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Post-learning stress reduces the misinformation effect: effects of psychosocial stress on memory updating

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ABSTRACT

Episodic memories can be modified when exposed to new and related information. This phenomenon, known as memory updating, is generally thought to be adaptive but can also lead to incorporating false information into a memory trace. Given the well-known effects of stress on episodic memory, we used a false information paradigm to investigate if acute stress during memory updating (i.e., post-learning stage) affected false memory formation. In a between-subject design, young healthy participants completed the initial phases of the misinformation experiment - they studied an event via a slideshow and then were exposed a related narrative that contained misleading information about that event. After, half of the participants were exposed to acute psychosocial stress and the other half completed a control task. Once stress levels returned to baseline, all of the participants completed the final phase of the experiment, which was a memory test for slideshow that included items containing true facts and misinformation. Participants in the stress condition showed a reduced misinformation effect and were better able to discriminate true from false information compared to control participants. This pattern of results held even when participants were tested on the same memory test after a multiple day delay, illustrating the long-lasting effects of stress on false memory formation specifically, and memory updating generally. We discuss how our results add to the understanding of the time-dependent factors that moderate stress effects on memory, and speculate how stress effects on memory updating can be positive, by limiting intrusions into encoded events, but also negative, by limiting the ability to integrate information with other concepts, harming memory generalization.

1. Introduction

Episodic memory representations can be altered after learning new and related information (for a review: Lee et al., 2017). This characteristic of memory can be viewed as adaptive because it allows encoded memories to be modified and updated with relevant information (Nader and Hardt, 2009; Schacter et al., 2011). However, it can also lead to distortions, causing false memories. One of the most prominent presentations of memory distortion is the misinformation effect, when misleading information presented after an event changes the memory of that original event (Loftus, 2005). One view is that the misinformation effect arises from memory updating mechanisms that will integrate newly learned (mis)information into the original memory representation (Loftus et al., 1985). Research indicates that memory updating is susceptible to the effects of stress, but that the nature of these effects depend on when the stress is induced (Dongaonkar et al., 2013). From these findings, we reasoned that stress will affect false memory formation in a similar time-dependent manner. Here, we tested the effects of inducing stress during a post-learning consolidation period on the misinformation effect (Loftus, 2005) – after both original and misleading memories have been formed. Based on the literature reviewed below, we test the specific hypothesis that stress during this stage of processing (i.e., consolidation) will reduce the ability to update and integrate memory representations of similar events, and thus will reduce the presence of memory intrusions.

Stress is a state in which situational demands are perceived to exceed one's personal resources to cope with the situation (Lazarus, 2006). Importantly stress has been shown to affect episodic memory processing mainly at the level of the hippocampus and prefrontal cortex (Bledowski et al., 2009; Nyberg et al., 2000). These brain areas are particularly sensitive to physiological responses of stress which include both, the fast-acting autonomic nervous system (ANS) response resulting in the release of catecholamines; and the slower acting hypothalamic-pituitary-adrenal (HPA) axis resulting in an increase of its

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downstream biomarker, the glucocorticoid hormone, cortisol (Johnson et al., 1992; Ulrich-Lai and Herman, 2009). These physiological responses determine the impact of stress at different stages of processing, namely encoding, consolidation, and retrieval (for reviews: Joëls et al., 2012; Schwabe et al., 2012). The ANS response is thought to enhance memory encoding, especially for arousing information (Kim and Diamond, 2002; Segal et al., 2012). The HPA too is thought to facilitate memory formation processes, in particular in the early stages of stress exposure, when the non-genomic glucocorticoid effects occur. At the same time glucocorticoids also suppress other cognitive operations such as memory retrieval, or the encoding of information not relevant to the stressful situation. With elapsing time however, genomic glucocorticoid actions set in which facilitate a memory storage mode that has a negative impact on encoding processes. This negative impact is particular robust during the later stages of a stressful experience (for reviews: McGaugh, 2015; Roozendaal, 2000; Schwabe, 2017).

There are indications that the negative impact of stress on hippocampus-mediated retrieval processes also impact memory consolidation and updating (i.e., re-consolidation) (for a review: Nader and Hardt, 2009). Early work has highlighted how this stress response can enhance the consolidation of episodic memories when induced post-learning (Roozendaal et al., 2006). Other work has suggested that stress placed during this post-learning consolidation period can influence memory updating by strengthening previously encoded memory traces. As an example, Bos et al. (2014) asked participants to learn a list of words, and after a delay, reminded participants of the words, so that the wordlist could be updated. The application of stress during this 'memory updating window' improved the later recall of the words. These results, and others of their kind, raise the rather paradoxical suggestion that the mechanisms of stress that reduce memory retrieval, can effectively enhance memory retrieval if applied during a post-learning consolidation period. Expanding this theory, some researcher have suggested that this effect of stress is due to the formation and maintenance of rigid memory traces that are not well integrated with other experiences and thus more resistant to updating (Dandolo and Schwabe, 2016).

