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Acute stress enhances general-knowledge semantic memory

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ABSTRACT

Acute psychological stress consistently impairs episodic memory, which consists of memory for events that are associated with a specific context. However, researchers have not yet established how stress influences semantic memory, which consists of general knowledge that is devoid of context. In the present study, participants either underwent stress induction or a control task prior to taking a trivia test that was designed to measure semantic memory. In contrast to the wealth of prior research on episodic memory, we found that stress enhanced semantic-memory retrieval. Supporting this finding, higher cortisol reactivity to stress was associated with better performance on the trivia test. Together with the results from previous studies of episodic memory, our findings suggest that stress differentially influences memory retrieval, depending on the degree to which the retrieval of a given memory relies on medial-temporal, neocortical, and striatal brain regions.

1. Introduction

The human stress response has generally been shown to impair memory retrieval (for reviews see Gagnon and Wagner, 2016; Shields et al., 2017; Smith and Thomas, 2017; but see Schoofs and Wolf, 2009; Schwabe et al., 2009). This effect has been attributed to a post-stress hormonal cascade that impairs activity in brain regions associated with retrieval (e.g., the hippocampus; Gagnon and Wagner, 2016; Schwabe et al., 2012; Wolf, 2017). However, research suggests that there are qualitatively-different types of memories, and the retrieval of some memories does not necessarily rely on brain regions that are down-regulated during the stress response. The present research aimed to determine how stress influences memories that do not depend on neural pathways that are disrupted by stress.

A consideration of the longstanding distinction between *episodic* and *semantic* memory is useful for addressing this aim (Tulving, 1972). Episodic memory consists of memory for events and information that are associated with the context in which they took place (e.g., your most recent birthday party), whereas semantic memory refers to our general knowledge of facts, concepts, and language that is independent of a learning context (e.g., *Asia is the largest continent*). Research into the effects of acute stress on memory retrieval has primarily focused on how stress influences episodic memory retrieval, and detrimental effects have been reported (Shields et al., 2017).

Episodic and semantic memory differ in their neural substrates. Most relevant to the present topic is the hippocampus, which is highly involved in establishing and retrieving the contextual elements of memory (e.g., time and place; Rugg et al., 2012). In research with healthy adults, both episodic- and semantic-memory retrieval have been shown to recruit the hippocampus (Burianova and Grady, 2007; Burianova et al., 2010; Catheline et al., 2015; Klooster and Duff, 2015). However, neuropsychological studies have shown that the hippocampus is only essential for the retrieval of episodic memories (Rosenbaum et al., 2008; Vargha-Khadem et al., 1997). When hippocampal functioning is reduced or eliminated, many semantic memories can still be retrieved (Graham et al., 1999; Manns et al., 2003; Moscovitch et al., 2005). This may occur because semantic memory retrieval recruits neocortical (Graham et al., 1999; Davey et al., 2015) and striatal (Scimeca and Badre, 2012) pathways, which provide retrieval routes that bypass the hippocampus.

Because semantic memories can be retrieved via extra-hippocampal pathways, the mechanism that presently explains the detrimental effects of stress on memory does not necessarily apply to semantic memory. Current theories posit that retrieval-related processing in the hippocampus is downregulated during the stress response, resulting in memory impairment (Gagnon and Wagner, 2016; Schwabe et al., 2012; Wolf, 2017). However, these theories are based on evidence from episodic-memory paradigms. In the context of a semantic-memory paradigm, retrieval may benefit from stress because the neocortical and striatal regions that support semantic memory also exhibit increased

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activity during the stress response (Hermans et al., 2014; Ito et al., 2003; Kohn et al., 2017). That is, despite reduced hippocampal support, semantic memory may be enhanced by stress because it does not require such support but does rely on neural networks that are upregulated during stress.

While over two dozen experiments have examined the effects of stress on episodic memory retrieval (see Shields et al., 2017), only one featured an intentional manipulation of stress prior to a semantic-retrieval task. In this study, researchers induced stress and measured subsequent performance on a true/false test involving statements of scientific concepts that are commonly acquired during childhood (e.g., *A moving bullet loses speed*; Merz et al., 2016). Relative to a non-stressed control group, stressed individuals did not demonstrate differences in true/false accuracy. In interpreting this finding, it is important to consider that, across studies on stress and episodic memory retrieval, the memory impairment that is typically observed occurs more commonly on effortful memory tests (e.g., free recall) than on easier tests (e.g., true/false; see Gagnon and Wagner, 2016). Thus, Merz et al.'s (2016) findings raise the question of whether their null results occurred because semantic memory for scientific concepts is immune to stress, or because low-demand memory tests like their true/false test tend to be unaffected by stress.

