Learning and Motivation 63 (2018) 20–26

Contents lists available at ScienceDirect

Learning and Motivation

journal homepage: www.elsevier.com/locate/l&m

Pre-exposure and retrieval effects on generalization of contextual fear

Dieuwke Sevenster[a,b,*], Lucas de Oliveira Alvares[c,d], Rudi D'Hooge[a]

[a] Laboratory of Biological Psychology, Department of Psychology, KU Leuven, Tiensestraat 102, B-3000 Leuven, Belgium
[b] Clinical Psychology, Utrecht University, Heidelberglaan 1, 3584 CS Utrecht, The Netherlands
[c] Neurobiology of Memory Lab, Federal University of Rio Grande do Sul, Porto Alegre, Brazil
[d] Neuroscience Graduate Program, Federal University of Rio Grande do Sul, Porto Alegre, Brazil

ARTICLE INFO

Keywords:
Context conditioning
Fear generalization
Pre-exposure
Retrieval

ABSTRACT

The degree of generalization from a fearful context to other contexts is determined by precision of the original fear memory. Experiences before and after fear learning affect memory precision. Pre-exposure to a similar context *before* context conditioning results in increased generalization to the similar context. In contrast, exposure to the conditioning context *after* fear learning reduces fear generalization. In the current study we aimed to investigate whether the events before and after fear learning interact. We hypothesized that pre-exposure-induced enhanced generalization could be reduced by a return to the conditioning context. We found that, in contrast to previous findings, pre-exposure did not affect generalization. However, a reminder of the conditioning context reduced generalization to both a similar and a different context. The results stress the dynamic nature of emotional memory.

1. Introduction

Generalization of fear allows a subject to treat a new situation that is similar to a threatening experience as potentially harmful (Dymond, Dunsmoor, Vervliet, Roche, & Hermans, 2015). It is no longer adaptive when a situation that only slightly resembles the threatening event evokes fear. To model fear generalization from one situation to another, animals are trained to fear a context by pairing the context with shock (unconditioned stimulus; US). Next, the animals are exposed to a similar context to test the ability to discriminate between the threatening (conditioning context) and a similar but safe context. A detailed memory of the context in which fear learning took place supports discrimination and reduces generalization (Hardt, Nader, & Nadel, 2013; Kheirbek, Klemenhagen, Sahay, & Hen, 2012; Sahay et al., 2011).

Memory has been shown to be far more dynamic than held possible by traditional consolidation views. It is no longer believed that consolidation results in a fixed memory representation but instead, memories are subject to change in interaction with other events (Forcato, Rodríguez, Pedreira, & Maldonado, 2010; Osan, Tort, & Amaral, 2011; Ramirez et al., 2013; Sevenster, Beckers, & Kindt, 2012; Sevenster, Beckers, & Kindt, 2013; Sevenster, Beckers, & Kindt, 2014). More specifically, the ability to discriminate between similar contexts is affected by experiences *before* and *after* fear learning. In the current study we investigated whether experiences before and after context conditioning interact in producing fear generalization.

First, pre-exposure to a context that is similar, but not the same or different, to the conditioning context enhances generalization on test. Crucial for the understanding of this increase in fear generalization is the phenomenon of pattern completion. If a new

* Corresponding author at: Utrecht University, Clinical Psychology, Heidelberglaan 1, 3584 CS Utrecht, The Netherlands.
E-mail address: d.sevenster@uu.nl (D. Sevenster).

https://doi.org/10.1016/j.lmot.2017.11.003
Received 22 September 2017; Received in revised form 14 November 2017; Accepted 14 November 2017
Available online 27 November 2017
0023-9690/

situation is sufficiently similar to or matches the stored representation of the context, pattern completion mechanisms will ensure retrieval of the existing representation (Blumenfeld, Preminger, Sagi, & Tsodyks, 2006; Hunsaker and Kesner, 2013; Leutgeb and Leutgeb, 2007; Osan et al., 2011). Hence, pattern completion will lead to the retrieval of the similar pre-exposure context during conditioning; both the pre-exposure and the conditioning context will become linked to the shock (Bae, Holmes, & Westbrook, 2015; O'Reilly & Rudy, 2001; Rudy and O'Reilly,1999), facilitating generalization to the pre-exposure context. Second, context re-exposure following fear learning can reduce fear generalization. A return to the conditioning context (without presentation of the US) after context conditioning reduces generalization to a similar context (de Oliveira Alvares et al., 2012, 2013; Wiltgen and Silva, 2007; Zhou and Riccio, 1994). It is well-known that the act of recall promotes memory maintenance (Roediger & Karpicke, 2006). Hence, recall stimulates context specificity of the aversive event, resulting in an increased ability to discriminate between similar contexts.

