Based on this information, Cohen’s d_z , another measure of effect size in within-

subject designs used by G*Power, can be calculated using the following formula (Lakens, 2013):

$$\text{Cohen's } d_z = \frac{t}{\sqrt{n}}$$

Using the values reported by Dunsmoor et al. (2015) yielded the following estimate for Cohen's d_z :

$$\text{Cohen's } d_z = \frac{2.48}{\sqrt{30}} = 0.45$$

We treated this effect size as a point estimate for the category-specific retroactive memory effect in our power analysis. This indicated that, using a two-tailed paired t -test with $\alpha = .05$, at least 41 participants would be required to detect such an effect with 80% certainty. This target sample size also represents an approximately 40% increase compared to the 24-h group in the original study ($n = 30$). Exclusion criteria for participation in this experiment comprised any current or past physical or mental illness, electric medical devices such as pacemakers, and pregnancy in women. Participants gave written informed consent prior to testing and received a monetary compensation of 20€ after completing the experiment. The ethics committee of the Faculty of Psychology and Human Movement Sciences of the University of Hamburg approved the study protocol.

Materials. As in the original study, stimuli were 180 color photographs of animals and 180 color photographs of tools isolated on white backgrounds. We acquired photographs from the Bank of Standardized Stimuli (Brodeur, Dionne-Dostie, Montreuil, & Lepage, 2010; Brodeur, Guérard, & Bouras, 2014) and from publicly available Internet sources. All photographs were of neutral valence and selected to be unique exemplars of their respective category. For example, there were not two different photographs of dogs or two different photographs of hammers. From the total pool of 360 photographs, 180 (90 animals, 90 tools) were randomly selected per participant to serve as learning items, while the remaining 180

served as lures for the surprise recognition test on the second experimental day. The 180 learning items were then randomly allocated to the three different incidental encoding phases for the first experimental day, such that each phase featured 30 photographs of animals and 30 photographs of tools.

Procedure. We aimed to follow the procedure of the original study (Dunsmoor et al., 2015) as closely as possible. The first experimental day featured an incidental encoding session with three phases: a pre-conditioning phase, a fear conditioning phase, and a post-conditioning phase. Approximately 24h later, participants completed a surprise recognition test for photographs that had been presented in all three encoding phases on the previous day. Unlike in the study by Dunsmoor et al. (2015), we did not vary the interval between encoding and recognition test between subjects, but kept it fixed at 24 h, as the 24 h group had previously shown the clearest evidence for both category-specific retroactive and prospective memory enhancement. Additionally, another study featuring a reward learning task also demonstrated category-specific retroactive memory enhancement only after a 24 h interval, but not in an immediate recognition test, suggesting a crucial role of a sufficiently long consolidation period before the recognition test (Patil et al., 2017).

Upon arrival on the first experimental day, participants gave written informed consent and received detailed written instructions about the following three learning phases. Importantly, they were not informed that the study investigated episodic memory, nor that a recognition test would follow on the second experimental day. In the *pre-conditioning phase*, participants saw 30 photographs of animals and 30 photographs of tools in a pseudo-randomized order, such that no more than three photographs from the same category could appear in a row. Each stimulus was presented for 2.5 s, during which participants should indicate whether the photograph showed an animal or a tool by pressing the ‘1’ or ‘2’ button on the computer keyboard (Figure 1). Each stimulus was followed by a black fixation cross

on a white background for $6s \pm 2s$. The allocation of buttons to each of the two categories was counterbalanced across participants. The total duration of the pre-conditioning phase was approximately 8 min.

Before the *conditioning phase*, we attached electrodes on the distal phalanx of the second and third finger of the left hand to record skin conductance responses (SCRs). Skin conductance was measured using a MP-160 BIOPAC system (BIOPAC systems, Goleta, CA). An additional STM-200 module (BIOPAC systems, Goleta, CA) was connected to the MP-160 for electrical stimulation. The stimulation electrode was placed on the right lower leg, approximately 25 cm centrally above the heel. To determine the individual stimulation intensity, we used a standardized procedure consisting of twelve 200 ms single pulse shocks with an initial intensity of 20 V. After each trial, participants rated the shock that they had just received as either painful or not painful in a forced-choice fashion. Whenever a shock was rated as not painful, its intensity was increased slightly in the following trial. Similarly, whenever participants rated a shock as painful, the intensity was decreased slightly. The goal was to select an intensity that participants perceived as unpleasant, but not painful.

The following conditioning phase again consisted of 30 photographs of animals and 30 photographs of tools, none of which had been presented before. As in the pre-conditioning phase, stimuli were presented in a pseudorandomized order, so that no more than three photographs from the same category appeared in a row. Each photograph was presented centrally on the screen for 4.5 s, during which participants were instructed to make a binary prediction about the possible occurrence of a following shock using the '1' and '2' buttons on the keyboard, corresponding to 'no shock' and 'shock', respectively. In 20 of the 60 trials in this phase, a 200 ms electric shock was presented immediately after the offset of the photograph. Importantly, shock contingencies were linked to the item categories, such that one image category (e.g. tools) served as the CS⁺ category, whereas the remaining category

(e.g. animals) was never paired with a shock and thus served as the CS⁻ category. Whether photographs of animals or tools served as the CS⁺ category was counterbalanced across participants. In CS⁺ trials, the shock probability was two-thirds, with a fixed number of 20 shocks occurring in the 30 CS⁺ trials. In CS⁻ trials, on the other hand, none of the photographs was followed by a shock. Participants were not informed about category-shock contingencies but had to learn them by trial and error. To avoid that participants could misinterpret shocks as consequences of their actions, they were explicitly told that their choices had no effect on the probability that a shock would occur (Dunsmoor et al., 2015). Each trial was followed by a black fixation cross on a white background for 8 ± 2 s, which enabled measuring the relatively slow SCRs elicited by electric shocks and allowed skin conductance levels to return to baseline before the next trials started. The total duration of the conditioning phase was approximately 12 min. After the conditioning phase, we removed both the SCR- and the shock-electrodes. Participants then rated the shock intensity on a scale from 1 (*not unpleasant at all*) to 10 (*extremely unpleasant*).

The subsequent *post-conditioning phase* consisted of 60 previously unseen photographs (30 animals and 30 tools) and otherwise followed an identical procedure as the pre-conditioning phase. Thus, the duration of the post-conditioning phase was approximately 8 minutes again.

Participants returned for a *memory test* 22h to 26h after encoding on the first experimental day. They first completed a short questionnaire to assess whether they had already anticipated the following recognition test. To this end, after being informed about the following memory test, they rated how surprised they were about the upcoming memory test on a scale from 1 (*not surprised at all*) to 5 (*very surprised*). Next, they received written instructions explaining details of the recognition test. In the recognition test, they were presented all 180 photographs from the three encoding phases of the previous day intermixed

with an equal number of “new” photographs (i.e., photographs that had not been presented previously). Half of these lures were photographs of animals and half were photographs of tools. Stimuli were presented one by one centrally on a white background. For each of these photographs, participants first decided whether it was “old” or “new” in a forced-choice fashion. Then, participants had to indicate how confident they were that this decision was correct by pressing buttons corresponding to “very unsure”, “rather unsure”, “rather sure” and “very sure”. If in any of the two stages no response was given within 5 s, the rest of the trial was skipped. Between trials, a black fixation cross on a white background was presented centrally for $1.5 \text{ s} \pm 0.5 \text{ s}$.

Data analysis. The statistical analysis was kept as close as possible to the analyses described in the original study by Dunsmoor et al., (2015). Specifically, memory analyses were performed on corrected recognition scores to account for different response criteria between subjects. These were derived by subtracting the individual per image category false alarm rate from the per image category and per phase hit rate. Responses were collapsed across confidence, that is, only the forced-choice decision between “old” and “new” items was considered for memory performance. Including only high-confidence responses (i.e., responses for which participants indicated that they were either “rather sure” or “very sure”) led to similar results.

As a manipulation check for successful fear conditioning, we analyzed skin conductance data obtained during the second encoding phase using a Continuous Decomposition Analysis as implemented in Ledalab Version 3.4.9. (Benedek & Kaernbach, 2010). First, the skin conductance signal was downsampled to a resolution of 50 Hz and optimized using four sets of initial values. The minimum amplitude threshold was set to $0.01 \mu\text{S}$. For each trial during the conditioning phase, we derived anticipatory SCRs as the average phasic driver within a response window of 0.5 s to 4.5 s after each stimulus onset.

Importantly, as shocks always appeared exactly 4.5 s after stimulus onset and therefore outside the response window, the resulting estimates could not have been biased by the UCS.

Results and discussion.

Successful fear conditioning. An analysis of skin conductance responses confirmed that our procedure successfully induced conditioned fear for items from the CS⁺ category. During the conditioning phase, participants showed significantly higher anticipatory SCRs to CS⁺ items compared with CS⁻ items, $t(43) = 4.79$, $p < .001$, $d_{av} = 0.52$ (Figure 2, left panel).

Anticipation of the recognition test. On the second experimental day, participants were first informed about the following recognition test for photographs from the previous day and then rated how surprised they were by this task on a scale ranging from 1 (*not surprised at all*) to 5 (*very surprised*). Responses from six participants were missing. The average response in the remaining sample was 2.92 ($SD = 0.97$), showing that, on average, participants were moderately surprised. Four participants indicated that they were *not surprised at all*. Exclusion of these four participants had no effect on the pattern of results. Therefore, these participants were still included in the following analysis.