There are still open questions about how stress affects this consolidation period that involves the integration of episodic memories with previously acquired information, which we refer to as updating. An effective tool to address this question is false memory experiments and particularly the misinformation experiment in which people are exposed to and often incorporate misleading information with a previously encoded event. To date, only a handful of studies have investigated the effects of acute stress with a misinformation experiment (e.g., Hoscheidt et al., 2014; Schmidt et al., 2013; Zoladz et al., 2017). One group that has studied stress with this paradigm induced stress before the beginning of the experiment, before participants encoded an to-be-recalled event that was presented in a slideshow and then exposed them to misinformation related to the slideshow two days later. When memory was later assessed, the authors found that the memories encoded under stress were recalled more accurately, however the endorsement of misinformation was not altered by stress (Hoscheidt et al., 2014). Another study conducted by Schmidt et al. (2013) induced stress after participants had encoded a to-be-remembered event (slideshow), but before they were exposed to the related (mis)information. When they assessed memory for the original slideshow event, stress induced at this time-point (i.e., encoding of misinformation) reduced the misinformation effect, such that participants who were under stress were less likely to confuse the (mis)information with the original encoded event.

To our knowledge, there are no studies that have looked at the effects of stress induction during a post-learning consolidation period of the misinformation experiment, during. What would happen if stress was induced during this period in which participants have already been exposed to both original event and misinformation? Based on the above-reviewed work, if stress impairs memory updating mechanisms when induced during this "post-learning consolidation" period, then the presence of stress at this time-point (i.e., consolidation) should reduce false memory formation by limiting how new information is integrated (i.e., updated) within an encoded memory (for a review: Nadel et al., 2012). In terms of the misinformation experiments used in the current study, this hypothesis leads to the prediction that acute psychosocial stress during a post-learning phase of the misinformation experiment will lead to a reduction in the misinformation effect.

2. Methods

2.1. Participants

Forty-six, healthy male university students (mean age of 21.89 years ± 2.97) participated in the current study. All participants were fluent in English and were free from factors that could affect stress reactivity (i.e., no previous exposure to the stress task, moderate alcohol (< 10 units per week) and tobacco consumption (< 5 cigarettes per day), no illicit drug use, and no endorsed symptoms of depression and/or anxiety). Participants provided informed consent prior to the study and were compensated 10$/hr. The study was approved by the McGill University Faculty of Science Institutional Review Board.

2.2. Experimental design

Participants were invited to the laboratory on two separate days, from herein referred to as "visit-1" and "visit-2," that occurred three days apart. Testing for both visits took place between 1 pm and 6 pm and in the same testing location. During visit-1, half of the participants were randomly assigned to the stress condition (TSST group) and the other half were assigned to the control condition (CTL group). As part of a larger testing battery, the experimental procedure of visit-1 began with a series of questionnaires, followed by the misinformation encoding phase, then the stress induction, and ended with a misinformation test phase. To test the endurance of the effects of acute stress on the long-term consolidation of misinformation, participants returned to the lab 3 days later for visit-2, during which they completed the same misinformation test phase as during visit-1. All tasks are described in further detail in the following sections. For a depiction of the experimental paradigm and timeline for visit-1, see Fig. 1.

2.3. Stress paradigm

Participants were assigned to either the Trier Social Stress Test (TSST; Kirschbaum et al., 1993) or a matched no-stress control task (CTL; Het et al., 2009). The TSST involves a mock-job interview; participants are given 10 min to prepare a speech to be given in front of a panel of expert judges. Following this anticipation period, participants perform a 5-minute speech task, followed by a 5-minute oral arithmetic task, in front of trained confederates (one male, one female). The TSST has been shown to reliably produce a significant increase in stress across a variety of markers: cortisol, ANS, and subjective stress (e.g., Ali and Pruessner, 2012; Dickerson and Kemeny, 2004; Goodman et al., 2017; Nater et al., 2005). The CTL condition involves similar procedures, but without the social evaluative component and thus does not elicit the psychological or biological stress response. Specifically, in the CTL condition, participants are led to an empty room and are instructed to talk about a recent event for 5 min and do simple arithmetic additions for another 5 min, in the absence of a committee or individual observers.