In sum, it is known that pre-exposure to a similar context *before* conditioning can enhance generalization whereas exposure to the conditioning context *after* fear conditioning can reduce generalization. In the current study we aimed to investigate whether experiences before and after fear conditioning interact. We hypothesized that enhanced fear generalization as a result of pre-exposure can be reduced by a reminder of the conditioning context. On day 1 mice were pre-exposed to a context that was similar to the conditioning context (context A), the to-be conditioning context (context B) or a context that was different from the conditioning context (context C). One day later animals were fear conditioned in context B. Half of the animals were tested first in context A (day 3), followed by test in context B (day 4). The other half were tested first in context B (day 3), followed by test in context A (day 4). All animals were tested in the different context C on day 5. We expected that generalization to context A would be enhanced in those animals that were pre-exposed to context A. Furthermore, we expected that this enhanced generalization would be reduced in those animals first tested in the conditioning context B. Finally, we did explorative analyses to investigate pre-exposure and retrieval effects on generalization to a different context (context C).

2. Methods and materials

2.1. Animals

Thirty female C57BL/6J mice 10–12 weeks of age were used. Animals were housed in a temperature and humidity controlled vivarium with a 12 h light – 12 h dark cycle. Food and water were available ad libitum. Experiments were performed during the light phase. All protocols complied with the European Community Council Directive and were approved by Animal Ethics Committees of the University of Leuven.

2.2. Apparatus

Testing occurred in two identical conditioning chambers (Panlab Startle & Fear Combined System, Panlab, S.L., Cornellà, Spain). The animal compartment (25 × 25 × 25 cm) had black methacrylate walls and a transparent front door and was located in a sound-attenuating cubicle. Shocks were delivered through a stainless steel grid floor. The freezing response was assessed as a measure of learned fear. Movement of the animal was tracked with a motion sensitive floor and registered with Panlab Freezing v1.3 software. Movement could range from 0 to 100; If movement on the sensitive floor remained below a 2.5 threshold for at least 1s, behaviour was classified as freezing. The conditioning chamber was adjusted to create a total of three different contexts (Fig. 1A).

2.3. Context manipulation

The conditioning context B was brightly illuminated (fluorescent lamp) and there was ambient noise produced from the ventilation fan (Fig. 1A). For generalization context A, a piece of cardboard was placed diagonally in the compartment to create a triangular chamber. The chamber was dimly illuminated (small cage lamp) and there was ambient noise produced by the ventilation fan. In context C, the grid floor was covered with a white sheet. There was no room illumination and no background noise. An odor cue was provided by placing a tube containing a cotton ball with a drop of mint solution next to the chamber. After every test session, the chamber was cleaned. Contexts A and B were cleaned with alcohol-detergent solution (70% alcohol, 30 percent detergent), while context C was cleaned with water. Thus, contexts A and B shared several features, including the grid floor, background noise and odor but differed in room illumination and shape of the chamber. Context C was designed to have no features in common (expect that the shape of the context was similar to that of context B).

2.4. Procedure

Testing procedures were adapted from Rudy and O'Reilly (1999) (Fig. 1B). Mice were randomly assigned to one of three pre-exposure conditions. On the first day of the experiment, mice were pre-exposed for 5 min to context A ($n = 10$), context B ($n = 10$), or context C ($n = 10$). One day later, context conditioning took place in context B. The mouse was placed in the conditioning chamber and 2 min later the first US was delivered (0.3 mA, 2 s). The second US was administered 2 min after the first US. One minute later the animal was returned to the home cage. Tests for conditioned fear in contexts A and B were counterbalanced and took place on day 3 and day 4. All animals were tested in context C on day 5. Thus, half of the animals were first tested in the similar context A (test order ABC on day 3, 4, 5, respectively), whereas the other half were reminded of the conditioning context before generalization test (test order BAC on day 3, 4, 5, respectively). Test duration in contexts A, B and C was 5 min. During pre-exposure and test no shocks were