Overall memory performance. Overall, participants performed well in the recognition task, as reflected in a markedly higher average hit rate for items from all three encoding phases (i.e., the rate of correctly classifying previously seen photographs as old) of 69.6% ($SD = .11$) than the false alarm rate (i.e. the rate of incorrectly classifying previously unseen photographs as old) of 24.4% ($SD = .09$). Notably, the false alarm rate for animals ($M = .28$, $SD = .12$) was significantly higher than for tools ($M = .21$, $SD = .09$), $t(43) = 4.90$, $p < .001$, $d_{av} = 0.68$. Since corrected recognition scores were calculated by subtracting false alarm rates from hit rates by category, this finding highlights the importance of counterbalancing the number of participants with animals vs. tools as the CS⁺ category, which we did here.

No evidence for category-specific retroactive memory enhancement. To address our main research question, we investigated how recognition performance for the photographs presented on the first experimental day was affected by the encoding phase (before, during or after the fear conditioning) and the conditioning category (CS^+ or CS^-) an item belonged to through a repeated-measures ANOVA on corrected recognition scores. For the factor phase, Mauchly's Test indicated that the sphericity assumption was violated, $W = 0.85$, $p = .030$. Hence, results for the factor phase are reported after applying a Greenhouse-Geisser correction. Overall, corrected recognition scores differed according to the phase an item was encoded in, $F(2, 86) = 17.1$, $p < .001$, $\eta^2_G = .05$ (Figure 3, left panel). Whether an item belonged to the conditioned category, on the other hand, had no significant overall effect on recognition performance, although a trend was visible, $F(1, 43) = 3.92$, $p = .054$, $\eta^2_G = .01$. There was no significant interaction between the encoding phase and the conditioning category an item belonged to, $F(2, 86) = 1.65$, $p = .20$, $\eta^2_G = .004$. We further performed paired t -tests comparing the corrected recognition for items from the CS^+ category vs. items from the CS^- category separately per phase. These confirmed previous findings of an enhanced memory formation for CS^+ items vs. CS^- items in the conditioning phase, $t(43) = 2.31$, $p = .025$, $d_{av} = 0.35$ (Figure 3, left panel; Dunsmoor et al., 2015). At trend level, there was evidence that this memory benefit persisted for CS^+ items over CS^- items in the post-conditioning phase, even though these photographs were never directly paired with the UCS, $t(43) = 1.82$, $p = 0.076$, $d_{av} = 0.29$. Critically, for items that were encoded during the pre-conditioning phase, there was no evidence for a category-specific retroactive memory enhancement for CS^+ items over CS^- items, $t(43) = 0.36$, $p = .719$, $d_{av} = 0.06$. Finally, we also tested for pre-conditioning items the previously reported positive linear relationship between the temporal distance to the conditioning phase and the size of category-specific retroactive memory enhancements (Dunsmoor et al., 2015). To this end, CS^+ and CS^- pre-conditioning

items were each binned in tertiles corresponding to trials 0-10, 11-20, and 21-30 relative to the conditioning phase. A repeated-measures ANOVA with the corrected recognition advantage for CS⁺ items compared to CS⁻ as the dependent variable and the time bin as a within-subject factor showed no significant effect of time bins, $F(2, 86) = 0.20$, $p = .82$, $\eta^2_G = .002$. In contrast with previous reports (Dunsmoor et al., 2015), this finding indicates that the relative time of encoding of an item within the pre-conditioning phase had no effect on a putative category-specific retroactive memory enhancement.

Experiment 1B

Despite successful fear conditioning and a close replication of the procedure and analysis strategy from Dunsmoor et al. (2015), we found no evidence for category-specific retroactive memory enhancements in Experiment 1A. It should be noted that, although conceptually very similar, Experiment 1A did not use the original stimulus set. Additionally, there were subtle differences in the procedure. For example, in our recognition test, “old” vs. “new” decisions and memory confidence were tested separately for each item, while this was a single step in the original study (Dunsmoor et al., 2015). Although there is no theoretical justification how these small deviations from the original study should prevent the detection of the proposed category-specific retroactive memory effect, we aimed to investigate whether we could replicate the findings when using the original stimulus set and sticking exactly to the original procedure. Therefore, we contacted the lead author of the original study and asked him to provide us the stimulus materials, including all experimental instructions, which were used in the original study (Dunsmoor et al., 2015). We received these materials and used them for a direct replication of the original study by Dunsmoor and colleagues (2015). Additionally, we substantially increased the sample size compared to Experiment 1A to minimize the chance of null findings due to insufficient statistical power.

Method.

Participants. Eighty-four healthy men and women between 19 and 35 years of age took part in Experiment 1B ($M = 25.23$, $SD = 4.08$). Four participants had to be excluded from the analysis, either because they did not return for the memory test on the second experimental day or because of technical and experimenter errors. Due to these exclusions, there was a slight imbalance regarding the between-subject factor ‘conditioned image category’, such that for 41 participants tools served as CS^+ category, while animals served as CS^+ category for only 39 participants. We examined whether this slight imbalance affected our results by randomly excluding two participants with tools as the CS^+ category from our analysis (10 permutations). Since the pattern of results remained unchanged, the following analyses were performed for the full sample of 80 participants. Again, the target sample size was determined using an a priori power analysis in G*Power 3 (Faul et al., 2007) with the aim to considerably increase the statistical power compared to Experiment 1A and thereby minimize the chance of null findings due to an insufficient sample size. As in Experiment 1A, we assumed $d_z = 0.45$ as a point-estimate for the previously reported category-specific retroactive memory effect (Dunsmoor et al., 2015). A two-tailed paired t -test with $\alpha = .05$ required at least 82 participants to achieve a statistical power of .98. Exclusion criteria were identical to Experiment 1A. None of the participants from Experiment 1A participated in this experiment. As before, participants received a monetary compensation of 20€. The study protocol was approved by the ethics committee of the Faculty of Psychology and Human Movement Science at the University of Hamburg.

Materials. For this experiment, we used the stimulus set from the study by Dunsmoor et al. (2015), consisting of 180 color photographs of animals and 180 color photographs of tools isolated on white backgrounds. As in Experiment 1A, photographs were of neutral valence and each tool and animal represented a unique exemplar of its respective category. The stimulus set was randomly divided into learning items and lures per participant and

learning items were allocated to the three encoding phases in the same manner as in Experiment 1A.

Procedure. The procedure in this experiment was largely identical to Experiment 1A, except for some minor changes to achieve consistency with the original study (Dunsmoor et al., 2015). More precisely, we changed the location of the stimulation electrode from the right lower leg to the right wrist. Since this area tends to be more sensitive to electric stimulation, we also reduced the initial intensity in the procedure for determining the pain threshold from 20V in Experiment 1A to 10V in this experiment. Furthermore, we replaced the two-step forced-choice decision in the surprise recognition test on the second experimental day with a task assessing both “old” vs. “new” decisions and certainty in a single step as reported in the original study (Dunsmoor et al., 2015). More precisely, for each stimulus in the recognition test, participants performed only a single button press with the four possible options that the currently presented item was either “definitely old”, “maybe old”, “maybe new”, or “definitely new” by pressing the “1”, “2”, “3”, or “4” button on the keyboard, respectively. Additionally, the 5 s time limit per response that was used in Experiment 1A was removed. In sum, Experiment 1B used exactly the same experimental procedure and stimuli as the study by Dunsmoor and colleagues (2015) but a significantly larger sample size.

Data analysis. The statistical analysis was identical to Experiment 1A and the statistical analysis of Dunsmoor and colleagues (2015).

Results and discussion.

Successful fear conditioning. An analysis of skin conductance data indicated that our procedure successfully induced conditioned fear for CS⁺ items. Specifically, during Pavlovian conditioning participants showed greater anticipatory SCRs to items from the CS⁺ category compared with items from the CS⁻ category, $t(79) = 4.32, p < .001, d_{av} = 0.35$ (Figure 2, center panel).

Anticipation of the recognition test. As in Experiment 1A, participants rated how surprised they were by the recognition test on a scale ranging from 1 (*not surprised at all*) to 5 (*very surprised*). On average, they indicated that they were moderately surprised ($M = 2.89$, $SD = 1.12$). Nine participants chose the *not surprised at all* option. Since excluding these participants did not affect the pattern of results, they were still included in the following analyses.

Overall memory performance. Participants performed overall very well in the surprise recognition test with an average hit rate for items from all three encoding phases of 60.9% ($SD = 0.14$) and an average false alarm rate of 25.2% ($SD = 0.10$). As in Experiment 1A, the false alarm rate for photographs of animals ($M = .31$, $SD = .13$) was significantly higher than for photographs of tools ($M = .20$, $SD = 0.10$), $t(79) = 7.79$, $p < .001$, $d_{av} = 0.96$.

No evidence for category-specific retroactive memory enhancement. We performed a repeated-measures ANOVA on corrected recognition scores to identify factors affecting memory formation over the task. As in Experiment 1A, the recognition performance generally differed between phases, $F(2, 158) = 26.8$, $p < .001$, $\eta^2_G = .06$. The recognition performance was also generally different between CS^+ and CS^- items, $F(1, 79) = 17.0$, $p < .001$, $\eta^2_G = .03$. Finally, there was a significant interaction between the encoding phase and the item category, indicating that the effect of membership of an item to the CS^+ vs. CS^- category differed between the encoding phases, $F(2, 158) = 6.66$, $p = .0017$, $\eta^2_G = .007$. To further qualify these results, we performed paired t -tests comparing corrected recognition scores for items belonging to the CS^+ vs. CS^- category separately per phase. For photographs presented during Pavlovian conditioning, we obtained an enhanced memory for CS^+ items compared to CS^- items, $t(79) = 4.89$, $p < .001$, $d_{av} = 0.53$ (Figure 3, center panel). This memory benefit for items belonging to the CS^+ category carried over to the post-conditioning phase, even though shock leads were removed beforehand, $t(79) = 3.32$, $p = .0014$, $d_{av} = 0.33$.

