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Using acute stress to improve episodic memory: The critical role of contextual binding

Matthew A. Sazma[a,*], Andrew M. McCullough[a], Grant S. Shields[a], Andrew P. Yonelinas[a,b]

[a] Department of Psychology, University of California, Davis, CA 95618, USA
[b] Center for Mind and Brain, University of California, Davis, CA 95618, USA

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ABSTRACT

Previous research has shown that encountering a brief stressor shortly after learning can be beneficial for memory. Recent studies, however, have shown that post-encoding stress does not benefit all recently encoded memories, and an adequate theoretical account of these effects remains elusive. The current study tested a contextual binding account of post encoding stress by examining the effect of varying the context in which the stressor was experienced. Participants encoded a mixture of negative and neutral images, immediately followed by a stressor (i.e., socially evaluated cold pressor) or a non-stress control task. Half of the participants received the stress/control manipulation in the same context as the study materials and half were moved to another context (i.e., a different room with a different experimenter). Two days later all participants returned to the original study room and received a recognition memory test. The results indicated that stress increased recognition memory only when the stressor occurred in the same context as the study materials, whereas stress did not benefit memory if the stressor occurred in a different context. Moreover, stress related increases in salivary cortisol were related to increases in memory when the stressor occurred in the same context as the study materials but not when the context changed. Similar effects were observed for negative and neutral materials and for males and females. These results are consistent with a contextual binding account and suggest that stress acts on memory by enhancing the encoding of the ongoing context of the stressor which benefits memory for the immediately preceding events that share the same context.

1. Introduction

Once an event has been encoded into memory, is there anything that can be done to strengthen that memory? A number of studies have shown that inducing a brief period of physical or social stress shortly after learning can be beneficial for memory (Beckner, Tucker, Delville, & Mohr, 2006; Cahill, Gorski, & Le, 2003; McCullough & Yonelinas, 2013). For example, in a classic study by Cahill et al. (2003), subjects were presented with a series of slides, and this was followed either by a non-stressful control task (i.e., holding their arm in lukewarm water), or a stressful cold pressor task (i.e., holding an arm in ice water) which produced a significant increase in the endogenous stress hormone cortisol. When recall for the slides was tested one week later, subjects who were stressed after encoding remembered significantly more information about the studied slides than did the non-stressed subjects. The beneficial effect of post encoding stress on episodic memory has now been well established in studies of both recall and recognition (For reviews see: Shields, Sazma, McCullough, & Yonelinas, 2017; Wolf, 2009).

Since the stress manipulation occurs after the study event in these paradigms, one potential explanation of these results is that stress may facilitate a consolidation process whereby newly encoded memories undergo a stabilization process that is essential for establishing long-term representations (McGaugh, 2000; Müller and Pilzecker, 1900). However, another potential explanation is that post encoding stress produces a salient episodic memory that benefits memory for items sharing the same context (i.e., a 'contextual binding' account). The idea is that a stressful event will lead to the formation of a particularly salient episodic memory, which will include information about the stressor and about the ongoing physical and mental context. To the extent that materials studied just prior to the stressor share the same context as the stressor, they will benefit by the strengthened context information produced by the encoding of the stressor. Thus, in episodic memory tests such as recall and recognition in which subjects are required to remember if items were presented in a particular experimental context (i.e., "Was this item presented in the earlier study list?"

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[*] Corresponding author.
E-mail address: msazma@ucdavis.edu (M.A. Sazma).

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or "Recall the items that were presented in the earlier study list."), stress will improve memory for items that were encoded just prior to the stressful event because they share a very similar strongly encoded context. Thus, contextual binding can explain why post-encoding stress improves memory relative to a non-stress control condition. If this account is correct, then if the context were to change dramatically between the presentation of the study items and the occurrence of the stressor, the studied items would no longer share a context with the stressor and so the beneficial effects of stress should be reduced. In fact, to the extent that the stressor reminds the subjects of a context that is substantially different from that of the study context, stress may even lead to a decrement in memory for the study items.