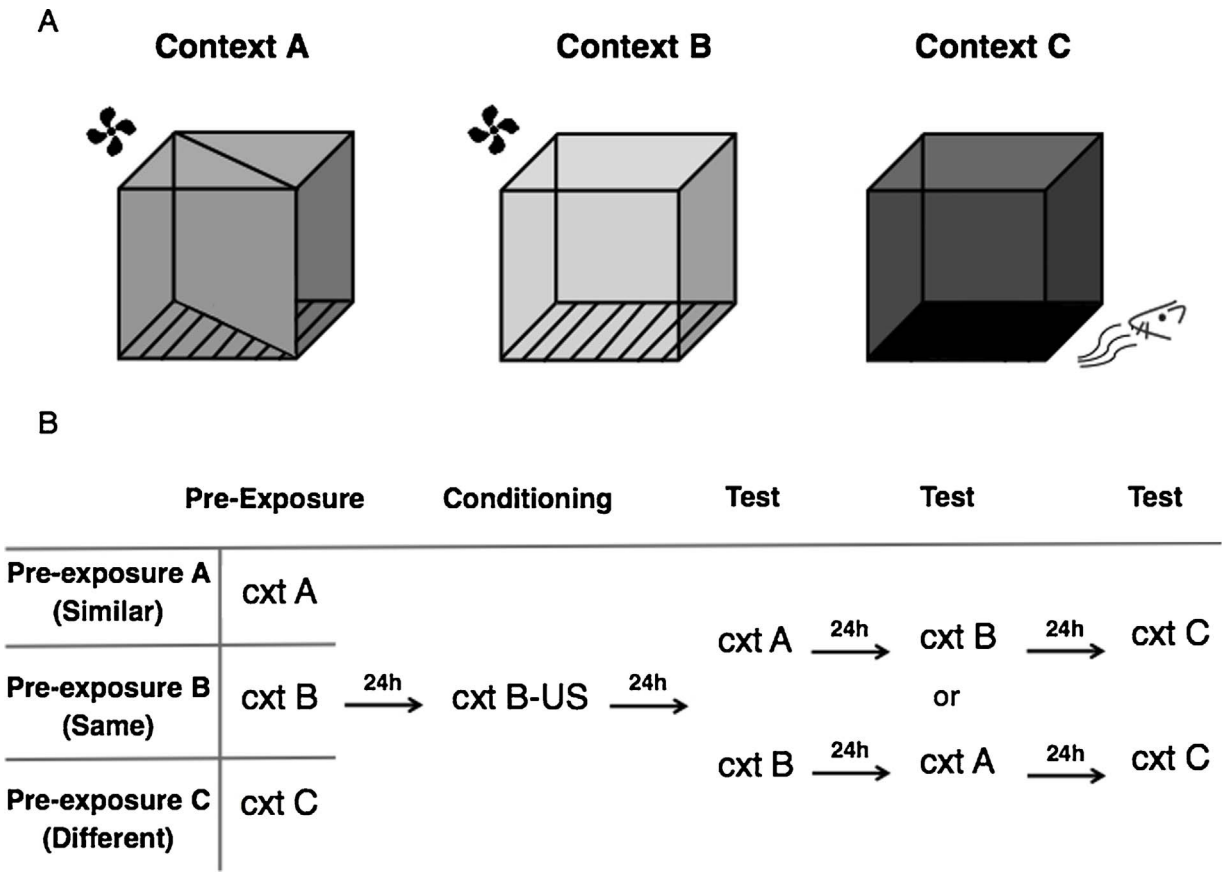

Fig. 1. Illustration of the three contexts (**A**). Schematic overview of the experimental design (**B**).

delivered. For a schematic overview see Fig. 1B.

2.5. Data analysis

Freezing levels during pre-exposure and test were averaged over 5 min. Conditioning data were averaged per minute to analyze the course of freezing behavior from the first to the last minute. To test the hypothesis that pre-exposure and a reminder of the conditioning context interact, freezing to the similar context A was subjected to a univariate ANOVA with condition (pre-exposure A; pre-exposure B; pre-exposure C) and trial order (no reminder [AB]; reminder [BA]) as between subjects factors. To follow up on a significant interaction between condition and trial order, analyses were performed for the three conditions separately to assess the effect of trial order. That is, a univariate ANOVA with trial order (no reminder [AB]; reminder [BA]) as a between subjects factor was conducted. We expected an effect of trial order only in those animals pre-exposed to the similar context A (pre-exposure A). In the absence of a significant interaction between condition and trial order, we investigated whether pre-exposure and trial order affected generalization separately. First, freezing levels to the similar context A were subjected to a univariate ANOVA with condition (pre-exposure A; pre-exposure B; pre-exposure C) as a between subjects factor. Second, freezing levels to the similar context A were subjected to a univariate ANOVA with trial order (no reminder [AB]; reminder [BA]) as a between subjects factor. Generalization to the different context was assessed by subjecting freezing levels to context C to a univariate ANOVA with condition (pre-exposure A; pre-exposure B; pre-exposure C) and trial order (ABC vs. BAC) as between subjects factors. Follow-up analyses were the same as described for context A. Due to technical failure, data from two subjects on day 1 (pre-exposure C condition) and data from two subjects on day 3 (pre-exposure B condition) were not registered. The alpha level was set at 0.05 for statistical analyses. A Greenhouse-Geisser procedure was used in case of violation of the sphericity assumption in ANOVAs. Data files are available at open science framework (OSF): https://osf.io/27e5b/?view_only=4c5815917c4049adb6ceae47c581ce3b.