Most importantly, despite the high statistical power in this replication study, we found no evidence for a retroactive memory enhancing effect for items from the CS^+ category over items from the CS^- category presented before the Pavlovian conditioning phase, $t(79) = 1.28$, $p = .20$, $d_{av} = 0.14$. As in Experiment 1A, we also tested for pre-conditioning items a possible linear relationship between their temporal distance and the size of the category-specific retroactive memory effect using the same procedure as in Experiment 1A. Contrary to this hypothesis, a repeated-measures ANOVA with the corrected recognition advantage for CS^+ items compared to CS^- items as the dependent variable and the time bin as a within-subject factor showed no significant effect of time bins, $F(2, 158) = 1.08$, $p = .34$, $\eta^2_G = .007$. This finding shows that the relative time of encoding of an item within the pre-conditioning phase had no effect on the proposed category-specific retroactive memory enhancement.

Experiment 1C

Thus far, in two replication attempts, we were unable to find any evidence for category-specific retroactive memory enhancements for weakly encoded stimuli belonging to a category that was later associated with the occurrence of shocks in a fear conditioning paradigm. Experiment 1B showed the absence of the category-specific retroactive memory effect could not be attributed to the stimulus set, nor to small deviations in the procedure. Additionally, as Experiment 1B had high statistical power, it is highly unlikely that the absence of the category-specific retroactive memory effect was due to an insufficient sample size.

This third replication attempt was designed to investigate one additional aspect that moderated the size of the category-specific retroactive memory effect in the original study, namely the interval between the encoding during the pre-conditioning phase and the subsequent fear-conditioning (Dunsmoor et al., 2015). It had been shown that items from the pre-conditioning phase that were presented the longest before fear-conditioning showed the

strongest category-specific retroactive memory enhancement, while this effect seemed to diminish the closer items were encoded relative to the conditioning phase (Dunsmoor et al., 2015). This finding was in line with previous work on non-specific behavioral tagging in rodents, which suggests that there might be a minimal interval between the weak encoding (setting the ‘tag’) and associated arousing event to enable retroactive memory enhancement (de Carvalho Myskiw et al., 2013; Moncada et al., 2015). Therefore, in this third experiment, we increased the interval between the pre-conditioning and the fear conditioning phase to investigate whether this change could produce the category-specific retroactive memory enhancement that was not detectable in the Experiments 1A and B. Apart from this single aspect, we retained both the procedure and the high statistical power from Experiment 1B.

Method.

Participants. Eighty-four healthy men and women between 18 and 33 years of age participated in this experiment ($M = 25.11$, $SD = 3.57$). Six participants had to be excluded from the analysis, either because they did not return for the memory test on the second experimental day or because of technical and experimenter errors. As in Experiment 1B, these exclusions led to a slight imbalance regarding the between-subject factor ‘conditioned image category’, such that for 40 participants tools served as CS^+ category, while animals served as CS^+ category for only 38 participants. Again, we examined whether this imbalance affected our results by randomly excluding two participants with tools as the CS^+ category from our analysis (10 permutations). Since the pattern of results remained unchanged, the following analyses were performed for the full sample of 78 participants. The target sample size was calculated using an a priori power analysis with identical parameters as in Experiment 1B. Exclusion criteria were identical as in Experiment 1A and 1B. None of the participants had previously participated in Experiment 1A nor in Experiment 1B. Again, participants received a monetary compensation of 20€. The study protocol was approved by

the ethics committee of the Faculty of Human Movement Science at the University of Hamburg.

Materials. We used the same stimulus set as in Experiment 1B, corresponding to the material used by Dunsmoor et al. (2015) and consisting of 180 color photographs of animals and 180 color photographs of tools isolated on white backgrounds. As in Experiment 1A and Experiment 1B, per participant, half of the stimuli from each category were randomly selected as learning items, while the remaining half served as lures. The learning items were allocated to each of the three encoding phases in the same manner as in Experiment 1A and Experiment 1B. Furthermore, the assignment of photographs of tools and animals as CS⁺ and CS⁻, respectively, was counterbalanced across participants.

Procedure. The only difference compared to the procedure in Experiment 1B was the extension of the interval between the pre-conditioning phase and the subsequent fear conditioning phase. This change was based on the finding that the category-specific retroactive memory effect was positively correlated with the temporal distance between the encoding of an item and the following fear conditioning procedure in the original study (Dunsmoor et al., 2015) as well as evidence from studies in rodents (de Carvalho Myskiw et al., 2013; Moncada et al., 2015). In this experiment, when participants finished the pre-conditioning phase - unlike in Experiment 1A and Experiment 1B - we did not immediately attach the electrodes. Instead, participants were first presented the following series of questionnaires: The State-Trait Anxiety Inventory (Spielberger, 1983), a multidimensional mood questionnaire (Steyer, Schwenkmezger, Notz, & Eid, 1997), a chronic stress questionnaire (Schulz, Schlotz, & Becker, 2004), the Beck Depression Inventory (Beck, Steer, & Brown, 1996), the Social Interaction Anxiety Scale (Mattick & Clarke, 1998), and the Positive and Negative Affect Schedule (Watson, Anna, & Tellegen, 1988). After participants had worked on these questionnaires for exactly 10 minutes, they were interrupted

and told that the remaining questions could be finished at a later stage. In fact, questionnaires were only added to keep participants occupied during the prolonged interval before the fear-conditioning. For this reason, we also chose a greater number of questionnaires than could usually be completed within 10 minutes, so that no participant would finish them earlier. Afterwards, the experiment continued in the same manner as described for Experiment 1B, by first attaching electrodes and determining the pain threshold before the start of the fear-conditioning phase, followed by the post-conditioning phase and the 24 hours-delayed recognition test.

Data analysis. The statistical analysis was identical to Experiments 1A and 1B.

Results and discussion.

Successful fear conditioning. As in both previous experiments, an analysis of skin conductance data confirmed that our procedure was successful in inducing conditioned fear for CS⁺ items. SCR data for one additional participant were missing due to experimenter error. For the remaining sample of 77 participants, during Pavlovian fear conditioning anticipatory SCRs to items from the CS⁺ category were significantly higher compared with items from the CS⁻ category, $t(76) = 4.10$, $p < .001$, $d_{av} = 0.30$ (Figure 2, right panel).

Anticipation of the recognition test. As in the previous experiments, participants rated how surprised they were by the recognition test on a scale ranging from 1 (*not surprised at all*) to 5 (*very surprised*). Data from one participant were missing due to experimenter error. On average, the remaining 77 participants indicated moderate levels of surprise ($M = 3.05$, $SD = 0.97$). Three participants chose the *not surprised at all* option. Since excluding these participants did not affect the pattern of results, they were still included in the following analyses.

Overall memory performance. As in Experiments 1A and 1B, participants performed overall very well in the surprise recognition test with an average hit rate for items from all

three encoding phases of 62.7% ($SD = 0.16$) and an average false alarm rate of 23.1% ($SD = 0.10$). As in Experiments 1A and 1B, the false alarm rate for photographs of animals ($M = .26$, $SD = .11$) was significantly increased compared to photographs of tools ($M = .20$, $SD = .12$), $t(77) = 4.76$, $p < .001$, $d_{av} = 0.57$.

No evidence for category-specific retroactive memory enhancement. To analyze factors affecting memory performance for the different phases of the task, we ran a repeated-measures ANOVA on corrected recognition scores. As in the two previous experiments, corrected recognition scores generally differed between phases, $F(2, 154) = 35.72$, $p < .001$, $\eta^2_G = .08$. Corrected recognition scores were also generally different between items from the CS^+ and CS^- categories, $F(1, 77) = 17.8$, $p < .001$, $\eta^2_G = .03$. Finally, this effect of item category membership differed between the encoding phases, as indicated by a significant interaction between the encoding phase and the item category, $F(2, 154) = 22.12$, $p < .001$, $\eta^2_G = .03$. To further qualify these results, we performed paired t -tests to compare corrected recognition scores for items belonging to the CS^+ vs. CS^- category separately per encoding phase. As in Experiments 1A and 1B, these showed an enhanced memory performance for CS^+ items encoded during Pavlovian conditioning compared to CS^- items encoded in the same phase, $t(77) = 6.60$, $p < .001$, $d_{av} = 0.77$ (Figure 3, right panel). As in Experiment 1A, there also was a trend towards improved recognition memory for CS^+ items encoded after Pavlovian conditioning compared to CS^- items encoded in the same phase, although unlike in Experiment 1B, this trend was not statistically significant, $t(77) = 1.90$, $p = .061$, $d_{av} = 0.19$. Above all, despite the increase in the interval between encoding and Pavlovian conditioning, we obtained no evidence for a retroactive enhancement of memory for CS^+ items compared to CS^- items encoded before Pavlovian conditioning, $t(77) = 0.17$, $p = .86$, $d_{av} = 0.02$. Notably, even at descriptive level, the memory difference between CS^+ and CS^- items encoded before fear conditioning was negligible. We again tested the possibility of a

previously suggested linear trend between pre-conditioning items' temporal distance to the conditioning phase and the size of retroactive memory enhancement using the same procedure as previously reported. As in Experiment 1A and 1B, a repeated-measures ANOVA with the corrected recognition advantage for CS⁺ items compared to CS⁻ items as the dependent variable and the time bin as a within-subject factor showed no significant effect of time bins, $F(2, 154) = 0.17, p = .85, \eta^2_G = .001$. This indicates that the relative time of encoding of an item within the pre-conditioning phase had no effect on putative category-specific retroactive memory enhancement.