The contextual binding hypothesis has never been directly tested, but there is some indirect evidence supporting this idea. For example, in a recent study we found that post-encoding stress led to a significant decrease, rather than an increase, in recognition memory (McCullough, Ritchey, Ranganath, & Yonelinas, 2015). The study used test procedures that had previously been shown to lead to significant post-encoding stress benefits in memory (e.g., McCullough & Yonelinas, 2013), so the results were somewhat surprising. However, this study was unusual in that subjects were moved to another room to complete the stress/control manipulation after learning, rather than receiving the stress manipulation in the same room as the study phase. One other study also failed to find a stress benefit in memory and they also had subjects move to another room to receive the stress/control manipulation (Trammell & Clore, 2014). Additionally, a recent meta-analysis suggested that post-encoding stress generally improved memory in studies in which the study materials were presented in the same room as the stressor manipulations, whereas stress led to a small decrease in memory in studies in which subjects changed rooms between the study phase and the stress manipulation (Shields et al., 2017). Although there are various procedural differences across these studies that could account for the differing results, the results are consistent with the idea that stress-related benefits in memory may rely on shared context. In addition, it is well established that changing the context in which materials are studied and tested generally reduces episodic memory (e.g., Godden & Baddeley, 1975), and these context switching effects have been found to be reduced if stress occurs prior to encoding or prior to retrieval (Schwabe, Böhringer, & Wolf, 2009; Schwabe & Wolf, 2009). Although the latter studies did not examine the effects of varying the context in which the stressor occurred, they do point to the importance of context in leading to other stress-related effects on memory.

In the current study, we tested the contextual binding notion by contrasting the effects of post-encoding stress when the stress/control manipulation occurred in the same context as the study materials, to conditions where the stress/control manipulation occurred in a different context, while keeping other aspects of encoding and retrieval identical between groups. This allowed us to determine whether the context of the stressor itself plays a causal role in producing post-encoding stress enhancements of memory. In addition, we included both negative and neutral materials to assess whether any potential context effects might be modulated by the emotionality of the materials. Although some previous studies have suggested that the post-encoding stress benefits on episodic memory are larger for negative than neutral materials (Cahill et al., 2003), other studies have found similar effects for negative and neutral materials (Andreano & Cahill, 2006; McCullough & Yonelinas, 2013; Preuss & Wolf, 2009; Yonelinas, Parks, Koen, Jorgenson, & Mendoza, 2011). On the basis of prior work, we expected that overall memory would be better for negative than neutral materials (for a review, see Kensinger, 2009), and that stress would benefit memory for both negative and neutral materials, but we did not have any a priori predictions about whether context changes would differentially impact the stress effects on negative and neutral materials.

In addition, we measured salivary cortisol before and after the stressor to verify that the stress manipulation led to a significant increase in this stress related hormone. Cortisol is a well-validated way to measure the stress response and is thought to play a key role in the effects of stress and memory (e.g., Roozendaal, 2002). Cortisol levels are highest in the morning and naturally drop throughout the day, unless a sufficiently stressful even is encountered to raise cortisol levels (Baum & Grunberg, 1995). We also wanted to determine if the stress effects on memory were related to the extent that individuals showed a cortisol increase, as has been reported in some previous work (e.g., Andreano & Cahill, 2006; McCullough & Yonelinas, 2013). In addition, we examined both males and females to determine if the effects generalized across both groups, as some studies have indicated that stress effects on memory may be more robust in males (McCullough et al., 2015; Yonelinas et al., 2011). Finally, we assessed memory using a recognition test in which subjects made a 'remember' response if they could recollect qualitative information about the specific study event in which the item was earlier presented, and they rated their confidence on a 1–5 scale for the non-recollected items. The method was used to assess memory sensitivity across levels of response bias, and to separate recollection from familiarity-based responses (Yonelinas, 2002). Prior work has indicated that post encoding stress can benefit both recollection (McCullough et al., 2015; Smeets, Otgaar, Candel, & Wolf, 2008) and familiarity (McCullough & Yonelinas, 2013; Yonelinas et al., 2011), but whether these effects are dependent on the context of the stressor is unknown.

2. Method

2.1. Participants

157 (69 male) undergraduates (average age = 19.9, age did not differ between groups, $p > .5$) from UC Davis gave informed consent and participated for course credit. Subjects were excluded if they were left-handed, smoked, used anti-depression or anti-anxiety medications. Additionally, participants were excluded if they were using hormonal contraceptives or currently in menses, based on a meta-analysis which found cortisol responses to stress were larger in studies that excluded these participants (Shields et al., 2017). Additionally, participants were e-mailed the day before the study and instructed to avoid eating for 1 h before the study and to avoid alcohol, caffeine, and more than 30 min of cardiovascular exercise for 4 h before the study. Fourteen of the participants could not be included in the analysis because they did not attend the second session when the memory test occurred (one of these participants had an adverse reaction to the socially evaluated cold pressor task, and another withdrew after seeing the negative stimuli). In addition, one participant was excluded due to a computer malfunction, and 11 participants were excluded for failing to complete at least 30 s of the cold pressor task (CPT). The final sample consisted of 34 Same Context Control (16 Male), 33 Same Context Stress (14 Male), 34 Different Context Control (15 Male), & 30 Different Context Stress (15 Male). All procedures were approved by the University of California Davis Institutional Review Board.