For both conditions, cortisol and salivary alpha amylase levels (sAA), an indirect marker of ANS activity (Nater et al., 2005), were collected via salivary samples to measure stress reactivity throughout this session. For each saliva sample, participants placed a cotton swab ("Salivette"; Sarstedt AG & Co, Nümbrecht, Germany) inside their mouth, for one minute. Cortisol levels (nmol/l) were measured using a

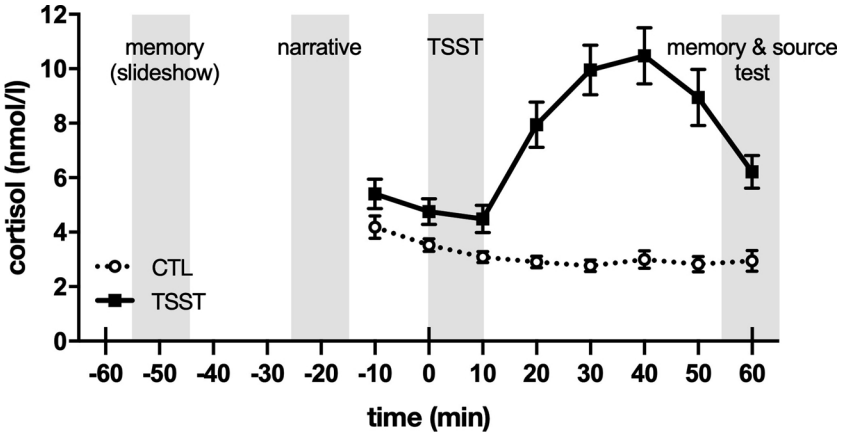

Fig. 1. Timeline of the experiment during visit-1, including the cortisol responses over time. First, participants viewed an event depict in a photographic slideshow (slideshow). Second, participants read text narratives that contained misinformation about the slideshow's event. Then, the stress induction (TSST group) or control task (CTL group) was administered. Finally, approximately 45 min after the end of the TSST or CTL task, participants completed a memory and source test for the slideshow event that contained true as well as misinformation items.

time-resolved fluorescence immunoassay described by Dressendörfer et al. (1992). SAA (U/ml) levels were determined using the enzyme kinetic method referred to in Engert et al. (2011). Subjective stress was evaluated using a visual analogue scale (VAS) at each saliva sampling. Participants marked an 'x' on a line with two anchors (0 = not at all, and 10 = very much) to indicate how stressed they felt at that moment (Ali et al., 2017). All measures were anchored to 7 time-points, in 10-min intervals, throughout the experiment from −10 to + 50 min.

2.4. Misinformation task

A modified version of the three-phase misinformation task by Okado and Stark (2005; also see: Patihis et al., 2013) was used in this study. During a two-phase encoding, participants were first shown a slideshow depicting an event over the presentation of 50 photographs, with each picture shown on-screen for a duration of 3500 ms. Before the beginning of the slideshow participants were instructed to watch carefully, as they would be asked questions concerning the content of the slideshow at a later point in the study. Then approximately 35 min after the slideshow, participants read a text narrative on a computer screen about the story described in the slideshow. The narrative was presented to the participants as a set of 50 sentences. Each sentence was displayed one at a time on the screen for 5.5 s. Participants were instructed to focus on the text presented and follow the story for the whole time of the presentation. Within the 50 sentence set, there were six sentences that contained misinformation (i.e., information that did not match the content of the previously presented slides).

The third test phase of misinformation task occurred about 95 min after the start of the encoding phase and about 45 min after the TSST or control task. This test phase contained two blocks. In the first block (memory test), participants were asked 18 questions assessing what they remembered from the original photographic slideshow. They were told to disregard information that was presented during the narrative. Questions were presented in multiple-choice format with three possible answers. One answer choice was always correct (i.e., shown in slideshow), and the other two choices were incorrect. For each participant, six of these questions contained a choice that was incorrect and contained misinformation (information not from the slideshow but from that was presented in the text narrative). If participants endorsed this incorrect misinformation choice, it was considered a memory distortion, which we refer to as overall false memory (OFM).

In the second block (source test), participants again saw the 18 multiple choice questions and recalled the source they used to answer the question. That is, they were asked to indicate which of the following five sources of information they used to answer the question. These sources were: (a) in the picture only, (b) in the narrations only, (c) in both, and they were the same, (d) in both, and they conflicted with each other, and (e) guessed. If a participant endorsed both a misinformation item in the memory test and indicated they remembered the information from the slides (a or c) during this source test, the information was considered a robust false memory (RFM).

When participants returned to the lab during visit-2, they completed the same test phase, first completed the memory test and then completed the source test.