Pooled analysis across Experiments 1A to C

Experiments 1A to 1C were designed to closely replicate the previously reported finding of a category-specific retroactive memory enhancement through subsequent electric shocks (Dunsmoor et al., 2015). Although we varied certain aspects regarding stimuli and the procedure between these experiments, the procedure of Experiments 1A to C was conceptually very similar. To summarize findings from the three studies in a combined statistical model, we pooled data across the three experiments and fit separate linear mixed-effects model using the *R* library *lme4* (Bates, Mächler, Bolker, & Walker, 2015) for each of the three conditioning phases. In each of these three models, the conditioned category an item belonged to (binary coding: 0 for CS⁻; 1 for CS⁺) was treated as a fixed effect (Hedges & Vevea, 1998) to explain corrected recognition scores. Additionally, random intercepts were fitted both per subject and per experiment, to account for differences in memory performance between participants and procedural differences between experiments, respectively. Even after pooling data from Experiments 1A to C with 202 unique participants, there was no evidence for category-specific retroactive memory enhancement, as indicated by no significant effect of conditioning category membership of pre-conditioning items on corrected recognition scores, $t(201) = 1.10, p = .27, \beta = 0.01$ (Figure 4). Note that β -estimates obtained can directly be interpreted as the difference

in proportional corrected recognition scores between CS⁺ and CS⁻ photographs. Therefore, even at descriptive level, these results only suggest approximately 1% difference between photographs of the subsequent CS⁺ and CS⁻ categories that were encoded during pre-conditioning. Although there was no evidence for a selective retroactive memory enhancement, the pooled analysis revealed that CS⁺ photographs encoded during fear-conditioning were significantly better recognized than CS⁻ photographs, $t(201) = 8.27, p < .001, \beta = 0.10$. Finally, the pooled analysis confirmed results from Experiment 1B that this memory enhancement for CS⁺ photographs relative to CS⁻ photographs carried over to the post-conditioning phase, even though these items were never directly paired with the UCS, $t(201) = 4.03, p < .001, \beta = 0.04$.

Experiment 2: Category-specific retroactive memory enhancement through a psychosocial stressor?

All three replication attempts described so far implemented aversive events through electric shocks in the context of a Pavlovian fear conditioning procedure. Notably, people face a large variety of aversive events in their everyday life, one of which is psychosocial stress. In this experiment, we tested whether a stressful encounter that resembles an everyday aversive event (i.e., a job interview) and thus has a higher ecological validity may be more potent to induce a category-specific retroactive memory enhancement. There is substantial evidence that stress can retroactively enhance memory for previously encoded stimuli (Cahill, 2003; McGaugh, 2015). So far, however, the literature suggested that these stress-induced memory enhancements are unspecific, given that there was no semantic link between encoded stimuli and the subsequent stressful event. Here, we targeted possible category-specific retroactive memory enhancement through stress by establishing a link between weakly encoded face stimuli and a subsequent psychosocial stress induction. Importantly, by including a non-stressed control group experiencing the same extend of social interaction in a non-stressful

way, this design allowed us to simultaneously observe both unspecific and category-specific retroactive memory enhancement through stress.

Method

Participants. Eighty-two healthy men and women between 18 and 34 years of age participated in this experiment ($M = 24.9$, $SD = 3.90$). Two participants did not return for the second experimental day and were excluded from the analysis. The target sample size was based on experience from previous studies on stress and memory processes (Schönfeld, Ackermann, & Schwabe, 2014; Simon-Kutscher, Wanke, Hiller, & Schwabe, 2019; Zerbes & Schwabe, 2019). While no prior research targeted retroactive memory enhancements specifically through social stress, our research design in this experiment was inspired by the study by Dunsmoor et al. (2015). The major difference compared to this original study was the replacement of aversive electric shocks during Pavlovian fear conditioning with an aversive psychosocial stress induction. Compared to the study by Dunsmoor et al. (2015), our sample size corresponded to an approximately 50% increase per group. Participants were recruited through flyers and a student job website. Exclusion criteria comprised any current or past physical or mental illness, current medication (including oral contraceptives in women), drug or tobacco use, and a body-mass-index outside the range of 19 to 26. Women were not tested during the menses phase of their menstrual cycle to avoid bias in their cortisol response (Genazzani et al., 1975). None of the participants had participated in any of the previous experiments. They received a compensation of at least 30€ and could, based on their performance in a second task on the first experimental day, earn an additional amount of up to 5.50€ (see Experiment 3 for details). The study protocol was approved by the ethics committee of the Faculty of Human Movement Science at the University of Hamburg.

Materials. Stimuli were 280 color photographs of White and Latino faces with a neutral expression, half of which were female. All photographs were taken from the Chicago

Face Database (Ma, Correll, & Wittenbrink, 2015). Per participant, 140 faces (70 male, 70 female) were randomly selected as learning items for the first experimental day, while the remaining 140 faces served as lures for the recognition task on the second experimental day. From the 140 learning items, two random subsamples consisting of 35 female and 35 male faces each were allocated to the pre- and post-stress incidental encoding phases.

Procedure. As in Experiments 1A to C, we used in Experiment 2 a two-day design with separate encoding phases on the first day and a surprise recognition test on the second day. While we also aimed to probe category-specific retroactive memory enhancements through an aversive experience related to previously presented stimuli on the first experimental day, in this study we utilized psychosocial stress instead of aversive electric shocks. To induce psychosocial stress, participants underwent either the Trier Social Stress Test (TSST; Kirschbaum, Pirke, & Hellhammer, 1993) or an equally interactive, but non-stressful control condition. We controlled for effects of the diurnal rhythm of the stress hormone cortisol by conducting all testing between 1 p.m. and 7 p.m. As in the previous experiments, participants were always tested individually.

On the first experimental day, participants gave written informed consent and provided a first saliva sample as a baseline measurement of the physiological stress marker cortisol. To verify a successful stress induction and track cortisol levels over the learning task, saliva samples were also taken right after the pre-stress encoding phase before the stress/control treatment (~28 min after arrival), directly following the stress/control treatment (~52 min after arrival), after the post-treatment encoding phase (~65 min after arrival), and after completion of a second reward learning task (see Experiment 3; ~104 after arrival). Another baseline saliva sample was taken at the beginning of the second experimental day before two surprise recognition tests. All samples were collected using Salivette collection devices (Sarstedt, Germany) and stored at -18°C. At the end of the experiment, samples from all

participants were analyzed together for free cortisol concentrations using a luminescence assay (IBL, Hamburg, Germany). We also measured baseline blood-pressure and heart rate as additional physiological stress indicators anytime a saliva sample was taken and additionally during the stress procedure using a Critikon Dinamap System (Tampa, FL) with the cuff placed around the nondominant arm. Finally, changes in subjective stress were tracked using a multidimensional mood questionnaire (Steyer et al., 1997) after each saliva sample had been collected.

To control for possible confounds to the stress reaction, participants also completed the State-Trait Anxiety Inventory (Spielberger, 1983), the Positive and Negative Affect Schedule (Watson et al., 1988), the Social Interaction Anxiety Scale (Mattick & Clarke, 1998), and a chronic stress questionnaire (Schulz et al., 2004).

After collecting baseline stress markers, participants received detailed written instructions for a face-categorization task. They were informed that, in two separate phases, they would be presented a series of faces and that their task would be to categorize each face as female or male (Figure 5). Importantly, we did not inform participants that the experiment targeted episodic memory nor that a memory test for the presented faces would follow. In the *pre-treatment phase*, 70 faces (35 female, 35 male) were presented in pseudo-randomized order, so that no more than three faces from the same gender appeared in a row. Each face was presented centrally on a gray background for 2.5 s, during which participants should make their decision about the gender of the face using the ‘left arrow’ and ‘right arrow’ buttons on the keyboard. The allocation of buttons to categories (i.e., female vs. male) was counterbalanced across participants. Between faces, a white fixation cross appeared centrally on a gray background for 2.5 s – 5.5 s.

Upon finishing the pre-treatment phase of the face categorization task, participants were brought to a separate room, where they underwent either the Trier Social Stress Test

(Kirschbaum et al., 1993) or an equally interactive, but non-stressful control treatment (friendly TSST). The TSST is a well-established, standardized procedure to reliably induce psychosocial stress, which manifests in increased activity of both the hypothalamus-pituitary-adrenal axis, leading to the release of corticosteroids (mainly cortisol in humans), and the autonomic nervous system, leading to the release of catecholamines and increases in blood pressure and pulse (Goodman, Janson, & Wolf, 2017; Kudielka, Hellhammer, & Clemens Kirschbaum, 2007). Briefly, in the TSST, participants completed a mock job interview comprised of a 5-minute free speech and a moderately difficult, 5-minute mental-arithmetic task (counting backwards from 2043 in steps of 17), while being videotaped and evaluated by two committee members dressed in white lab coats. Importantly, in the TSST, these two lab members remain cold towards the participant, providing no feedback and answering no questions.

In contrast, participants in the control treatment interacted with a committee that was warm, welcoming, and reacted empathically to statements made by the participant. Instead of a mock job interview, control participants could freely choose their own conversation topic. The mental-arithmetic task from the original TSST was replaced by an interactive counting game (counting from 1 while leaving out any numbers containing '7' as a digit or evenly divisible by 7) in which the two committee members also took part. Furthermore, there were no video recordings during this control procedure.