2.2. Stimuli

We used a set of 368 pictures (8 pictures for practice) used in previous research (McCullough et al., 2015; McCullough & Yonelinas, 2013); half of these pictures were negative and half were neutral. The photoset used in the current study has been used extensively in previous stress and memory research (McCullough et al., 2015; McCullough & Yonelinas, 2013; Sharot, Delgado, & Phelps, 2004; Sharot & Yonelinas, 2008; Yonelinas et al., 2011). The images were selected from the International Affective Photo Series (Lang, Bradley, & Cuthbert, 2008; IAPS), but were supplemented with additional images in order to equate the negative and neutral images for the presence of humans and differences in visual complexity. Subjective ratings of valence and arousal (Sharot et al., 2004) indicated that the neutral photos were rated as neutral ($M = 3.75$, $SD = 1.07$, on a 9-point scale) and emotional photos as negative ($M = 7.69$, $SD = 0.52$); $t(10) = 14.23$, $p < .0001$. In addition, neutral photos had lower arousal ratings ($M = 3.03$, $SD = 0.83$), than emotional photos ($M = 6.79$, $SD = 1.15$); $t(11) = 10.67$, $p < .0001$. Images were approximately 315 square pixels with minor variations of this size. Participants encoded 120 pictures (60 negative), and at retrieval, participants were presented with all 120 studied pictures, along with 120 new pictures (60 negative). In total participants saw a subset of 240 pictures from the set of 360 (as well as 8 pictures for practice). Stimuli were counterbalanced across subjects.

2.3. Procedure

Participants were tested individually between the hours of 9am-5 pm. After arriving, participants had a 5-minute acclimation period where they filled out informed consent, basic demographics forms, and then relaxed until the first task. Participants then incidentally encoded 120 pictures (60 negative and 60 neutral) and rated each one for visual complexity on a 1–6 scale. Participants were told to make their best subjective judgment about how "busy" or complex the pictures appeared, without any further guidance. This task was intended to ensure that participants attended to each image, and these complexity ratings were not analyzed. Pictures were presented in a random order for 800 ms each, followed by a 2 s blank period for participants to make their complexity rating. There was then a 500 ms inter-trial interval. These timings were based on prior studies using these materials to lead to memory performance that avoids floor and ceiling effects (McCullough et al., 2015; McCullough & Yonelinas, 2013). After this encoding period, participants had 10 min where they either stayed in the same context with the same experimenter or changed contexts. Context was manipulated by changing both the physical and mental context. Participants in the different context condition were informed they were going to be participating in a separate study for the remainder of the study time, and were walked outside by the experimenter and introduced to another experimenter, then led inside the adjacent building. The starting room was counterbalanced, and the testing rooms differed in several ways. One room was larger and rectangular in shape, had yellow walls, contained 4 computers on one long desk separated by dividers, and had tile flooring. The other room was square in shape, had white walls, contained 2 separate desks with computers, and had carpeted flooring.

This 10-minute transition period also included time to complete short sleep and food surveys, basic medical questions, and pre-stress anxiety and nervousness questions. The questionnaires and an initial saliva sample were followed by either the stress or the control task. The stress task was a socially evaluated cold pressor task (Schwabe, Haddad, & Schachinger, 2008) where participants were told to submerge their non-dominant arm in ice water (0–3 °C) for 3 min, or as long as they could stand, and they were told they were being recorded by a webcam and the experimenter would be evaluating their facial expressions as they completed the task. The experimenter remained standing with a clipboard and pen to simulate evaluation, but the webcam was not actually recording their expressions. In the control task participants submerged their non-dominant arm in room temperature water for 3 min (19–22 °C), without any mention of facial expression evaluation, and no clipboard was used to simulate evaluating the participants.

Participants then dried off their arms and completed a post-stress questionnaire in which they rated their levels of anxiety and nervousness. A second saliva sample was then taken (approximately 15 min after the end of the stress task). For the time between the questionnaire and the saliva sample, and for a similar period immediately after the saliva sample, all subjects were engaged in an 8 min block of an unrelated working memory change detection task (i.e., one block included pairs of houses and another included colored squares). The results of the filler tasks are not related to the current study and will be reported in a subsequent paper.