2.5. Analyses plan

We first conducted a one-way MANOVA with age and BMI as dependent variables to ensure that groups did not differ on these variables. Similarly, we performed a repeated measures ANOVA with group and testing day (visit-1, visit-2) on correct responses from memory test. To compare the stress biomarkers for both groups, we conducted a MANOVA with the AUCis for cortisol, sAA, and VAS as dependent variables. Prior to the analysis, we performed logarithmic conversions to the cortisol and sAA data to account for skewness. Subsequently, areas under the curve (AUCis) for cortisol, sAA, and subjective stress (VAS) were calculated using the previously described formula by Pruessner et al. (2003).

Since our measures for misinformation (i.e., OFM, RFM) represent count data, and to account for repeated measures data for each person (visit-1, visit-2), we conducted generalized linear mixed models with poisson distribution (GLMM; Baguley, 2012; Bolker et al., 2009; Holmes Finch et al., 2014) for both OFM and RFM respectively, with group (0 = CTL; 1 = TSST), as a between-subject factor, and time (0 = visit-1, 1 = visit-2), as a within-subject factor, both as fixed-effects. Subject-id was included as a random-effect (cf. Barr et al., 2013). In order to assess the misinformation effect, d-prime (d') and bias measures were calculated using the formulas described by Stanislaw and Todorov (1999), and Macmillan and Creelman (2004). Here, d' represents the ability to discriminate between a correct responses (true information) and incorrect responses (misinformation), whereas bias describes the degree to which "yes" (lower values), or "no" (higher values), responses dominate. Higher d'-values represent better ability to differentiate between true and misinformation; conversely, higher values for the bias-criterion represent subjects' bias to respond no, and is deemed a conservative response (Macmillan and Creelman, 2004; Stanislaw and Todorov, 1999). Two repeated-measure ANOVAs were conducted with d' and bias as dependent variables respectively, day of testing (visit-1 vs visit-2) as within-subject, and group (TSST vs CTL) as between-subject factors. In order to probe the association of d's during visit-1 with cortisol, we conducted a multiple linear regression with d' during visit-1 as dependent variable and group (0 = CTL; 1 = TSST) and cortisol (AUCi) as predictor variables. Some recent studies have reported differential results for memory performance for low- and high-cortisol responders (e.g., Dandolo and Schwabe, 2016; McCullough et al., 2015; Zoladz et al., 2017), thus, in an exploratory analysis, we therefore

Table 1
Means of demographics, memory performance, and stress markers in the CTL and TSST group.

	CTL	TSST
Age	21.91 (3.13)	21.91 (2.85)
BMI	23.73 (2.55)	23.22 (2.58)
CR visit-1	66.40 (3.29)	70.80 (2.82)
CR visit-2	61.60 (3.78)	67.90 (3.31)
OFM visit-1	13.0 (1.70)	9.18 (1.70)
OFM visit-2	12.3 (1.56)	9.18 (1.93)
RFM visit-1	4.59 (1.14)	1.69 (0.65)
RFM visit-2	3.38 (0.91)	1.69 (0.74)
Cortisol (AUC)	−2.95 (1.23)	18.10 (2.39)
sAA (AUC)	4.36 (1.11)	11.25 (1.39)
VAS (AUC)	2.34 (1.16)	30.21 (4.44)

Note: CTL = control group; TSST = stress group. Group means and SD in parentheses for participants' age, BMI, and stress markers (AUCs). CR memory represents the mean percentage of correctly recalled true information during visit-1, or visit-2 respectively, with SE in parentheses. OFM represents the mean percentage of misinformation items endorsed during visit-1, or visit-2 respectively, with SE in parentheses; RFM = represents the mean percentage of robust false memory during visit-1, or visit-2 respectively, with SE in parentheses. AUC = area under the curve; sAA = salivary alpha amylase; VAS = subjective stress.

included a squared orthogonal polynomial regression-term, to probe for non-linear effects of cortisol (also see: Aiken et al., 1991; Kachanoff et al., 2016; cf. Miller et al., 2013). Confidence intervals were bootstrapped. All statistical analyses were conducted using R (R Core Team, 2017) and the lme4-package for GLMM (Bates et al., 2015).

3. Results

3.1. Demographics

We ran a MANOVA to test for potential differences on demographic variables between the TSST and the CTL group. The results revealed no significant differences between the TSST and CTL groups on age or BMI (age: $F(1,44) = 0.0$, $p = 0.96$; BMI= $F(1,44) = 0.45$, $p = 0.51$). See Table 1.