In this experiment, both the TSST and its friendly control counterpart featured two single-gender committee members allowing us to target specific retroactive memory enhancement for previously encoded faces that were either congruent or incongruent with the gender of the committee. This procedure was conceptualized as the event that would supposedly trigger category-specific retroactive memory enhancements and follows a similar logic as the Pavlovian fear conditioning procedure featured in the study by Dunsmoor et al.

(2015). In the present experiments' procedure, initially neutral male and female faces were encoded before the psychosocial stressor, which related back to half of the previously encoded faces whose gender matched that of the stress committee. Analogously, Dunsmoor et al. (2015) presented initially neutral photographs and half of those photographs belonged to the item category that predicted aversive electric shocks in a Pavlovian fear conditioning procedure. In the study by Dunsmoor et al. (2015), the category predicting electric shocks (i.e., either tools or animals) was counterbalanced across participants. Likewise, in the present study, we counterbalanced the committee's gender (i.e., either exclusively female or exclusively male) across participants. We hypothesized that if there was a category-specific retroactive memory enhancement, this should lead to a memory enhancement specifically for faces encoded during the pre-treatment phase of the gender that corresponded to the gender of the TSST committee members.

After completion of the stress/control treatment, participants in both groups rated the procedure regarding its difficulty, unpleasantness and stressfulness on scales ranging from 0 (not at all) to 100 (very much). Thereafter, they completed a *post-treatment encoding phase* of the face categorization task. This phase followed an identical procedure as the pre-treatment phase, but featured 70 previously unseen faces (35 female, 35 male). On the first day, participants also completed three phases of a reward learning task featuring photographs of animals and tools that was irrelevant for this experiment (see Experiment 3 for details).

Twenty-two to 26 hours later, participants returned to the lab and first completed a questionnaire assessing their expectations for the second experimental day. After they were informed about the following recognition tests, they rated how surprised they were on a scale from 1 (*not surprised at all*) to 5 (*very surprised*). They then received written instructions for the following recognition test of faces from the previous day. In this test, all 140 'old' faces from both encoding phases (i.e., pre- and post-treatment) were presented randomly

intermixed with an equal number of previously unseen, ‘new’ faces (70 male, 70 female). For each face, participants had a maximum of 6 s to make an old vs. new classification by pressing the ‘left arrow’ and ‘right arrow’ key, respectively, and an additional 5 s to indicate their certainty regarding this classification with response options of “very unsure”, “rather unsure”, “rather sure”, and “very sure” corresponding to the “1”, “2”, “3”, and “4” keys, respectively. Whenever participants failed to respond quickly enough, the rest of the trial was skipped. Between individual trials, a white fixation cross was displayed on a gray background for 1 – 2 s.

Data analysis. To test the success of the stress manipulation, salivary cortisol concentrations, vital signs and subjective stress ratings were subjected to mixed-design ANOVAs with the between-subject factor treatment (stress vs. control) and the within-subject factor time. To additionally test for group differences at certain time points, independent *t*-tests were used.

To address our main research question, our memory analyses focused on corrected recognition scores, in accordance with previous studies on category-specific retroactive memory enhancements (Dunsmoor et al., 2015; Oyarzún et al., 2016; Patil et al., 2017). These were derived per participant by subtracting the average false alarm rate per stimulus category (i.e., female vs. male) from the average hit rate per phase and per stimulus category. We performed mixed-design ANOVAs with the between-subject factor treatment (i.e., stress vs. control) and the two within-subject factors gender congruency (i.e., whether there was a match between the gender of the presented face and the gender of the committee in the stress/control procedure) and encoding phase (i.e., pre- vs. post-treatment). These were followed by *t*-tests comparing the corrected recognition for faces encoded before the treatment that were congruent vs. incongruent with the committee’s gender separate for stress and control participants.

Results and discussion

Successful stress induction. Physiological and subjective measures confirmed a successful stress induction in participants who underwent the TSST (Figure 6). To investigate how salivary cortisol concentrations were affected by our treatment, we performed a mixed-design ANOVA with the treatment (stress vs. control) as a between subjects factor and the point in time at which each sample was collected as within subject factor. Cortisol concentrations could partially not be determined for three participants because their samples contained an insufficient amount of saliva. Therefore, the following analysis included only 77 participants for which all six samples could be analyzed. Results indicated that cortisol levels differed significantly between the two treatment groups, $F(1, 75) = 6.91, p = .01, \eta^2_G = .05$. Mauchly's test indicated that the sphericity assumption was violated for both the factor time ($W = 0.07, p < .001$) and the condition $\times$ time interaction ($W = 0.07, p < .001$). Therefore, p -values are reported after applying a Greenhouse-Geisser correction. There was a significant main effect of time, indicating that cortisol levels fluctuated over the course of the experiment, $F(5, 375) = 23.02, p < .001, \eta^2_G = .12$. Most importantly, we found a significant interaction between condition and time, indicating that the time course of the cortisol responses differed between the two groups, $F(5, 375) = 6.75, p < .001, \eta^2_G = .04$. This was confirmed by additional t -tests showing that the stress manipulation, compared to the control condition, had elevated cortisol levels 19 min after treatment onset ($t(75) = 2.59, p = .011, d = 0.59$), with a peak approximately 32 min after treatment onset ($t(75) = 3.40, p = .001, d = 0.78$), whereas there were no group differences before the stress/control manipulation (approximately 30 min before treatment: $t(75) = 1.42, p = .16, d = 0.32$; approximately 2 min before treatment: $t(75) = 0.62, p = .54, d = 0.14$). Even 71 minutes after treatment onset, participants in the stress group still had elevated cortisol level compared to controls, $t(75) = 2.20, p = .031, d = 0.50$.

Next, we applied the same mixed-design ANOVAs with the treatment as a between subject-factor and the time each sample was taken as a within-subject factor to the measures of pulse and blood pressure, which reflect the more rapid stress-component, compared to the slower cortisol response (Joëls & Baram, 2009). For the pulse, we found general changes over the experiment, $F(6, 468) = 37.5, p < .001$ (Greenhouse-Geiser corrected), $\eta^2_G = .11$. There also was a significant treatment $\times$ time interaction, $F(6, 468) = 9.90, p < .001$ (Greenhouse-Geiser corrected), $\eta^2_G = .03$. A follow up t -test confirmed that, as expected, this interaction was qualified by an increased pulse for participants during the stress treatment, compared to control participants, $t(78) = 2.85, p = .006, d = 0.64$ (Figure 6, top-right panel). For systolic blood pressure, we again found general changes over the task, $F(6, 468) = 22.1, p < .001$ (Greenhouse-Geiser corrected), $\eta^2_G = .06$. There also was a significant treatment $\times$ time interaction, $F(6, 468) = 4.08, p < .001$ (Greenhouse-Geiser corrected), $\eta^2_G = .01$. Post-hoc t -tests showed that during the treatment procedure (approximately 8 min after stress onset), systolic blood pressure was significantly elevated for participants in the stress group compared to control participants, $t(78) = 2.56, p = .012, d = 0.57$. For the diastolic blood pressure, there was a main effect of time, reflecting that diastolic blood pressure levels generally changed over the task, $F(6, 468) = 80.1, p < .001$ (Greenhouse-Geiser corrected), $\eta^2_G = .22$. There was no significant main effect of treatment, nor a significant treatment $\times$ time interaction (both F s < 1.53 , both p s $> .21$).

At the subjective level, the post-treatment questionnaire indicated that, compared with control participants, stress participants rated the treatment as significantly more difficult, $t(78) = 9.96, p < .001, d = 2.16$, reported feeling significantly more uncomfortable, $t(78) = 8.71, p < .001, d = 1.95$, and rated the procedure as significantly more stressful, $t(78) = 9.55, p < .001, d = 2.14$.

Anticipation of the recognition test. At the beginning of the second experimental day, participants rated how surprised they were by the following recognition test on a scale from 1 (*not surprised at all*) to 5 (*very surprised*). Data from one participant were missing. On average, participants reported that they were moderately surprised ($M = 3.09$; $SD = 0.99$). Only three participants indicated that they were *not surprised at all*. Excluding these three participants did not change the pattern of results. Therefore, they were still included in the following analyses.

Overall memory performance. On average, participants correctly classified 57.8% ($SD = .16$) of all faces they had seen on the previous experiment day as old (hit rate). In comparison, the false alarm rate (i.e., incorrectly classifying a previously unseen face as old) was relatively low at 25.6% ($SD = .12$). Participants gave a significantly greater number of false alarms for female faces ($M = .27$, $SD = .13$) than for male faces ($M = .24$, $SD = .12$), $t(79) = 2.82$, $p = .006$, $d_{av} = 0.25$. As the number of participants facing male vs. female committees was counterbalanced, this difference in false alarm rates could not bias the corrected recognition scores.

No evidence for category-specific retroactive memory enhancement through psychosocial stress. To test for a category-specific retroactive memory enhancement after a psychosocial stress exposure, we performed a mixed-design ANOVA with the encoding phase (pre- vs. post-stress) as a within subject-factor, the congruency between the gender of the panel conducting the stress/control treatment (match vs. no match) as a within-subject factor and the treatment condition (stress vs. control) as a between-subject factor. This revealed that memory formation differed for items encoded before vs. after the stress/control treatment, $F(1, 78) = 58.11$, $p < .001$, $\eta^2_G = .08$. Whether the gender of a face was congruent with the gender of the panel during the stress/control treatment, on the other hand, had no general effect on face recognition, $F(1, 78) = 0.03$, $p = .87$, $\eta^2_G = .0005$. Likewise, there was

no main effect of the treatment condition, indicating that stress did not generally affect memory formation, $F(1, 78) = 1.62, p = .21, \eta^2_G = .01$. However, there was a significant interaction between the encoding phase and the treatment condition, suggesting that stress might have different effects on memory formation depending on the relative timing of the encoding to the treatment. To further analyze what was driving the interaction between treatment condition and phase, we performed independent t -tests comparing correct recognition scores of stressed vs. control participants separate for both encoding phases. Results showed an improved face recognition for items encoded before the TSST, compared to the control manipulation, $t(78) = 2.15, p = .035, d = 0.48$. In other words, stress after encoding led to an unspecific enhancement for previously encoded faces (Figure 7). The recognition performance for items encoded after the stress/control treatment on the other hand, remained unaffected by the stress treatment, $t(78) = 0.03, p = .97, d = 0.007$.