Participants returned 48 h after starting the first session, and again acclimated to the lab for 5 min before beginning the free recall memory task. In the recall test, participants were given 10 min to write down descriptions of as many of the pictures as they could; participants were encouraged to write as many details as possible and to try for the entire 10 min even if they thought they could not remember any more items. Since there were so many items presented with a very brief encoding time, free recall performance was very low (~8%), and so we focus on the recognition memory results. Following free recall, a recognition memory test was given where participants saw all 120 studied pictures, along with 120 new pictures. They were instructed to rate their memory on a "1–5 or recollect scale". Recollect meant that participants could remember an associated detail from the study event. If they were unable to recollect details of studying the picture, they were instructed to use the 1–5 confidence scale where 1 indicated that they were sure it was new and 5 indicated that they were sure it was old. Each picture was presented on the screen for 1500 ms, but the confidence scale stayed on the screen until a response was made. There was a 500 ms inter-trial interval after each response.

2.3.1. Analysis of salivary cortisol

Two saliva samples (pre- and post-stress manipulation) were collected from each participant using the passive drool method. Participants were given a piece of Trident original sugar-free gum to aid in saliva production. After collection, samples were frozen at −20 °C until analysis. All saliva analysis took place after data collection, so samples were stored between 1 and 8 months. Saliva samples were assayed in duplicate using Salivary Cortisol ELISA Kits (Salimetrics LLC, State College, PA) according to manufacturer instructions. The sensitivity of the assay kit is 0.193 nmol/L. Five participants' cortisol concentrations were too low at one or both time points to be accurately measured, and their cortisol data were excluded. The inter-assay CV was 13.11% and the average intra-assay CV was 3.23%. All cortisol concentration measurements were converted to nmol/L to be consistent with the literature. To calculate cortisol change, we subtracted measured cortisol at time 1 (baseline) from measured cortisol at time 2 (15 min post-stress).

2.3.2. Analysis of memory

Recognition memory performance was measured by calculating d' based on hits and false alarms (i.e., R, 5, 4 and 3 responses for old and new items respectively) for each participant (Macmillan & Creelman, 2004). In addition, participants' confidence judgments were also used to plot Receiver Operating Characteristics (ROCs) with cumulative hit rates plotted on the y-axis and false alarm rates on the x-axis. Estimates of recollection and familiarity were calculated for each participant by fitting a dual-process signal detection model to their observed data and minimizing the sum of squared errors (Yonelinas, 1994). The parameter estimate of recollection corresponds to the point at which the ROC crosses the y-axis, and represents the proportion of items recollected. The parameter estimate of familiarity is based upon d', but using all confidence ratings rather than just the midpoint (for the exact equations used, see Yonelinas, 1994). All memory measures were tested with separate 3-way mixed ANOVAs with stress and context as between-subject factors and emotion as a within-subject factor. For correlations between cortisol change and recollection, we calculated Pearson's R between individual participants' recollection estimate and their cortisol change from time 1 to time 2. We excluded 4 participants as outliers (2 for being more than 3 SD's higher for cortisol change, and 2 for being more than 3 SD's higher for recollection than the mean). Including these outliers in the analysis slightly increased the observed correlation in the same context condition, and did not change the relationship in the different context.

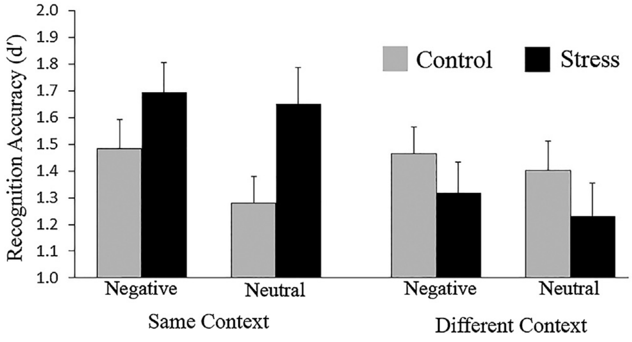

Fig. 1. Recognition memory performance for negative and neutral materials. When the stressor occurred in the same context as learning, stress benefited memory, whereas when the stressor occurred in a different context there was no benefit of stress on memory.

3. Results

Using G*Power (Version 3.1.9.2; Faul, Erdfelder, Buchner, & Lang, 2007), we estimated that with a total sample of 128 participants, we would have 80% power to detect a medium interaction effect, $f = 0.25$, given an α level of 0.05. Therefore, we targeted a final sample size of approximately 130 usable participants.