3.2. Stress administration

We ran a MANOVA testing for group differences in overall stress reactivity for cortisol, sAA, and VAS. Results showed significant group effects for cortisol, $F(1, 44) = 30.01$, $p < 0.001$, $\eta^2 = 0.41$, sAA, $F(1, 44) = 7.37$, $p = 0.009$, $\eta^2 = 0.14$, and VAS, $F(1,44) = 18.05$, $p < 0.001$, $\eta^2 = 0.29$. Pairwise comparison revealed that the TSST successfully induced an increase in stress-markers in the experimental group, compared to the CTL group. For cortisol, TSST: mean = 18.10, SD = 2.39; CTL: mean= -2.95, SD = 1.23. For sAA, TSST: mean = 11.25, SD = 1,39; CTL: mean = 4.36, SD = 1.11. For VAS, TSST: mean = 30.21, SD = 4.44; CTL: mean = 2.34, SD = 1.16. In order to test for an anticipated baseline return we compared the baseline cortisol measure to cortisol levels at the time of memory testing (time-point 1 vs. time-point 8; $t(37) = -0.69$, p = 0.49, (n.b., cortisol levels during the memory testing at time-point 8 were unavailable for 7 participants), indicating a return to pre-stress levels of cortisol. See Fig. 1 for the cortisol response over time.

3.3. Memory performance

3.3.1. Memory test: correct responses

To examine differences in correct responses from the memory test between the TSST group and the CTL group, for each day, we ran a repeated measures ANOVA. Group (TSST = 0, CTL = 1) was entered as a between-subjects factor and time (visit-1 vs visit-2) was entered as within-subject. factor. The test revealed no group differences ($F(1,44) = 1.49$, $p = 0.23$, $\eta^2 = 0.03$). However, there was a main effect of visit ($F(1,44) = 4.94$, $p = 0.03$, $\eta^2 = 0.08$.), indicating a decrease in memory accuracy over time for both the TSST and CTL groups. The interaction between group and time was not significant ($F(1,44) = 0.3$, $p = 0.58$, $\eta^2 = 0.00$). See Table 1 and Fig. 2.

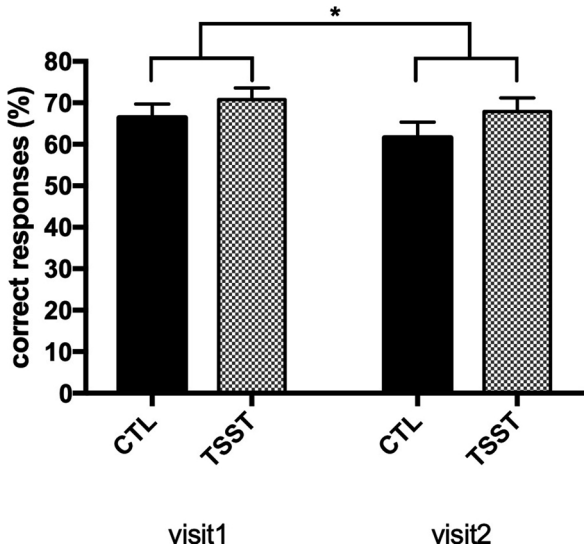

Fig. 2. The average number of correct responses for the two groups (control group, CTL; stress group, TSST) during the two testing visits. This figure illustrates that the number of correct responses did not differ between the groups, but was significantly lower during visit-2 than for visit-1. Standard error bars are shown.

3.3.2. Memory test: overall false memory

98% of individuals in the control group endorsed at least one misinformation item (i.e., OFM), compared to 74% in the stress group, when the data was collapsed across testing visits. Next, we examined whether or not there was a difference in OFM between groups, using a GLMM predicting OFM, with group and time (visit) as fixed effects, and subject as a random factor. This analysis did not reveal a significant group difference, $b = -0.35$ (se = 0.20; 95% - CI[-0.73, 0.02]), $z = -1.75$, $p = 0.08$, and no effect of time, $b = -0.03$ (se = 0.15, 95% - CI [-0.35, 0.25]), $z = -0.22$, $p = 0.82$.

3.3.3. Source test: robust false memory

Across testing visits, 50% of individuals in the control group showed robust false memory (RFM), compared to 24% in the stress group. We examined whether or not there was a difference in RFM between groups, using a GLMM predicting RFM, with group and time as fixed effects, and subject as a random factor. This analysis revealed a significant effect of group, $b = -0.89$ (se = 0.40; 95% - CI[-1.59, -0.10]), $z = -2.2$, $p = 0.03$, but no effect of time, $b = -0.21$ (se = 0.29, 95% - CI [-0.93, 0.36]), $z = -0.73$, $p = 0.47$. Compared to the CTL group, the TSST group showed lower rates of RFM, a metric of source memory intrusions, on both testing visits. Including interaction terms between time and group did not result in significant predictors for either of the models.