Critically and contrary to our hypotheses, there was no evidence for a significant three-way interaction between encoding phase, stimulus-committee congruency, and treatment condition, $F(1, 78) = 0.95, p = .33, \eta^2_G = .0006$. To specifically target the hypothesized category-specific retroactive memory enhancements in this task, we next performed paired t -tests comparing the corrected recognition for congruent vs. incongruent items encoded before the treatment phase separately for both treatment conditions. An item was defined as congruent when the gender of the displayed face matched the gender of the committee in the stress/control procedure. Results provided no evidence that memory for congruent faces was retroactively promoted more strongly than for incongruent faces when participants were exposed to stress after encoding, $t(39) = 0.75, p = .46, d_{av} = 0.08$. Likewise, we found no retroactive memory enhancement for congruent over incongruent items for participants in the control condition, $t(39) = 1.06, p = .30, d_{av} = 0.16$. None of the remaining interactions in the mixed-design ANOVA were statistically significant, both F s < 0.86 , both p s $> .36$.

Control variables. At the beginning of the first experimental day, participants completed several questionnaires to control for possible confounds to the stress reaction. Independent sample *t*-tests indicated that stress and control group did not differ with respect to fearfulness of social interaction (measured through the Social Interaction Anxiety Scale; Mattick & Clarke, 1998), trait anxiety (measured through the State-Trait Anxiety Inventory; Spielberger, 1983), chronic stress (measured through the Trierer Inventar für chronischen Stress; Schulz et al., 2004), and positive and negative affect (measured through the the Positive and Negative Affect Schedule; Watson et al., 1988), all *ts* < 1.67, all *ps* > .098.

Experiment 3: Testing the reward-related, category-specific retroactive memory enhancement

The shared goal of all experiments presented in this manuscript was to investigate category-specific retroactive memory enhancements. The four experiments described so far attempted to induce retroactive memory enhancement of initially weakly encoded stimuli by a subsequent, conceptually linked aversive event (i.e., electric shocks in Experiments 1A to C and psychosocial stress in Experiment 2). However, it is important to note that such category-specific retroactive memory enhancements are not necessarily confined to the aversive domain but might also be triggered through appetitive events.

So far, two published studies have investigated category-specific retroactive memory enhancement through appetitive events. In one study following a similar classical conditioning procedure as the study by Dunsmoor et al. (2015), the authors replaced aversive electric shocks through monetary rewards (Oyarzún et al., 2016). These rewards failed to produce retroactive memory enhancement for conceptually linked neutral stimuli that were encoded before the reward phase. In a later study, the same group of authors that introduced the concept of category-specific retroactive memory enhancements in the aversive domain (Dunsmoor et al., 2015) employed an operant conditioning procedure wherein participants

gained rewards for correct reactions in a delayed matching-to-sample task (Patil et al., 2017). They found evidence for category-specific retroactive memory enhancements for stimuli that were encoded before the reward phase and that later belonged to high rewarded compared with a low rewarded category.

Here, we aimed to closely replicate the later experiment, thus testing whether we can find evidence for category-specific retroactive memory enhancements due to later rewards. Again, we focused on the 24 h retrieval group, that, unlike an immediate retrieval group, showed evidence for category-specific retroactive memory enhancement through reward in the original study (Patil et al., 2017).

Method

Participants. The sample in this experiment was identical to Experiment 2. Only participants from the control group of Experiment 2 were included as we aimed to closely replicate previous findings of category-specific retroactive memory enhancement in a non-stressed sample. This subsample consisted of 40 healthy men and women between 18 and 34 years of age ($M = 25.8$, $SD = 4.21$). A post-hoc power analysis enabled us to determine the probability of obtaining a significant retroactive memory effect specifically for high-reward vs. low-reward items based on statistics reported by Patil et al. (2017). While the authors provided no direct measure of effect sizes for the retroactive memory effect for high- vs. low-rewarded items, these can be derived from their first experiment's sample size of $n = 24$ and the reported t -value of 2.98 in a dependent means t -test using the previously described formula (Lakens, 2013):

$$\text{Cohen's } d_z = \frac{2.98}{\sqrt{24}} = 0.61$$

The post-hoc power analysis for a two-tailed paired t -test with $\alpha = .05$ and our sample size of $N = 40$ revealed that an effect of $d_z = 0.61$ (i.e. the point-estimate obtained from the original study) should be detectable with 96.4% certainty. As participants were a subsample of

Experiment 2, the same exclusion criteria and monetary compensation applied. The study protocol was approved by the ethics committee of the Faculty of Human Movement Science at the University of Hamburg.

Materials. Stimuli consisted of the same 180 color photographs of animals and 180 color photographs of tools isolated on white backgrounds as in Experiment 1B and Experiment 1C (Dunsmoor et al., 2015). Per participant, of the 180 photographs from each category, 60 were randomly selected to serve as targets and 60 to serve as distractors for the delayed-match-to-sample task. These were distributed equally to the three encoding phases (see Procedure). The remaining 60 photographs per category served as lures for the surprise recognition test on the second experimental day.

Procedure. The procedure of this experiment was mostly adapted from the original study (Patil et al., 2017), apart from the addition of an encoding phase following the reward phase that was inspired by previous findings of proactive memory enhancements in aversive learning (Dunsmoor et al., 2015; Experiments 1A to C). The three encoding phases of this experiment followed directly after the post-treatment encoding phase in Experiment 2 (see above). Each encoding phase consisted of a delayed-matching-to-sample task (Figure 8). In each trial, participants were presented a unique photograph of either an animal or a tool centrally on a gray background for 2 s, followed by a white fixation cross for 5 s. Then, the just presented photograph (target) was presented side-by-side with a previously unseen photograph from the same category (distractor). Participants had 0.6 s to react by indicating which side the target was on by pressing either the '1' or '2' key, corresponding to left and right respectively. The target position was randomly determined and counterbalanced across categories in each phase. Between trials, a white fixation cross on a gray background was presented for 1.5 s. In each of the three encoding phases, participants saw 40 unique targets (20 animals and 20 tools) and 40 distractors from the same category. In both the pre- and the

post-reward phases, they did not receive any form of feedback. Conversely, in the reward-phase, whenever participants made the correct choice within the allocated time, they received either a white star, corresponding to a low reward, or a green star, corresponding to a high reward. Rewards were displayed for 1 s immediately after the match-to-sample part of each trial. When participants made incorrect choices or reacted too slowly in the reward phase, they saw a corresponding message instead of the reward. They were explicitly instructed that collecting at least 90% of all possible white stars (i.e., low rewards) would increase their final compensation by 0.50€, while collecting at least 90% of all possible green stars (i.e., high rewards) would increase their final compensation by another 5€. Importantly, rewards were linked to stimulus categories, such that correct responses in trials in which one category was presented would always yield high rewards, while correct responses in trials in which the other category was presented would always yield low rewards. Allocation of categories to be linked with either high or low rewards was randomized and counterbalanced across participants. Participants were not informed about the link between categories and rewards but were expected to learn these by themselves.

On the second experimental day, a recognition test for the 120 photographs that had served as targets in all three phases of the delayed match-to-sample task followed directly after the recognition task from Experiment 2 (see above). In random succession, these were presented individually, intermixed with the same number of previously unseen photographs (i.e., photographs that served neither as targets nor as lures). For each photograph, participants had a maximum of 6 s to make both their classification of the current photograph as ‘old’ or ‘new’ as well as their certainty with this decision by pressing the ‘1’, ‘2’, ‘3’, or ‘4’ buttons corresponding to the options of “definitely old”, “maybe old”, “maybe new”, or “definitely new”, respectively. Between individual photographs, a white fixation cross appeared centrally on a gray background for 1.5 s.

Data analysis. In line with the original study (Patil et al., 2017), our memory analyses focused on corrected recognition scores. These were derived by subtracting each participant's false alarm rate per category (i.e., animals and tools) from the hit rate per category and per phase. To investigate variables affecting the recognition performance, we performed a repeated-measures ANOVA on corrected recognition scores with the within-subject factors reward category (high vs. low) and phase (pre-reward, reward, and post-reward). These were followed up with paired *t*-tests comparing corrected recognition scores for high vs. low rewarded items separately per phase.

Results and discussion

Performance in the delayed matching-to-sample-task. Averaged across all three encoding phases, participants performed the correct action in the match-to-sample task within the given response time in 88.9% ($SD = 0.31$) of all trials. Consistent with findings in the original study (Patil et al., 2017), a repeated measures ANOVA revealed neither a significant main effect of the encoding phase (pre-reward, reward, post-reward), nor a main effect of the reward category (low vs. high reward), nor an interaction between these two on the performance in the match-to-sample task, all F s < 2.62 , all p s $> .10$.