An examination of recognition accuracy (i.e., sensitivity measure *d'*; Macmillan & Creelman, 2004) indicated that context and stress interacted ($F(1,127) = 5.26$, $p = .023$, $\eta_p^2 = 0.04$), such that changing the context of the stressor significantly altered the effects of stress on memory performance (Fig. 1). This reflected the fact that in the same context condition, stress increased memory ($t(65) = 2.15$, $p = .036$, $d = 0.52$), whereas when the context of the stressor was different from learning, stress led to a numerical, but not statistically significant decrease in recognition ($t(62) = -1.08$, $p = .28$, $d = 0.30$). There was a main effect of emotion, indicating recognition memory was better for negative than neutral items ($F(1,127) = 7.44$, $p = .007$, $\eta_p^2 = 0.055$), but there were no other significant main effects or interactions (all p's > 0.13), indicating similar effects of stress for both negative and neutral items.

We then examined whether gender altered the observed stress by context interaction. Performing the ANOVA with gender included as an additional factor revealed no significant differences in the effects observed in males and females (Stress*Context*Sex interaction $p > .8$, see Table 1). Additionally, performing a 3-way ANCOVA with time of day as a covariate (Baum & Grunberg, 1995) did not impact the significant Stress*Context interaction ($F(1,126) = 6.10$, $p = .015$, $\eta_p^2 = 0.045$).

Several additional analyses were conducted to further characterize the observed memory effects. First, rather than assessing sensitivity using a single point measure of d' we examined area under the curve (AUC) to incorporate performance across all confidence ratings. As can be seen in Fig. 2, in the same context condition performance was higher for the stress than control conditions whereas the effect reverses in the different context condition across levels of response confidence. This was reflected in a significant context by stress interaction ($F(1,127) = 5.02$, $p = .027$, $\eta_p^2 = 0.038$). Moreover, when scoring only the most confidently recognized items (i.e., those where participants reported having recollected detailed episodic memory for the item), context and stress interacted ($F(1,127) = 5.94$, $p = .016$, $\eta_p^2 = 0.045$), indicating that stress benefitted recollection in the same context ($t(65) = 2.54$, $p = .014$), but not when stress occurred in a different context ($t(62) = -0.91$, $p = .37$). We also examined responses that were made when participants lacked detailed episodic memory (i.e., recognition in the absence of recollection). In this case, the interaction of context and stress was not significant ($F(1,127) = 1.61$, $p = .21$, $\eta_p^2 = 0.012$), suggesting that it is primarily recollection rather than

Table 1
Various memory measures (d', Recollection, Familiarity) for each experimental group (Stress*Context), split by gender (Male or Female in each row) and by item valence (Negative or Neutral in each column). Standard errors of the mean (SEM) are in parenthesis. See the method section for more details on how the memory scores were calculated.

	d' Negative Items	d' Neutral Items	Recollection Negative Items	Recollection Neutral Items	Familiarity Negative Items	Familiarity Neutral Items	Area Under Curve Negative Items	Area Under Curve Neutral Items
Same Context Control - Female	1.39 (0.52)	1.13 (0.40)	0.12 (0.22)	0.12 (0.20)	1.31 (0.50)	1.10 (0.76)	0.803 (0.024)	0.766 (0.021)
Same Context Control - Male	1.58 (0.76)	1.44 (0.74)	0.13 (0.18)	0.11 (0.20)	1.40 (0.76)	1.29 (0.62)	0.812 (0.029)	0.787 (0.031)
Same Context Stress - Female	1.51 (0.61)	1.58 (0.78)	0.19 (0.14)	0.16 (0.17)	1.41 (0.73)	1.44 (0.55)	0.830 (0.027)	0.826 (0.029)
Same Context Stress - Male	1.94 (0.65)	1.75 (0.79)	0.34 (0.22)	0.25 (0.11)	1.47 (0.68)	1.20 (0.62)	0.868 (0.024)	0.808 (0.027)
Different Context Control - Female	1.44 (0.46)	1.46 (0.60)	0.21 (0.14)	0.20 (0.16)	1.22 (0.56)	1.22 (0.39)	0.816 (0.017)	0.811 (0.019
Different Context Control - Male	1.50 (0.73)	1.33 (0.68)	0.23 (0.18)	0.18 (0.10)	1.35 (0.72)	1.28 (0.70)	0.826 (0.024)	0.797 (0.025)
Different Context Stress - Female	1.24 (0.67)	1.16 (0.65)	0.17 (0.18)	0.17 (0.16)	1.12 (0.73)	0.95 (0.89)	0.784 (0.028)	0.752 (0.030)
Different Context Stress - Male	1.40 (0.60)	1.31 (0.70)	0.22 (0.25)	0.13 (0.24)	1.19 (0.65)	1.18 (0.55)	0.801 (0.025)	0.767 (0.031)