3.3.4. Discrimination (d') and bias scores

We ran a repeated-measures ANOVA testing for group differences in d', across visits (time). The results revealed a significant main effect of group on d', $F(1,44) = 5.26$, $p = 0.026$, $\eta^2 = 0.11$. There was no effect of time, nor was there an effect for the group x time interaction, all $ps > 0.1$.TSST: mean = 1.87, se = 0.33; CTL: mean = 0.74, se = 0.19. Fig. 3 illustrates that participants in the stress (TSST) group has higher d' scores than the control group. To test the relationship of d' scores

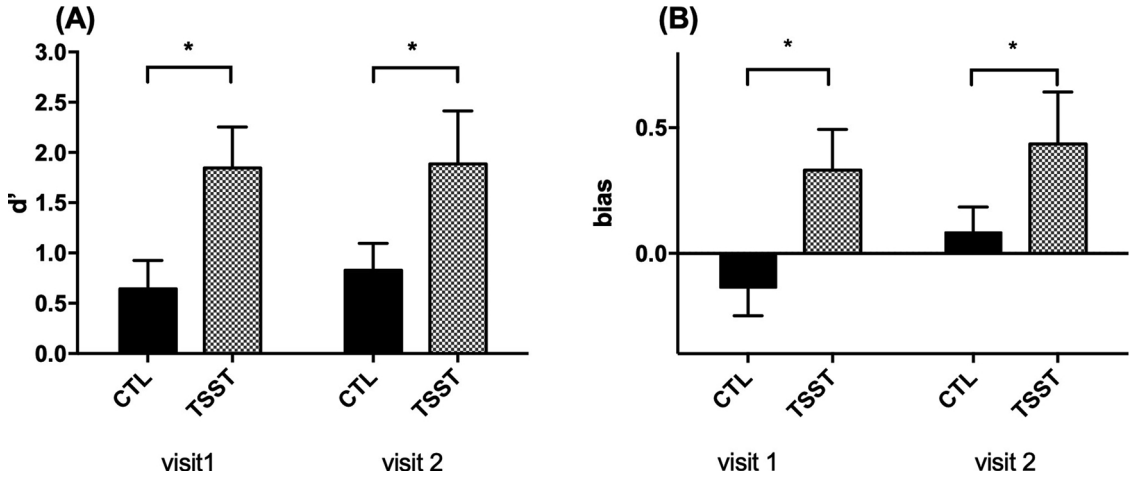

Fig. 3. (A) The average d' values (a metric of the ability differentiate between true and misinformation) for the control (CTL) and the stress (TSST) groups, during visit-1 and visit-2 respectively. (B) The average bias scores (a metric of the likelihood to response yes or no to recognition memory questions) measures for the control (CTL) and the stress (TSST) groups, during visit-1 and visit-2. Standard error bars are shown in both panels.

between visits, we then ran a subsequent Pearson correlation for each group. This analysis revealed a significant relationship between d'-values during visit-1 and visit-2 for the TSST group, but not the CTL group (TSST: $r = 0.74$, $p < 0.001$; CTL: $r = 0.39$, $p = 0.07$); a Fisher r-to-z transformation revealed a significant difference for the two correlation-coefficients, z = 2.14, p = 0.03 such that there was a stronger correlation for the stress group than the control group.

We ran a repeated-measures ANOVA testing for differences in bias scores between groups and testing days. The results revealed a significant effect of group on bias, $F(1,44) = 4.96$, $p = 0.03$, $\eta^2 = 0.1$. There was no effect of time, nor was there a group x time interaction effect, all *ps* > 0.1. A Pairwise comparison revealed that the TSST group had higher bias-scores, compared to the CTL group (TSST: mean = 0.38, se = 0.13; CTL: mean = -0.03, se = 0.08). See Fig. 3.

3.3.5. Discrimination (d') scores and cortisol response

We ran a multiple linear regression analysis predicting d' during visit-1 with group and cortisol as independent variables. The analysis revealed a significant regression equation, $F(1.6,43) = 3.84$, $p < 0.016$, with an R^2 of 0.22 and an adjusted R^2 of 0.16. Both group, $\beta = 0.5$, $p < 0.01$, as well as the squared polynomial regression-term for cortisol, $\beta = 0.3$, $p < 0.029$, significantly predicted d' during visit-1. To identify the exact regions of the curve in which the simple slope is significant, we used the Johnson-Neyman Technique. Results showed a U-shaped function for cortisol, with values falling within observable range of centered cortisol-data (-1.5, 2.9), indicating a decline in slope for values below -0.76, and a rising slope for values higher than 1.9. See Fig. 4.