Overall memory performance. On average, participants correctly recognized 66.3% ($SD = .16$) of the animals and tools they had seen in all three encoding phases (hit rate). In comparison, the false alarm rate (i.e., incorrectly classifying a previously unseen item as 'old') was relatively low at 21.2% ($SD = .13$). As in our previous experiments utilizing the same two image categories (i.e., Experiment 1A to C) participants gave a significantly higher number of false alarms for photographs of animals than for photographs of tools, $t(39) = 2.74$, $p = .009$, $d_{av} = 0.27$.

No evidence for category-specific retroactive memory enhancement through reward. To test for a potential category-specific, retroactive memory enhancement by

rewards, we first performed a repeated-measures ANOVA on corrected recognition scores with the encoding phase and the reward category of an item as within-subject factors. This revealed that the corrected recognition differed between encoding phases, $F(2, 78) = 6.01$, $p = .004$, $\eta^2_G = .013$. In contrast to previous findings (Patil et al., 2017), we found no general memory difference between low and high rewarded items, $F(1, 39) = 0.03$, $p = .87$, $\eta^2_G < .001$. Moreover, there also was no significant interaction between the encoding phase and the reward category, $F(2, 78) = 0.96$, $p = .39$, $\eta^2_G = .002$.

Follow-up paired t -tests provided no evidence for a memory advantage for high over low rewarded items encoded during the reward phase, $t(39) = 0.69$, $p = .49$, $d_{av} = 0.12$ (Figure 9). Likewise, there was no evidence of a memory advantage for items belonging to the high reward category compared to low rewarded items that were encoded after the reward phase, $t(39) = 0.24$, $p = .81$, $d_{av} = 0.03$. Most importantly and in contrast to previously reported findings, we found no evidence for a category-specific retroactive memory enhancement for pre-reward items that belonged to the later high-rewarded vs. low-rewarded category, $t(39) = 0.72$, $p = .47$, $d_{av} = 0.09$.

General discussion

Adaptive episodic memory has been theorized to preferentially store motivationally significant experiences that can be useful to guide future behavior (Nairne & Pandeirada, 2008; Nairne et al., 2007; Shohamy & Adcock, 2010). Recently, a possible underlying mechanism has been identified that retroactively and selectively promotes memory for initially neutral items when their respective category is later predictive of either aversive or appetitive events (Dunsmoor et al., 2015; Patil et al., 2017). In a series of five experiments, we aimed to replicate, both closely and conceptually (Bonett, 2012), such category-specific retroactive memory enhancement. In all experiments, participants encoded a series of initially neutral stimuli from two categories. Subsequent aversive (Experiment 1A to C, Experiment

2) or appetitive (Experiment 3) events were conceptually linked to one of the two previously encoded categories. Experiments 1A to C aimed to replicate findings from the first published study showing category-specific retroactive memory enhancements for initially neutral stimuli through a following Pavlovian fear-conditioning procedure that linked aversive electric shocks to only one category of stimuli (Dunsmoor et al., 2015). Inspired by this paradigm, in Experiment 2, we investigated whether this idea would generalize when aversive shocks would be replaced by a more ecologically valid aversive event, namely psychosocial stress. Again, a conceptual link between initial learning material and the following aversive event was established by linking the gender of faces presented during encoding to the gender of members of a committee that led participants through the psychosocial stress procedure. Finally, in Experiment 3, we aimed to closely replicate findings indicating that category-specific retroactive memory enhancements are not confined to the aversive domain, but can also be observed for initially neutral stimuli belonging to a category that is later associated with increased monetary rewards (Patil et al., 2017). Based on recent reports (Dunsmoor et al., 2015; Patil et al., 2017), we expected in all experiments that memory for the initially neutral items would retroactively be enhanced when these are later revealed to belong to a relevant category, as indicated by an improved recognition performance in a following surprise memory test. In sharp contrast to our hypotheses, all five experiments consistently failed to produce any evidence for category-specific retroactive memory enhancement.

How can the inconsistencies between the previous reports of category-specific retroactive memory enhancements and the current findings be explained? One might argue that these inconsistencies are owing to slight deviations in our experimental procedure. However, Experiments 1A, 1B, and Experiment 3 were designed to replicate the procedure of the previous studies as closely as possible regarding various aspects such as timing,

instructions, and stimuli. After the failure to replicate the previous findings of category-specific retroactive memory enhancement through aversive events in Experiment 1A, we contacted the authors of the previous study and received original stimuli and instructions, which were incorporated in Experiment 1B. This change had no effect on the pattern of results, even after substantially increasing the sample size in Experiment 1B. The increase in sample size is particularly relevant because non-significant findings in replications can sometimes be attributed to insufficient statistical power (Asendorpf et al., 2013; Maxwell, Lau, & Howard, 2015). Notably, in all four close replications (i.e., Experiments 1A to C and Experiment 3), sample sizes were approximately 1.5 to 3 times higher as in the 24h delay group in the study of Dunsmoor and colleagues (2015). A-priori power analyses were conducted to predetermine target sample sizes in Experiment 1A to achieve the overall smallest, but still acceptable statistical power of approximately 80%. In Experiment 1B and 1C, using a priori-power analyses, we chose target sample sizes that should detect previously reported effect sizes with at least 95% probability. Similarly, a post-hoc power analysis in Experiment 3 indicated that we had achieved statistical power of over 95%. Therefore, unless effect sizes were substantially inflated in the original studies, it is highly unlikely that the present lack of a category-specific retroactive memory enhancement was due to insufficient statistical power. Additionally, at the mere descriptive level, all observed effect sizes for category-specific retroactive memory enhancements were either small or close to zero which further contradicts the notion that further increasing sample sizes would yield different results. A pooled analysis over Experiment 1A to C further provided no statistically significant evidence for this effect and overall observed corrected recognition differences between CS^+ and CS^- items encoded during pre-conditioning were only approximately 1%. Thus, procedural differences or a lack of statistical power are extremely unlikely to explain

the failure to replicate the category-specific retroactive memory enhancement in the present series of experiments.

A factor that has been suggested to moderate the extent of category-specific memory enhancement is the interval between the encoding of initially neutral stimuli and the following significant (either aversive or appetitive) event (Dunsmoor et al., 2015). Specifically, a previous study reported a linear trend between the distance of learning items to the following significant event and the strength of category-specific retroactive memory enhancement. This linear trend is in line with previous work on non-specific behavioral tagging in animals suggesting that a minimal interval between initial learning and following event is necessary for such effects to unfold (de Carvalho Myskiw et al., 2013; Moncada et al., 2015). One might argue that, since the duration of this interval was mostly determined by the duration of the shock intensity adjustment in Experiment 1A and 1B this putatively critical interval was controlled insufficiently, although the same would be true in the original study. We specifically addressed this issue in Experiment 1C, where we extended this interval by ten minutes in which participants completed task-irrelevant questionnaires. However, even after extending the interval between initial encoding and the arousing encounter, we found neither evidence for an increase of the effect at descriptive level, nor any significant evidence for the effect per se. Also, neither of Experiments 1A to C provided any evidence for the previously reported linear trend between a pre-conditioning item's temporal distance to the conditioning procedure and the size of category-specific retroactive memory enhancement.

Retroactive memory effects have been theorized to only strengthen initially weak memories. When an item is encoded strongly, on the other hand, subsequent significant events are assumed to have no additional memory enhancing effect on them (Moncada & Viola, 2007; Wang et al., 2010). Dunsmoor et al. (2015) found converging evidence that this

also appears to be true for category-specific retroactive memory enhancement. In a separate group of participants, they manipulated encoding strength by presenting each stimulus three times during pre-conditioning, instead of just once as in the remaining groups. As expected, participants that saw each stimulus repeatedly showed a better overall recognition performance when tested 24h later. More importantly, they also showed no evidence for category-specific retroactive memory enhancement. The authors attributed this lack of an improvement to ceiling effects for already strongly encoded stimuli. Even though we followed the exact procedure as the authors of the original study to produce weak initial encoding, one possibility might still be that our sample of participants included better learners, which would be observable as a generally improved recognition performance and could be used as an explanation for missing category-specific retroactive memory enhancement. However, comparing recognition performances across all learning phases in Experiments 1A to C and Experiment 3 to those found by Dunsmoor et al. (2015) and Patil et al. (2017), respectively, indicated a largely comparable memory performance. Therefore, it is unlikely that the lack of category-specific retroactive memory enhancement is due to an already strong initial encoding of stimuli.

It should be noted that, while none of our five experiments provided any evidence for the existence of category-specific retroactive memory enhancement, they showed that memory processes can be modulated in important ways by arousing events. Across Experiments 1A to C we consistently found a memory advantage for items from the CS⁺ category that were presented during Pavlovian fear conditioning compared to items from the CS⁻ category encoded in the same learning phase. This finding is in line with previous evidence showing enhanced memory for stimuli linked to arousing events (Salehi, Cordero, & Sandi, 2010; Vogel & Schwabe, 2016). In the context of adaptive memory, such a mechanism could help to identify possibly threatening situations in the future by

preferentially forming episodic memories for stimuli that are currently associated with threat (Nairne & Pandeirada, 2008; Nairne et al., 2007). In Experiment 2, the fear conditioning procedure was replaced by a psychosocial stress induction during which no learning items were presented, so that such an effect could not be evaluated here. Experiment 3 featured a reward phase with high vs. low reward opportunities. Here, we found no differences in recognition memory for high vs. low rewarded items that were encoded during the reward procedure. This is surprising given that the original study found not only evidence for a category-specific retroactive memory effect of reward, but also clear evidence for enhanced memory formation for high-rewarded items encoded during the reward-learning phase (Patil et al., 2017). Since we found no memory differences between high vs. low rewarded items in any learning phase, one might suspect that this distinction was not salient enough in our experiment. However, our procedure, instructions, and stimuli were designed to closely match those of the original study, so it remains unclear why salience would have been larger in the study by Patil et al. (2017).