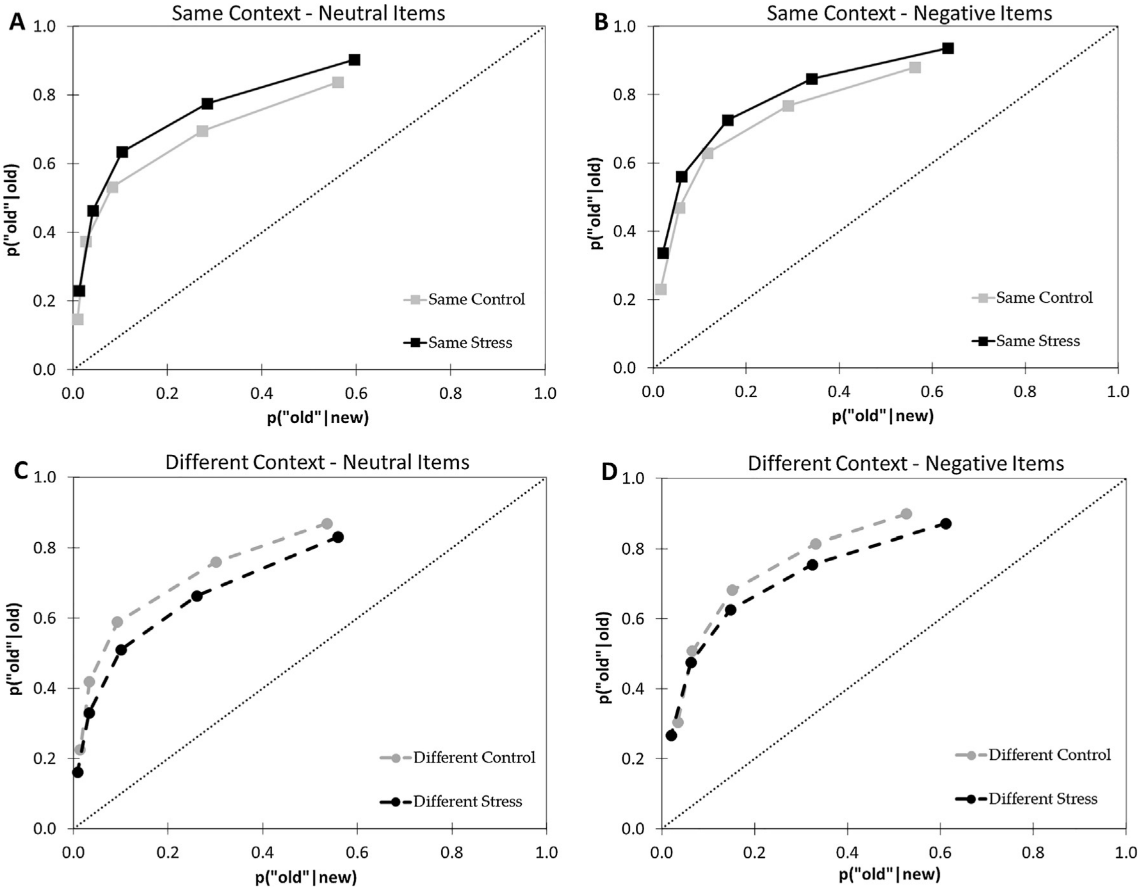

Fig. 2. Recognition memory ROCs for the stress and non-stress control groups, for neutral (left panels) and negative items (right panels), when the stressor occurred in the same context as the study materials (top panels) or in a different context (bottom panels). Stress improved memory only when it occurred in the same context as the study materials.

familiarity that was affected by stress and context.

Salivary cortisol measured prior to the stress manipulation was similar for the stress and control groups ($M = 8.22$ nmol/L and $M = 7.23$ nmol/L, respectively, $p = .33$), whereas after the stress manipulation, cortisol was significantly higher in the stress than the control condition ($M = 13.67$ nmol/L and $M = 5.76$ nmol/L, respectively, $p < .001$), indicating that the stress manipulation led to the expected increase in cortisol. In addition, the context change did not interact with stress ($p = .88$), indicating that the cortisol reactivity for groups depended on the stress condition, and not on the context condition. Calculating Pearson's R correlation, change in salivary cortisol from time 1 (baseline) to time 2 (15 min post-stressor) was positively correlated with individuals estimates of recollection ($r(66) = 0.44$, $p < .001$), but only for individuals in the same context condition. For subjects in the different context conditions, there was no significant relationship between changes in cortisol and recollection ($r(61) = -0.02$, $p = .86$, see Fig. 3). These results indicate that although stress led to increases in cortisol for both context groups, this was related to an increase in recollection only when the stressor occurred in the same context as the learning materials. A similar, but only marginally significant effect was observed when correlating cortisol change with d'. Specifically, if stress occurred in the same context, changes in cortisol were positively related to d' ($r(66) = 0.23$, $p = .07$), but if stress occurred in a different context, cortisol change was not related to d' ($r(61) = -0.11, p = .39$). We also examined the correlation between cortisol change and familiarity and found no effects for either context condition (p's > 0.5).