3. Results

3.1. Pre-exposure

Manipulation of the conditioning chamber itself did not affect behavior, since freezing levels during pre-exposure did not differ in

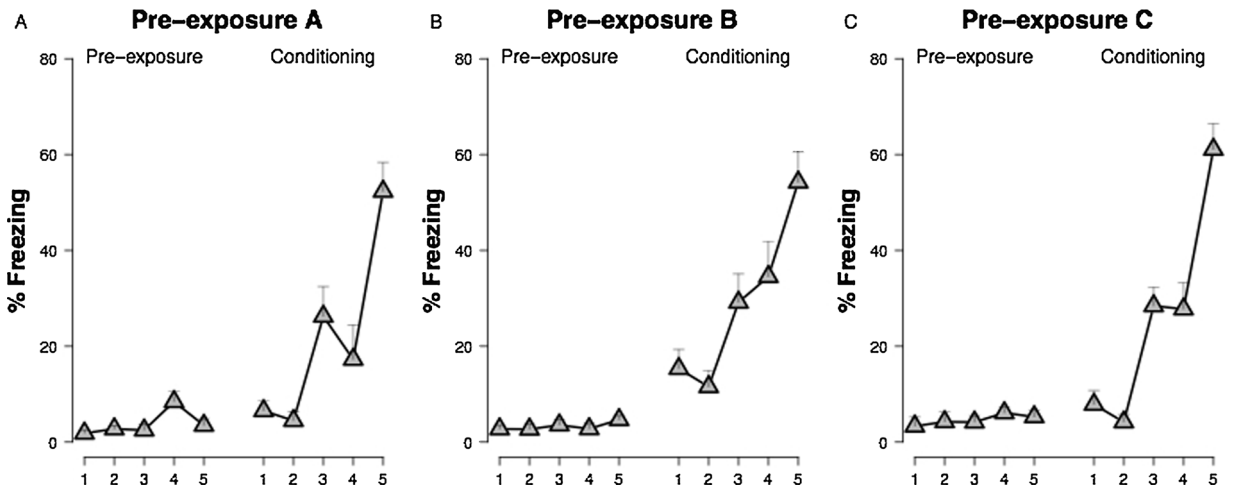

Fig. 2. Mean levels of freezing per minute to the pre-exposure context (day 1) and the conditioning context B (day 2) for the pre-exposure A condition (**A**), the pre-exposure B condition (**B**), and the pre-exposure C condition (**C**). Error bars represent s.e.m.

the different contexts (main effect condition; $F_{(2,25)} < 1$) (Fig. 2A–C; Table 1).

3.2. Conditioning

There was an increase in freezing behavior from the first to the last minute of conditioning (main effect time; $F_{(1,27)} = 175.92$, $p < 0.001$, $\eta_p^2 = 0.87$) that did not differ between conditions (time x condition; $F_{(2,27)} < 1.42$). There was no difference between conditions in overall level of freezing during the first and last minute of conditioning (main effect condition; $F_{(2,27)} < 1$) (Fig. 2A–C; Table 1).

3.3. Generalization to the similar context A

Contrary to expectation, pre-exposure before and exposure after conditioning did not interact in affecting freezing levels in the similar context A (condition x test order; $F_{(2,26)} < 1$) (Table 2). Next, analyzing the effect of pre-exposure alone revealed that pre-exposure did not affect generalization to the similar context A (main effect condition; $F_{(2,26)} < 2.04$) (Fig. 3A). Note that when we analyzed freezing levels in context A only in those animals that were first tested in context A, similar to the experiments by Bae et al. (2015) and Rudy and O'Reilly (1999), we also did not observe differences between conditions ($F_{(2,11)} < 1$) (Table 2). Note that there was substantial generalization to context A, as freezing in animals tested in context A on day 3 did not differ from animals tested in context B on day 3 (main effect context; $F_{(1,26)} < 1$).