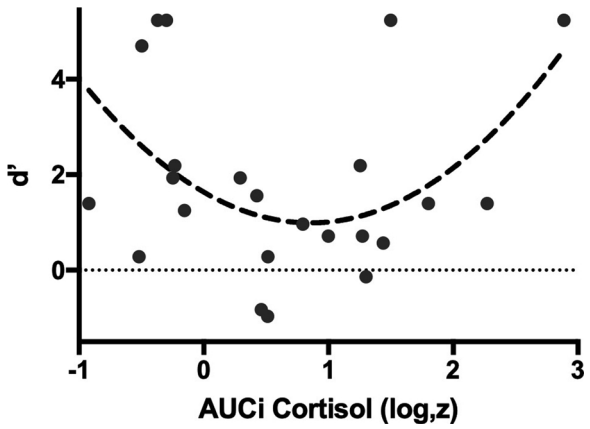

Fig. 4. An illustration of the curve linear relationship between cortisol response levels (log transformed cortisol area under the curve measures, AUCi Cortisol) and on d' in the stress (TSST) group.

4. Discussion

In the presented study, we investigated the effects of acute psychosocial stress on memory distortions during a 'post-learning consolidation' phase of memory processing, when memory updating is thought to occur. We hypothesized that stress induced during this phase of processing would disrupt the memory updating mechanisms that are needed to integrate related information resulting in fewer memory intrusions on a false memory measure (Dongaonkar et al., 2013; Smeets et al., 2008). Using the well-validated misinformation paradigm (Loftus, 2005), participants studied an event depicted through a photographic slideshow and were then given a narrative with misinformation about that event. After seeing both the photographic event and the misinformation text (i.e., during post-learning consolidation), we exposed participants either to acute psychosocial stress (stress group) or a non-stressful control task (control group) and then tested their memory for the original event once stress levels have returned to baseline. We report no difference between the stress and control group in recognizing *true* information from that event, but as hypothesized, participants in the stress group endorsed fewer misinformation items than the control group. Moreover, those in the stress group were better able to discriminate the source of the tested event information than the controls, suggesting that their memory traces of the true and misinformation events were less integrated relative to the control group. We further found these group differences remained after a three-day delay, indicating the lasting effects of post-learning consolidation stress on memory retrieval. Together, these data add to the literature that describes how stress effects on memory, particularly memory updating mechanisms, as a function of time while also providing new insights into how the false memory effects arise when individuals are stressed.

First, our work extends research on the effects of stress on false memory formation. Stress has been shown to enhance the initial encoding of (true) information (Hoscheidt et al., 2014; Smeets et al., 2008; Zoladz et al., 2017). In addition, Schmidt et al. (2013) showed that stress induced prior to the presentation of new (mis)information reduces the later endorsement of misinformation as veridical. Thus, demonstrating how stress *during* encoding affects misinformation. However it was not clear how stress *after* encoding, i.e., during a consolidation period that would integrate the encoded true events with misinformation, would be affected by stress. We addressed this

knowledge gap and showed that acute stress during this time-point reduced the incorporation of misinformation to true events.

In terms of mechanisms, stress during encoding is thought to enhance the strength of the original true memory (for a review: Schwabe, 2017), making the original memory resistant to intrusion from a potentially weakly encoded misinformation event, or vice versa (Ayers and Reder, 1998). In our study, stress effects during the post-learning consolidation period cannot be explained with these mechanisms since it occurs after these encoding events. We speculate that stress during this phase of memory is targeting and disrupting memory updating mechanisms that are necessary for integrating encoded information and thus reducing the misinformation effect. Evidence for this idea comes from work outside the domain of false memory that indicate that stress can have a harmful effect on memory updating processes that are supported by the hippocampus, a brain region sensitive to stress (for reviews: Kim and Diamond, 2002; Lupien and Lepage, 2001; McEwen, 2007). Yet, an alternate account of our results is that the reduced misinformation effect when stress occurs during post-learning consolidation comes from stress affecting retrieval mechanisms during the memory test. It is true that the participants in the tested stress group were still within a 'window' of elevated cortisol levels when their memory was tested (45 min after the stressor) during visit-1, relative to the control group. However, if this account were true, then we should have found that participants in the stress group were impaired at retrieving misinformation as well as true event information relative to the controls, which we did not find. Stress did not affect the ability to retrieve the originally encoded memory as indicated by comparable correct response rates between the groups (e.g., Buchanan et al., 2006; de Quervain et al., 1998).