4. Discussion

The current results show that the beneficial effects of post encoding stress are critically dependent on the context of the stressor, such that stress leads to an increase in recognition memory when the stressor occurs in the same context as the study materials, whereas it leads to a slight (non-significant) decrease in memory when the stressor occurs in a different context. These results provide a key to understanding why post-encoding stress benefits have been reported on some studies but not others. Most of the prior studies that found that post-encoding stress benefitted memory had the stressor occur in the same context as the studied materials (e.g., Beckner et al., 2006; Cahill et al., 2003; Felmingham, Tran, Fong, & Bryant, 2012; Smeets, Sijstermans, et al., 2008). Many of the earlier studies that did not find beneficial effects of stress inadvertently introduced the stressor in a different context from the learning materials (McCullough et al., 2015; Trammell & Clore, 2014). Although these across-experimental differences could have been produced by any number of procedural differences, the current study holds all other factors constant, demonstrating that maintaining the same context between study and stress is essential in order to observe the beneficial effects of post-encoding stress. In addition, the current results indicate that the context effects were quite general in the sense that they were observed for both negative and neutral materials, and for both males and females. A similar pattern was observed when examining changes in cortisol across individuals. When stress occurred in the same context as the study materials, subjects who showed a larger cortisol increase showed greater recollection, whereas in the different context condition, cortisol increases were no longer related to recollection.

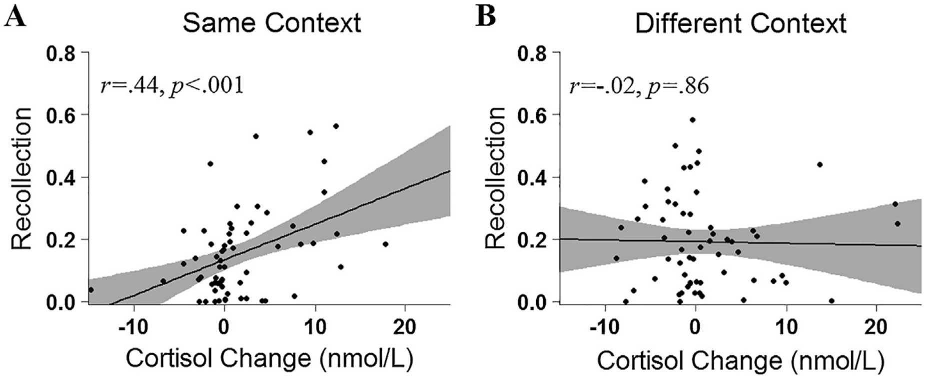

Fig. 3. Correlation between participants' cortisol change and recollection scores. Panel A shows a significant correlation between recollection and cortisol change when stress occurred in the same context as learning, while panel B shows no relationship when context was changed between learning and stress.

The current results are consistent with the predictions of the contextual binding account of post-encoding stress which proposes that the stressor itself serves as a memorable event that benefits memory for the earlier encoded items because they share a similar context. Critically, as predicted by this account when the context of the stressor is no longer the same as that of the studied items the stress benefit was eliminated. In fact, the numerical reduction in memory in the different context condition could have arisen because the stressor effectively strengthened a context that was different from the study list.

Although the current results lend support to the contextual binding account, future studies will be important in testing this account further. For example, the account may prove useful in helping to understand the effects of pre-encoding stress on memory. That is, when acute stress occurs prior to encoding, some studies show that this benefits episodic memory (e.g., Henckens, Hermans, Pu, Joels, & Fernandez, 2009; Hoscheidt, Labar, Ryan, Jacobs, & Nadel, 2013; Smeets, Giesbrecht, Jelicic, & Merckelbach, 2007), whereas others have found that it reduces memory (Maheu, Collicutt, Kornik, Moszkowski, & Lupien, 2005; Taverniers, Taylor, & Smeets, 2013; Wirkner, Weymar, Löw, & Hamm, 2013), but the reason for this discrepancy is not yet clear. One possibility is that the pre-encoding effects of stress may also be dependent on contextual binding. That is, to the extent that stress strengthens contextual binding, this would also be expected to benefit memory for items encoded immediately after the stressor (in addition to the benefit for items encoded prior to stress as seen in the current study). In fact, several studies in which the stressor occurred immediately prior to the encoding phase have reported increases in memory (e.g., Wiemers, Sauvage, Schoofs, Hamacher-Dang, & Wolf, 2013; Zoladz et al., 2011), whereas several other studies in which the stressor occurred much earlier than the study items reported decreases in memory (e.g., Taverniers et al., 2013; Zoladz et al., 2011). One potential account of these results is that increases in the delay between the stressor and the study items reduces the similarity of the study and the stressor contexts, thus reversing any beneficial effects of stress.