Analysis did reveal a significant effect of test order ($F_{(1,27)} = 4.99, p < 0.034, \eta_p^2 = 0.16$); a reminder of the conditioning context B one day before the generalization test reduced freezing levels to context A (Fig. 4A). It could be argued, however, that these results are merely order effects rather than the effect of retrieval. That is, the first test will generally excite more fear behavior than the second test, regardless of the test context. It is important to note that freezing levels in context B were not affected by test order ($F_{(1,27)} < 1.05$). Hence, it is unlikely that reduced responding in context A when first tested in context B was the result of extinction.

Table 1
Means (M) and standard deviations (SD) for freezing levels during pre-exposure (day 1) and conditioning (day 2) for the pre-exposure A, pre-exposure B, and the pre-exposure C conditions.

		Pre-Exposure day 1					Conditioning day 2				
Pre-exposure A	Minute	*1*	*2*	*3*	*4*	*5*	*1*	*2*	*3*	*4*	*5*
	M	1.83	2.73	2.48	8.43	3.47	6.51	4.47	26.23	17.24	52.32
	SD	2.12	1.94	3.81	6.62	4.32	6.42	5.84	19.62	22.74	19.05
Pre-exposure B	Minute	*1*	*2*	*3*	*4*	*5*	*1*	*2*	*3*	*4*	*5*
	M	2.73	2.67	3.54	2.76	4.65	15.33	11.53	29.16	34.52	54.24
	SD	2.49	3.61	3.79	3.64	2.81	12.61	10.78	18.81	23.34	20.24
Pre-exposure C	Minute	*1*	*2*	*3*	*4*	*5*	*1*	*2*	*3*	*4*	*5*
	M	3.30	4.22	4.15	6.09	5.25	7.85	4.17	28.43	27.75	61.08
	SD	5.48	5.81	3.74	3.66	3.75	9.15	5.10	12.36	17.31	17.09

Table 2
Means (M) and standard deviations (SD) for freezing levels during test in context A, context B, and context C for the pre-exposure A, pre-exposure B, and the pre-exposure C conditions, separated for trial order. Animals that were tested following trial order ABC (No Reminder) were tested in context A on day3, in context B on day 4, and in context C on day 5. Animals that were tested following trial order BAC (Reminder) were tested in context B on day3, in context A on day 4, and in context C on day 5.

		Trial Order ABC (No Reminder)			Trial Order BAC (Reminder)		
		Test A day 3	Test B day 4	Test C day 5	Test B day 3	Test A day 4	Test C day 5
Pre-exposure A	Minute	*1–5*	*1–5*	*1–5*	*1–5*	*1–5*	*1–5*
	M	40.50	25.81	27.27	38.72	19.81	1.24
	SD	20.65	17.80	16.94	17.21	7.20	1.44
Pre-exposure B	Minute	*1–5*	*1–5*	*1–5*	*1–5*	*1–5*	*1–5*
	M	61.78	59.06	27.43	46.32	42.82	8.14
	SD	32.40	37.00	16.84	7.51	24.10	3.91
Pre-exposure C	Minute	*1–5*	*1–5*	*1–5*	*1–5*	*1–5*	*1–5*
	M	55.25	45.35	37.44	72.89	35.68	17.63
	SD	30.10	28.19	11.88	7.55	13.97	6.26