The present study addressed these unresolved questions by examining the effects of stress on free recall of semantic memories. To summarize the literature reviewed thus far, research suggests that episodic-memory retrieval requires hippocampal support, whereas semantic-memory retrieval can be accomplished via neocortical and striatal pathways. Models that specify the effects of stress on neural activity suggest that stress reduces retrieval-related hippocampal activity but increases activity in neocortical and striatal brain regions. Thus, we hypothesized that acute stress would enhance semantic-memory retrieval because it does not rely on the hippocampus (downregulated during stress) but does capitalize on neocortical and striatal pathways (upregulated during stress). Further, because stress suppresses episodic-memory retrieval and associated brain regions, stress may serve to streamline memory retrieval of semantic knowledge by reducing interference from episodic memory processing.

2. Method

2.1. Design

The experiment featured two between-subjects variables and one within-subjects variable. The first between-subjects variable pertained to which condition of the Trier Social Stress Test for groups (TSST; von Dawans et al., 2011) each participant completed. Participants either completed the stress or control tasks associated with the TSST. The second between-subjects variable was gender (male or female), and the within-subjects variable was question difficulty on the general knowledge test.

2.2. Participants

Ninety-two Tufts University students participated in the experiment (63 women, *M* age = 19.57, *SD* age = 2.83). Participants were recruited through introductory psychology courses to fulfill a research participation requirement. All participants reported that they had not consumed caffeine or nicotine in the 6 h prior to the experiment. Forty-six participants were randomly assigned to each TSST group (stress or control). There were 34 women in the stress group, and 29 women in the control group.[1]

2.3. Materials

2.3.1. General knowledge test

The general knowledge memory test consisted of 122 trivia questions from a recently-normed database containing 244 questions (Fastrich et al., 2017). We sorted the questions according to their memorability, and chose the most memorable half of the items. According to the established norms, these items ranged from 37% recallability to 92% recallability, on average. On the memory test, questions were presented randomly, one at a time, for 15 s each using *E*-Prime software (Version 2.1; Schneider et al., 2001). There was a box in the upper-left corner of the screen in which participants could enter their answer for each question.

2.3.2. State-trait inventory for cognitive and somatic anxiety (STICSA)

We administered the STICSA to assess participants' self-reported levels of pre- and post-stress anxiety (Grös et al., 2007). STICSA scores range from 0 to 80 and higher scores are indicative of higher self-reported anxiety.

2.4. Procedure

Testing sessions occurred during a single session between 2:30 p.m. and 5:30 p.m. to control for variability in diurnal cortisol secretion (e.g., Weitzman et al., 1971). Participants in the stress group were always tested two at a time according to TSST protocol (von Dawans et al., 2011). Participants in the control group were tested either individually or two at a time.

Upon arriving to the lab, participants rinsed their mouth out with water to prepare for providing subsequent saliva samples. They then read through and signed the consent forms (~5 min). Participants next completed the first STICSA and provided the first saliva sample as baseline measures of psychological and physiological stress. They then began the tasks associated with either the stress or control version of the TSST (von Dawans et al., 2011).

The stress group was given 4 min to prepare a speech in which they would be applying for a hypothetical job as a Teaching Assistant. Their notes were then taken away, and they delivered their speeches extemporaneously for 2 min each. During speech delivery, participants were video-recorded and the experimenter pretended to take notes on a clipboard. In instances where participants finished their speech early, the experimenter told them to continue until 2 min had passed. After both participants had delivered their speeches, the experimenter then called on them at random to solve math subtraction problems aloud (e.g., 4573 – 17) for 6 min. Participants continued to be video recorded and observed by the experimenter during the math phase.