In addition, the contextual binding account may also be useful in helping to understand results from rodent studies of post-encoding stress and memory. For example, a number of studies have examined the effects of post encoding stress on object recognition and maze learning tasks, and have generally reported that stress leads to a decrease, rather than an increase, in memory (e.g., Guercio et al., 2014; Kogan & Richter-Levin, 2010; Li, Fan, Wang, & Tang, 2012; Maroun & Akirav, 2008). Why the results from rodent studies differ from those of humans is not clear, but one noticeable difference between the rodent studies and those of human subjects is that in all of the published rodent studies that we are aware of, the animals were removed from the learning environment in order to complete the stress manipulations. Thus, those studies may be similar to the 'different context' condition in the current study. Future studies that look to see if stress may benefit memory in rodents when the context is held constant would serve as an important test of the contextual binding hypothesis.

An open question is whether the context binding account is useful in accounting for stress effects on other forms of memory such as fear conditioning and avoidance learning where the encoded materials themselves are highly stressful. Those types of paradigms have been used quite extensively in behavioral and pharmacological studies of rodents and have strongly suggested that those memory benefits may reflect a strengthened consolidation process. The initial stressful event leads to a cascade of hormones (including corticosterone, the rodent equivalent of cortisol) that is thought to alter long-term potentiation to benefit memory (e.g., McGaugh, 2000; Roozendaal, 2002). Although some recent studies have indicated that the effects in those studies can be sensitive to contextual manipulations such as habituation (e.g., Roozendaal, Okuda, Van der Zee, & McGaugh, 2006), as far as we know no studies have directly manipulated the stressor context.

The current results extend work indicating the importance of physical and mental context in determining the effects of stress on memory during encoding and retrieval. For example, when stress is experienced during memory retrieval, it generally results in a decrease in memory performance (for a review see Wolf, 2009), but this decrement is eliminated if a distinctive learning context is reinstated at test (Schwabe & Wolf, 2009). Moreover, stress experienced prior to encoding reduces the facilitative effects of reinstating a distinctive context during retrieval (Schwabe et al., 2009). Based on these types of results it has been suggested that stress impacts frontally-mediated attentional processes involved in effective encoding as well as executive control processes engaged during memory retrieval (Gagnon & Wagner, 2016; Joëls, Pu, Wiegert, Oitzl, & Krugers, 2006; Shields, Sazma, & Yonelinas, 2016). The current results extend this work by showing that the context in which the stressor occurs plays an essential role in producing stress effects, even if stress occurs after the learning event. Future work will be needed to determine the neural processes underlying these effects, but we propose that post-encoding stress benefits newly encoded memories by enhancing the binding of mental and physical context with the stressful event. This indirectly improves memory for other events that occur in a similar context. Presumably, this acts in part through the increase in cortisol, which may focus attention through the frontally-mediated attentional network, as well as facilitating medial temporal lobe regions critical for associating the objects encountered within an event to the ongoing context (Diana, Yonelinas, & Ranganath, 2007; Howard & Kahana, 2002).

While the current study reveals a critical role of context in stress effects on memory, the specific aspects of context that are most important are not yet known. Changes in the physical environment such as spatial location likely play a critical role (the meta-analysis by Shields et al., 2017 used spatial context change when finding the significant effects of context), but other aspects of context, such as the presence of different people (social context), as well as accompanying changes in emotional and cognitive states (mental context) may also play an important role (Newtson & Engquist, 1976; Zacks et al., 2001). Future work should address these questions. Moreover, the use of post-encoding stress has been applied in educational settings to enhance learning (Nielson & Arentsen, 2012), and pharmacological interventions targeting the stress system have been useful in clinical settings—such as helping patients suffering from post-traumatic stress disorder (Steckler & Risbrough, 2012). The current results suggest that the effectiveness of these interventions may critically depend on when and where the stress related manipulations occur, although the exact relationship between context and a chronic stressor such as post-traumatic stress disorder remains to be elucidated.

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Author contributions

M. Sazma, A. McCullough, & A. Yonelinas were responsible for study design. M. Sazma & A. McCullough were responsible for data collection. M. Sazma was responsible for data analysis. G. Shields, M. Sazma, A. McCullough were responsible for analyzing cortisol data. All authors contributed to the manuscript.

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