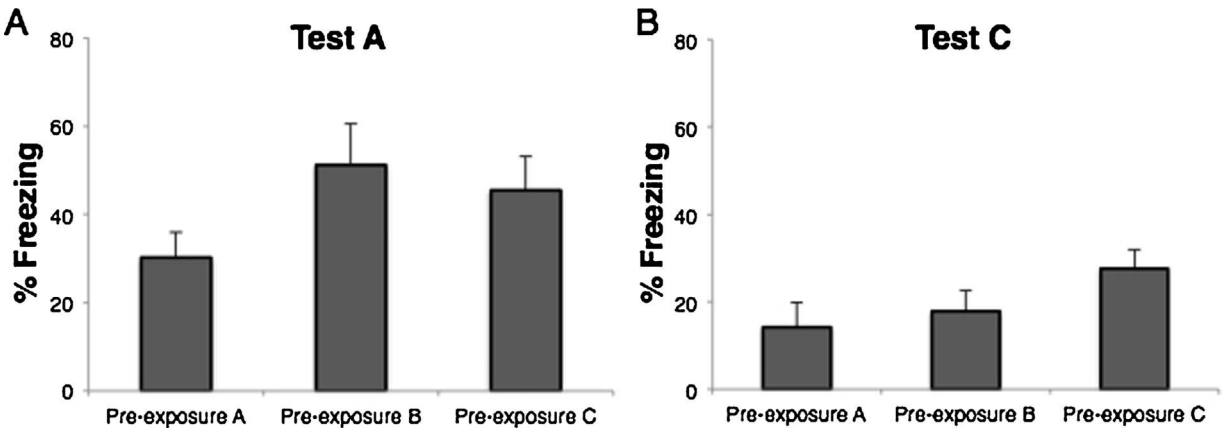

Fig. 3. Mean levels of freezing to (**A**) the similar context A and (**B**) different context C for the pre-exposure A condition, the pre-exposure B condition, and the pre-exposure C condition, irrespective of trial order. Error bars represent s.e.m.

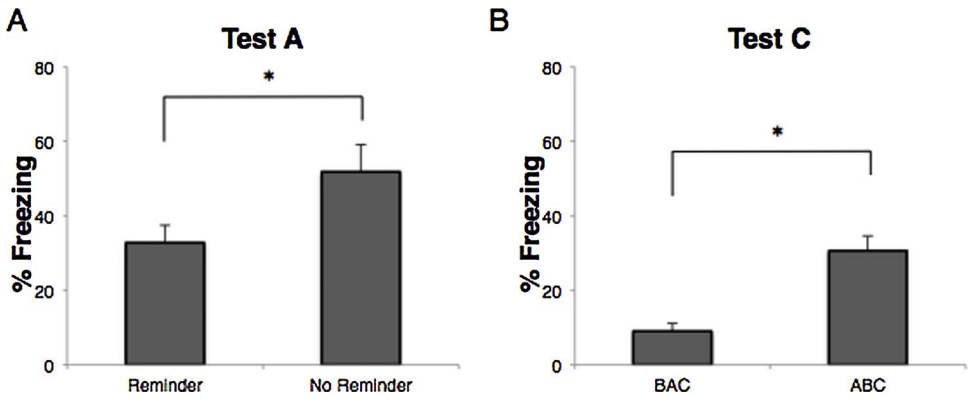

Fig. 4. Mean levels of freezing to the similar context A for those first tested in the conditioning context (Reminder) and those first tested in the similar context A (No Reminder) (**A**). Mean levels of freezing to the different context C for test order BAC and test order (ABC) (**B**), irrespective of condition. Asterisk indicates a significant difference between groups. Error bars represent s.e.m.

3.4. Generalization to the different context C

Pre-exposure did not interact with test order for generalization to the different context C (condition x test order; $F_{(2,27)} < 1$) (Table 2). Pre-exposure also did not affect generalization to context C (main effect condition; $F_{(2,27)} < 1.91$) (Fig. 3B). Finally, test order did affect generalization to the different context C; we observed lower levels of freezing in those animals that were first tested in

context B (main effect test order; $F_{(1,28)} = 24.23, p < 0.001, \eta_p^2 = 0.46$) (Fig. 4B). Note that test in context C was always preceded by exposure to both contexts A and B. It is therefore surprising to find that a reminder of the conditioning context B was no longer effective when given after exposure to the similar context A.

4. Discussion

In contrast to previous findings (Bae et al., 2015; O'Reilly and Rudy, 2001; Rudy and O'Reilly, 1999), we did not observe enhanced generalization as a result of pre-exposure to a context that shares features with the conditioning context. Overall, there was substantial generalization to the similar context one day after conditioning, given that it did not differ from freezing in context B. Hence, a possible explanation for this failure to replicate could be that the generalization context was in fact too similar to the conditioning context; this similarity was effective in inducing generalization to such an extent that it did not allow for further enhanced generalization. In fact, freezing levels to context A did not differ from those in context B one day after conditioning. While the similar context A and the conditioning context B differed on several aspects, context odor was the same. Given that mice have a highly sensitive olfactory system (Buck & Axel, 1991; Tazir, Khan, Mombaerts, & Grosmaitre, 2016), differences between visual aspects in contexts can be overruled by a common scent. While we aimed to reproduce the contexts used in previous studies (Bae et al., 2015; O'Reilly and Rudy, 2001; Rudy and O'Reilly, 1999) as closely as possible, subtle changes from one set-up to another can seriously affect generalization. Careful selection of overlapping and different context features is indispensible. Finally, note that the analyses of pre-exposure effects on generalization to context A in those animals that were first tested in context A were performed on subgroups of only 4–5 animals. The absence of an effect of context pre-exposure could be attributed to these small sample sizes.