For this reason, we interpret our results to indicate deficits in memory updating mechanisms, particularly since these mechanisms are known to be sensitive to stress (for a review: Akirav and Maroun, 2013). More specifically, it is likely that the reported reduction of the misinformation effect of stress is because cortisol limited the hippocampal-mediated updating processes that are required to integrate the misinformation with the original event memory (e.g., Kluen et al., 2017; Vogel et al., 2018). Interestingly, when we explored the link between the level of cortisol released in response to acute stress and the false memory effect, we found a non-linear effect of cortisol on the ability to differentiate between the photographic and narrative event (i.e., the susceptibility to false memory). That is, low and high levels of cortisol responses were linked to a reduced misinformation effect, whereas medium levels of cortisol were associated with a larger misinformation effect. This result aligns well with prior studies that have described a U-shaped function in the negative impact of cortisol on hippocampal function (Joëls, 2006; Lisman et al., 2011; Roozendaal et al., 2004), lending to the hypothesis that the stress induction in our study targeted hippocampal processes needed to integrate memories, but likely in a more nuanced fashion.

On a final note, we interpret our results alongside a recent study that found that inducing stress before a memory generalization task resulted in the formation of more rigid and less generalizable memories (Dandolo and Schwabe, 2016). Generalization tasks require memories to be updated much like false memories (for reviews: Loftus, 2005; Schacter and Loftus, 2013). With our results, this study points to the fact that stress effects on memory updating can have both beneficial and impairing effects. From our study, stress improved the ability to represent two related events as discrete, and thus led to reduced misinformation and a 'true' remembering of the past. The Dandolo and Schwabe (2016) results generally suggest that the same effect of stress on the misinformation effect may have resulted in memory traces that are less flexibly integrated together, leading to more rigid remembering that is less able to be applied (generalize) to new situations (Dandolo and Schwabe, 2016). In summary, we suggest that depending on the nature of a memory task, stress induced during a post-learning consolidation period can be viewed as beneficial - as is the case of false memories - or as maladaptive, when information needs to be integrated in pre-existing knowledge structures to guide behavior (Carpenter and Schacter, 2017; Schacter et al., 2011; Schlichting and Preston, 2015).

5. Conclusions and limitations

Although the current study makes an important contribution to understanding the integration of misinformation under stress specifically, and the effects of stress on memory updating more generally - there are additional factors to consider. For example, one factor is the emotional valence of information presented, which is known to impact memory processing under stress (e.g., Payne et al., 2007). Under stress, emotional content tends to be encoded better, and thus better recalled later on, compared to neutral content (Hoscheidt et al., 2014; Joëls et al., 2011; Sheldon et al., 2018). Relevant to our current study, Hoscheidt et al. (2014), used the misinformation paradigm to show that acute psychosocial stress increases the encoding of arousing events, which the authors speculated could be due to a modulation of consolidation processes via amygdala connections to the hippocampus (for a review: McGaugh, 2004). In the present investigation, the stimuli presented in the current study were not designed with a particular valence in mind. Thus, future work should specifically investigate the effect of valence, by including emotionally arousing - or for the stress situation, salient - information, in order to thoroughly assess the effects of stress during post-learning consolidation on the misinformation effect specifically and memory updating more generally. Another factor to consider is that in the current study, we only tested male participants. Given that the female stress response differs from males' in several aspects, such as a reduced endocrinological stress response (e.g., Kirschbaum et al., 1999; Kudielka and Kirschbaum, 2005), and differential effects on memory functioning (e.g., Buchanan and Tranel, 2008; Smeets et al., 2006; Wolf et al., 2001), it is important to investigate these effects in samples with a different gender/sex composition.

Despite these limitations, our study provides new insight into how stress can affect memory processing even when it occurs after learning. With the misinformation paradigm, we demonstrate that participants exposed to stress at this time-point showed fewer memory intrusions among these events, compared to a group not exposed to stress. Since this phase of memory processing is thought to activate memory updating mechanisms, we interpret our pattern of results as indicating that stress decreased the ability to update memory representations, which may ward off against false memory. On a final note, we consider that this effect could have deleterious effects. Under other memory conditions, this impact of stress on memory updating as could impair the ability to integrate related memories to generalize the information to new situations. In this way, our results highlight the dynamic relationship between stress and memory by providing evidence that the effects of stress are not simply beneficial or detrimental but depend on how memory is used.

Conflict of interest

This study was funded by an NSERC Discovery grant awarded to SS (#RGPIN-04241). JPN holds a Doctoral scholarship from Fonds de Recherche du Québec - Société et culture (FRQSC).

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SS developed the study concept and study design with input from all authors. SC performed data collection under the supervision of JPN. JPN conducted the data analyses. JPN and SS wrote the manuscript. SC, JAB and JCP provided critical revisions. All authors approved the final version of the manuscript for submission. This study was funded by an NSERC Discovery grant awarded to SS (#RGPIN-04241). JPN holds a Doctoral scholarship from Fonds de Recherche du Québec - Société et culture (FRQSC). The authors have no financial or other conflicts of

interest to declare.

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