In the time-matched control group, participants read silently from a biology textbook for 8 min. Prior to beginning, they were told that they would not be tested on the reading material and that the task was simply for their enjoyment. Afterward, participants were given 6 min to solve the same math problems that were presented to participants in the stress group, but solved the problems using pen and paper. Further, they were instructed that their answers would not be graded. Participants in the control group were not video recorded during these tasks, and the experimenter sat at a desk and did not observe them.

Following the TSST tasks, all participants viewed 10 min of an episode of the BBC series *Planet Earth*. They then provided the second saliva sample as a post-stress measure of cortisol. Participants next completed the general knowledge test, as described in the Materials section. The test took 31 min to complete. Afterward, participants were debriefed and excused.

[1] Women sometimes demonstrate a blunted cortisol response to psychological stress, particularly when in the follicular phase of their menstrual cycle or when taking oral contraceptives (Kajantie and Phillips, 2006). We opted to not control for these variables in order to gather a representative and generalizable pattern of data.

2.5. Scoring

The following types of responses were scored as correct on the general knowledge test: (1) perfect matches for the correct answer, (2) misspellings that were easily extrapolated (e.g., dinsaur instead of dinosaur), (3) correct answers that were inappropriately pluralized or capitalized, (4) common synonyms for correct answers (e.g., ping pong instead of table tennis), and (5) partial answers in which the first four letters matched the correct response (e.g., Euro instead of Europe). The latter exception occurred in instances in which the participant's response was cut off at the 15 s time limit. Cases in which participants provided multiple answers, including the correct one, were scored as incorrect. Two researchers independently scored all responses and the interrater reliability was 98.45%. Rare instances of disagreement were discussed and resolved.

2.6. Cortisol measurement and data management

Cortisol data for three participants were excluded from analysis due to error in data processing. Saliva samples were stored at −20 °C until the completion of data collection, after which they were shipped to Salimetrics, LLC (Salimetrics, LLC, State College, PA) for analysis. Samples were assayed in duplicate, and the mean cortisol concentration for the two values served as the dependent measure. The inter- and intra-assay coefficients of variability were 7.50% and 2.03%, respectively. We converted cortisol concentrations from μg/dL to nmol/L for consistency with human stress literature.

3. Results

3.1. Physiological stress response

We conducted a 2 (TSST Group: Stress or Control) × 2 (Sample Timing: Pre-TSST or Post-TSST) × 2 (Gender: Male or Female) mixed model ANOVA to determine whether the TSST groups differed in their pre- and post-TSST cortisol levels. Gender was included as a variable because gender can influence the physiological response to psychological stress. For instance, women who are in the follicular phase of their menstrual cycle or who take oral contraceptives generally demonstrate a blunted cortisol response to psychological stress (Kajantie and Phillips, 2006). Most notably, we found a significant TSST Group by Sample Timing interaction, $F(1, 85) = 18.57$, $p < .001$, $\eta_p^2 = 0.18$. As shown in Fig. 1, participants in the control group did not experience an increase in cortisol from pre- to post-TSST ($M_{pre} = 5.27$, $SEM_{pre} = 0.40$ vs. $M_{post} = 5.66$, $SEM_{post} = 0.40$), whereas those in the stress group did ($M_{pre} = 5.07$, $SEM_{pre} = 0.35$ vs. $M_{post} = 7.87$, $SEM_{post} = 0.65$). We also found a Gender by Sample Timing interaction, $F(1, 85) = 4.47$, $p = .037$, $\eta_p^2 = 0.05$. Men experienced a more pronounced increase in cortisol from pre- to post-TSST ($M_{pre} = 4.85$, $SEM_{pre} = 0.47$ vs. $M_{post} = 7.11$, $SEM_{post} = 0.80$) than women ($M_{pre} = 5.33$, $SEM_{pre} = 0.32$ vs. $M_{post} = 6.55$, $SEM_{post} = 0.43$). Last, we found a main effect of Sample Timing, as participants generally showed lower pre- than post-TSST cortisol (averaged across TSST Group), $F(1, 85) = 31.59$, $p < .001$, $\eta_p^2 = 0.27$.