While our results oppose the notion of category-specific retroactive memory enhancement, the possibility of similar enhancements in the opposite, proactive direction remains. Our results regarding such an encoding bias for items belonging to a relevant category first presented after a significant event were rather inconsistent. Consistent with findings from Dunsmoor et al. (2015), in Experiment 1B, stimuli from the CS⁺ category that were encoded after the fear conditioning procedure were later recognized significantly better than CS⁻ items presented in the same learning phase. In both Experiment 1A and 1C we observed trends in the identical direction, although both not significant. After pooling data from Experiments 1A to C, however, we found clear evidence for this effect. Contrarily, in Experiment 2, which was also in the aversive domain, but replaced aversive electric shocks with a social stress procedure, there was no evidence that memory for faces congruent with

the psychosocial stressor was proactively promoted compared with incongruent faces, although here the link between arousing event and subsequent encoding was less clear than in Experiment 1A to C. The same was true for Experiment 3, where we found no differences in recognition performance for items that were encoded after the reward phase and belonged to the high-rewarded category compared with low-rewarded items from the same encoding phase.

Experiment 2 was unique in that it potentially allowed us to simultaneously observe both category-specific and general (i.e., category-unspecific) retroactive memory enhancement within a single experimental design. According to a category-specific retroactive memory enhancement, it was hypothesized that, within the stress group, only faces with a congruent gender as the committee in the social stress manipulation should receive a retroactive memory promotion. Unspecific retroactive memory-enhancement, on the other hand, could be observed as retroactively promoted memory for all previously encoded faces (regardless of gender) in stressed but not control participants. Results were consistent with the latter, but not the former effect. In other words, psychosocial stress led to an unspecific retroactive memory enhancement, a finding that is congruent with the existing literature on facilitated memory consolidation by stress (Andreano & Cahill, 2006; Beckner, Tucker, Delville, & Mohr, 2006; Cahill, 2003; McGaugh & Roozendaal, 2002; Roozendaal, Castello, Vedana, Barsegyan, & McGaugh, 2008; Schwabe, Joëls, Roozendaal, Wolf, & Oitzl, 2012).

Together, our results suggest that there might be different mechanisms to prioritize memory specifically for self-relevant stimuli, both while a threat is present (e.g., during the fear conditioning procedure in Experiments 1A to C) and immediately after threat (e.g., in the post conditioning phase in Experiments 1A to C). This selectivity in episodic memory has considerable impact on the architecture of our autobiographical memory and, although being

generally adaptive, may propel dysfunctional memory in a variety of psychiatric disorders, such as anxiety disorders (Airaksinen, Larsson, & Forsell, 2005; Coles, Turk, & Heimberg, 2007; de Quervain, Schwabe, & Roozendaal, 2017), post-traumatic stress disorder (Brown et al., 2014; Isaac, Cushway, & Jones, 2006), or depression (Airaksinen, Wahlin, Forsell, & Larsson, 2007; Lemogne et al., 2006; McDermott & Ebmeier, 2009). The lack of evidence for category-specific retroactive memory enhancement raises the question how the brain might adapt when certain stimuli only gain relevance after their initial encoding. One solution that has been presented here is by unspecifically promoting recent memories regardless of their relation to the relevant event. Another solution that has not been considered by the literature so far could be that in these cases, an even more specific retroactive enhancement takes place, that does not apply to a relatively wide array of stimuli of the same category, but only strengthens the memory trace of a single stimulus. Relating back to the example of the bank costumer's encounter with the bank robber, importance lies on the memory for only the specific face of the robber and not for other faces seen shortly before (e.g. that of all men). Therefore, adaptive memory would call for a memory promotion of only the specific face and not other faces from the same abstract category. Whether such a mechanism exists, however, is currently still unknown and should be addressed in future research.

In summary, the present series of experiments searched for category-specific retroactive memory enhancement of initially neutral stimuli as suggested by the so far only two published accounts of this effect (Dunsmoor et al., 2015; Patil et al., 2017). Our data yielded no evidence for a category-specific retroactive memory enhancement and cast doubt whether such an effect exists. Elucidating how our memory balances the need for efficiency on the one hand and the need for an enhanced storage of experiences that preceded a significant event on the other hand remains a challenge for future research.

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Figure 1. Procedure in Experiments 1A to C. In each phase, participants saw 60 unique photographs of animals and tools. During pre- and post-conditioning, they were instructed to categorize each photograph as an animal or tool. During fear conditioning, photographs from one category (CS⁺; animals in the example above) were followed by an electric shock in two-thirds of all trials, while photographs of the remaining category (CS⁻; tools in the example above) were never followed by a shock. Whether photographs of animals or tools served as the CS⁺ category was counterbalanced across participants. For each photograph, participants were instructed to indicate whether they expected that a shock would follow. Note that in Experiment 1C, the interval between pre-conditioning and Pavlovian fear conditioning was increased by 10 min, based on previous reports that this would lead to increased category-specific retroactive memory enhancement (Dunsmoor et al., 2015). Approximately 24h after encoding, participants completed a surprise recognition test in which they saw all previously presented photographs of animals and tools together with the same number of ‘new’ photographs and indicated for each of them whether they thought it had been presented on the previous day.

Figure 2. Successful fear conditioning as indicated by average anticipatory skin conductance responses (SCRs) in Experiments 1A, 1B, and 1C. SCRs were estimated using a continuous decomposition analysis (CDA) in Ledalab (Benedek & Kaernbach, 2010). In all three experiments, participants showed significantly greater anticipatory skin-conductance responses during fear conditioning to CS⁺ items compared with CS⁻ items, confirming a successful fear induction. Error bars represent ± 1 standard error of the mean. *** $p < .001$.

Figure 3. Recognition performance expressed as hit rate minus false alarm rate in Experiments 1A, 1B, and 1C by encoding phase and conditioning category. In all three experiments, recognition was improved for items from the CS⁺ category that were encoded during Pavlovian fear conditioning. Only in Experiment 1B, this effect significantly carried over to items encoded after the end of the fear conditioning. Most importantly, none of the three experiments provided any evidence for category-specific retroactive memory enhancement. Error bars represent ± 1 standard error of the mean. * $p < .05$, ** $p < .01$, *** $p < .001$.

Figure 4. Results of a pooled analysis across data from Experiments 1A, 1B, and 1C using linear-mixed effect models. CS⁺ items encoded during both Pavlovian fear conditioning and after fear conditioning were recognized significantly better compared to CS⁻ items encoded within their respective phase. Critically, even after pooling data from three experiments with over 200 unique participants, there was no evidence for category-specific retroactive memory enhancement. Error bars represent 95% confidence intervals. *** $p < .001$.

Figure 5. Procedure in Experiment 2. Similarly to Experiments 1A to C, in both the pre-and the post-treatment phase, participants encoded 70 unique faces of men and women. In both encoding phases, their task was to indicate the gender of each face using one of two keys. In an intermediate treatment phase, they interacted with two experimenters that were both either male or female. In a standardized procedure, the two experimenters were either cold and non-responsive towards the participant to induce social stress (Kirschbaum et al., 1993), or they were friendly and reinforcing, which served as a control condition. Both the gender of the experimenters in the treatment and the treatment type were counterbalanced across participants. Approximately 24h after encoding, participants completed a surprise recognition test in which they saw all previously presented faces together with the same number of ‘new’ faces and indicated for each face whether they thought it had been presented on the previous day.

Figure 6. Successful stress induction in Experiment 2. Results show a substantial increase in salivary cortisol levels in participants from the stress condition compared to controls that emerged after the completion of the treatment and was still observable approximately 75 min after treatment onset. Likewise, both pulse and systolic blood pressure were significantly increased during the treatment in stress participants, reflecting the more rapid component of the stress response. Error bars represent ± 1 standard error of the mean. * $p < .05$, ** $p < .01$

Figure 7. Recognition performance in Experiment 2 by encoding phase, treatment, and congruency. Relative to controls, stress unspecifically retroactively promoted memory for items encoded before the treatment. However, this effect was irrespective of the gender congruency between faces encoded as learning items and the single-gender committee performing the treatment. Therefore, results are consistent with general, but not with category-specific retroactive memory enhancement. Error bars represent ± 1 standard error of the mean. * $p < .05$.

Figure 8. Procedure in Experiment 3. In each of the three encoding phases, participants performed a delayed match-to-sample task. In each trial, a photograph of either an animal or a tool was presented (target) and followed by a centrally presented fixation cross. Then, the target reappeared next to a distractor item from the same category and participants should quickly indicate which side the target was on. In the pre- and post-reward phase, participants received no feedback. In the reward phase however, participants were rewarded with white and green stars for each correct response. They were instructed that collecting at least 90% of all possible white stars would increase their final compensation by 0.50€ (low reward condition), while collecting at least 90% of all possible green stars would increase their final compensation by 5.00€ (high reward condition). Importantly, whether a correct response would yield a green or a white star was deterministically linked with the category of the photographs (i.e., animals and tools). Participants were not informed about this contingency. Allocation of photograph categories to the low vs. high rewarded category was counterbalanced across participants.

Figure 9. Recognition performance in Experiment 3 by encoding phase and reward opportunities. R^+ and R^- refer to items associated with high vs. low reward opportunities, respectively. Surprisingly, reward opportunities affected recognition performance in none of the three encoding phases. Error bars represent ± 1 standard error of the mean.