A reminder of the conditioning context reduced generalization to a similar context, in line with previous findings (de Oliveira Alvares et al., 2012, 2013; Wiltgen and Silva, 2007; Zhou and Riccio, 1994). Given the high similarity between context A and context B, a reminder of the conditioning context was crucial for reduction of fear generalization to the highly similar context. But discrimination between the conditioning context and the more different context C also benefitted from re-exposure to the conditioning context. Possibly, the strengthening of context specificity is achieved through updating of a retrieved memory. An abundance of studies shows that Information present at the time of memory retrieval can be integrated in the retrieved memory (Forcato et al., 2010; Pedreira, Pérez-Cuesta, & Maldonado, 2004; Sevenster et al., 2012, 2013). As such, the content of the retrieved memory can be changed. A return to the conditioning context enhances context specificity by strengthening the memory for the context. Rodent studies demonstrated that reduced generalization by a reminder of the conditioning context was prevented by injection of nimodipine, a memory destabilization-blocking agent, before memory retrieval (de Oliveira Alvares et al., 2013). Thus, when memory destabilization could not occur, the reduction in generalization was not observed, confirming the idea that through memory retrieval context specificity can be enhanced.

Interestingly, a reminder of the conditioning context only reduced generalization to context C when applied before exposure to the similar context A (test order BAC). In contrast, re-exposure to the conditioning context was no longer effective in reducing generalization when animals were first tested in context A (test order ABC). This could be explained by previous findings showing that following conditioning (context B), exposure to a similar context (context A) facilitates generalization to a more different context (context C) (de Oliveira Alvares et al., 2013). In other words, updating of the memory to a more general representation resulted in overgeneralization of fear. Enhanced generalization to a different context could be prevented by a nimodipine injection before retrieval (de Oliveira Alvares et al., 2013); when memory destabilization could not occur, the memory was not updated and the original memory content was preserved. Thus, memory retrieval in similar context A changes the original memory. This updated memory is less precise than the original memory, impairing the ability to discriminate between the conditioning context and the more different context C. Remarkably, once the memory is updated, exposure to the original conditioning context does not return it to its original state, given that generalization to context C is not reduced when preceded by exposures to contexts A and B. Hence, under the conditions of the current study, a more general memory cannot regain memory specificity.

In sum, we did not observe enhanced generalization as a result of pre-exposure. Instead, there were strong effects of memory retrieval following fear conditioning. A reminder of the conditioning context substantially reduced generalization to similar and more different contexts.

Conflicts of interest

The authors declare no conflict of interest.

Acknowledgements

DS was supported by an FWO-Flanders postdoctoral fellowship (12P8715N). The authors thank G. Soogen for data collection.

References

Bae, S. E., Holmes, N. M., & Westbrook, R. F. (2015). False context fear memory in rats. *Learning & Memory, 22*, 519–525. http://dx.doi.org/10.1101/lm.039065.115.

Blumenfeld, B., Preminger, S., Sagi, D., & Tsodyks, M. (2006). Dynamics of memory representations in networks with novelty-facilitated synaptic plasticity. *Neuron, 52*, 383–394. http://dx.doi.org/10.1016/j.neuron.2006.08.016.

Buck, L., & Axel, R. (1991). A novel multigene family may encode odorant receptors: A molecular basis for odor recognition. *Cell, 65*, 175–187. http://dx.doi.org/10.

1016/0092-8674(91)90418-X.
de Oliveira Alvares, L., Einarsson, E.Ö., Santana, F., Crestani, A. P., Haubrich, J., Cassini, L. F., ... Quillfeldt, J. A. (2012). Periodically reactivated context memory retains its precision and dependence on the hippocampus. *Hippocampus, 22*, 1092–1095. http://dx.doi.org/10.1002/hipo.20983.
de Oliveira Alvares, L., Crestani, A. P., Cassini, L. F., Haubrich, J., Santana, F., & Quillfeldt, J. A. (2013). Reactivation enables memory updating, precision-keeping and strengthening: Exploring the possible biological roles of reconsolidation. *Neuroscience, 244*, 42–48. http://dx.doi.org/10.1016/j.neuroscience.2013.04.005.
Dymond, S., Dunsmoor, J. E., Vervliet, B., Roche, B., & Hermans, D. (2015). Fear generalization in humans: Systematic review and implications for anxiety disorder research. *Behavior Therapy, 46*, 561–582. http://dx.doi.org/10.1016/j.beth.2014.10.001.
Forcato, C., Rodríguez, M. L. C., Pedreira, M. E., & Maldonado, H. (2010). Reconsolidation in humans opens up declarative memory to the entrance of new information. *Neurobiology of Learning and Memory, 93*, 77–84.
Hardt, O., Nader, K., & Nadel, L. (2013). Decay happens: The role of active forgetting in memory. *Trends in Cognitive Sciences, 17*, 111–120. http://dx.doi.org/10.1016/j.tics.2013.01.001.
Hunsaker, M. R., & Kesner, R. P. (2013). The operation of pattern separation and pattern completion processes associated with different attributes or domains of memory. *Neuroscience & Biobehavioral Reviews, 37*, 36–58. http://dx.doi.org/10.1016/j.neubiorev.2012.09.014.
Kheirbek, M. A., Klemenhagen, K. C., Sahay, A., & Hen, R. (2012). Neurogenesis and generalization: A new approach to stratify and treat anxiety disorders. *Nature Neuroscience, 15*, 1613–1620. http://dx.doi.org/10.1038/nn.3262.
Leutgeb, S., & Leutgeb, J. K. (2007). Pattern separation, pattern completion, and new neuronal codes within a continuous CA3 map. *Learning & Memory, 14*, 745–757. http://dx.doi.org/10.1101/lm.703907.
O'Reilly, R. C., & Rudy, J. W. (2001). Conjunctive representations in learning and memory: Principles of cortical and hippocampal function. *Psychological Review, 108*, 311–345. http://dx.doi.org/10.1037/0033-295X.108.2.311.
Osan, R., Tort, A. B., & Amaral, O. B. (2011). A mismatch-based model for memory reconsolidation and extinction in attractor networks. *PLoS One, 6*, e23113.
Pedreira, M. E., Pérez-Cuesta, L. M., & Maldonado, H. (2004). Mismatch between what is expected and what actually occurs triggers memory reconsolidation or extinction. *Learning & Memory, 11*, 579–585.
Ramirez, S., Liu, X., Lin, P.-A., Suh, J., Pignatelli, M., Redondo, R. L., ... Tonegawa, S. (2013). Creating a false memory in the hippocampus. *Science, 341*, 387–391. http://dx.doi.org/10.1126/science.1239073.
Roediger, H. L., & Karpicke, J. D. (2006). Test-enhanced learning taking memory tests improves long-term retention. *Psychological Science, 17*, 249–255. http://dx.doi.org/10.1111/j.1467-9280.2006.01693.x.
Rudy, J. W., & O'Reilly, R. C. (1999). Contextual fear conditioning, conjunctive representations, pattern completion, and the hippocampus. *Behavioral Neuroscience, 113*, 867–880. http://dx.doi.org/10.1037/0735-7044.113.5.867.
Sahay, A., Scobie, K. N., Hill, A. S., O'Carroll, C. M., Kheirbek, M. A., Burghardt, N. S., ... Hen, R. (2011). Increasing adult hippocampal neurogenesis is sufficient to improve pattern separation. *Nature, 472*, 466–470. http://dx.doi.org/10.1038/nature09817.
Sevenster, D., Beckers, T., & Kindt, M. (2012). Retrieval per se is not sufficient to trigger reconsolidation of human fear memory. *Neurobiology of Learning and Memory, 97*, 338–345. http://dx.doi.org/10.1016/j.nlm.2012.01.009.
Sevenster, D., Beckers, T., & Kindt, M. (2013). Prediction error governs pharmacologically induced amnesia for learned fear. *Science, 339*, 830–833. http://dx.doi.org/10.1126/science.1231357.
Sevenster, D., Beckers, T., & Kindt, M. (2014). Prediction error demarcates the transition from retrieval, to reconsolidation, to new learning. *Learning & Memory, 21*, 580–584. http://dx.doi.org/10.1101/lm.035493.114.
Tazir, B., Khan, M., Mombaerts, P., & Grosmaitre, X. (2016). The extremely broad odorant response profile of mouse olfactory sensory neurons expressing the odorant receptor MOR256-17 includes trace amine-associated receptor ligands. *European Journal of Neuroscience, 43*, 608–617. http://dx.doi.org/10.1111/ejn.13153.
Wiltgen, B. J., & Silva, A. J. (2007). Memory for context becomes less specific with time. *Learning & Memory, 14*, 313–317. http://dx.doi.org/10.1101/lm.430907.
Zhou, Y. L., & Riccio, D. C. (1994). Pretest cuing can alleviate the forgetting of contextual stimulus attributes. *Learning and Motivation, 25*, 233–244. http://dx.doi.org/10.1006/lmot.1994.1013.