3.2. Psychological stress response

To test whether the TSST tasks increased subjective anxiety, we ran a 2 (TSST Group: Stress or Control) × 2 (STICSA Timing: Pre-TSST or Post-TSST) mixed model ANOVA comparing pre- and post-TSST STICSA scores for the stress and control groups. Supporting the results of the analysis on cortisol, we found a significant TSST Group by STICSA Timing interaction, $F(1, 90) = 40.89$, $p < .001$, $\eta_p^2 = 0.31$. Participants in the control group did not experience an increase in subjective stress from pre- to post-TSST ($M_{pre} = 28.87$, $SEM_{pre} = 0.81$ vs. $M_{post} = 28.26$, $SEM_{post} = 0.90$), whereas those in the stress group did ($M_{pre} = 29.57$, $SEM_{pre} = 0.98$ vs. $M_{post} = 35.57$, $SEM_{post} = 1.28$). We also found a main effect of STICSA Timing, as participants generally showed lower subjective stress before the TSST than after it, $F(1, 90) = 27.21$, $p < .001$, $\eta_p^2 = 0.23$. Last, we found a significant main effect of TSST Group, as participants in the stress group generally reported higher anxiety (averaged across pre- and post-TSST measurements) than those in the control group, $F(1, 90) = 9.06$, $p = .003$, $\eta_p^2 = 0.09$.

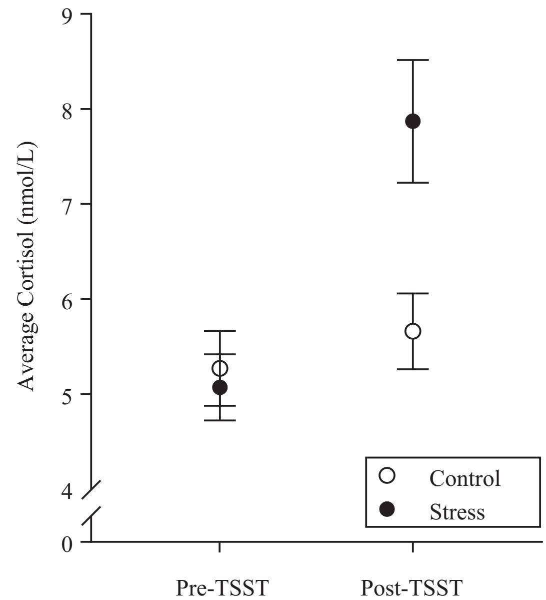

Fig. 1. Average pre- and post-TSST cortisol concentrations for the stress and control groups. Error bars represent standard errors of the mean.

3.3. Memory performance under stress

3.3.1. Accurate responses

Memory accuracy for each participant was calculated as the proportion of correct responses out of 122 total questions on the general knowledge test. The variables Gender (Male or Female) and Question Difficulty (ordinally ranked from 1 to 122) were considered as potential moderators of the influence of TSST Group (Stress or Control) on memory for general knowledge facts.

Initial inspection of the data showed no interaction between Question Difficulty and TSST Group. Specifically, as shown in Fig. 2, the Stress and Control groups showed similar patterns of decreasing performance as item difficulty increased, but no interaction was evident. Furthermore, when average performance on the easier half of items was compared to average performance on the harder half of the items, a 2 (Question Difficulty: High or Low) × 2 (TSST Group: Stress or Control) ANOVA did not reveal a significant interaction, $F(1, 90) = 0.88$, $p = .351$. Thus, Question Difficulty was not included as an independent variable of interest in our main analyses.

As depicted in Fig. 3, further inspection of the data did reveal an influence of Gender on memory accuracy. As is commonly found on tests of general knowledge, men ($M = 0.24$, $SEM = 0.01$) demonstrated higher accuracy than women ($M = 0.20$, $SEM = 0.01$) (Lynn and Irwing, 2002; Lynn et al., 2001). A 2 (Gender: Male or Female) × 2 (TSST Group: Stress or Control) ANOVA on average accuracy confirmed a main effect of Gender, $F(1, 88) = 9.65$, $p = .003$, $\eta_p^2 = 0.10$. Most notably, we found a main effect of TSST Group, $F(1, 88) = 5.81$, $p = .018$, $\eta_p^2 = 0.06$. Regardless of question difficulty, participants in the stress group ($M = 0.23$, $SEM = 0.01$) demonstrated higher accuracy on the general knowledge test than those in the control group ($M = 0.20$, $SEM = 0.01$). The interaction between Gender and TSST

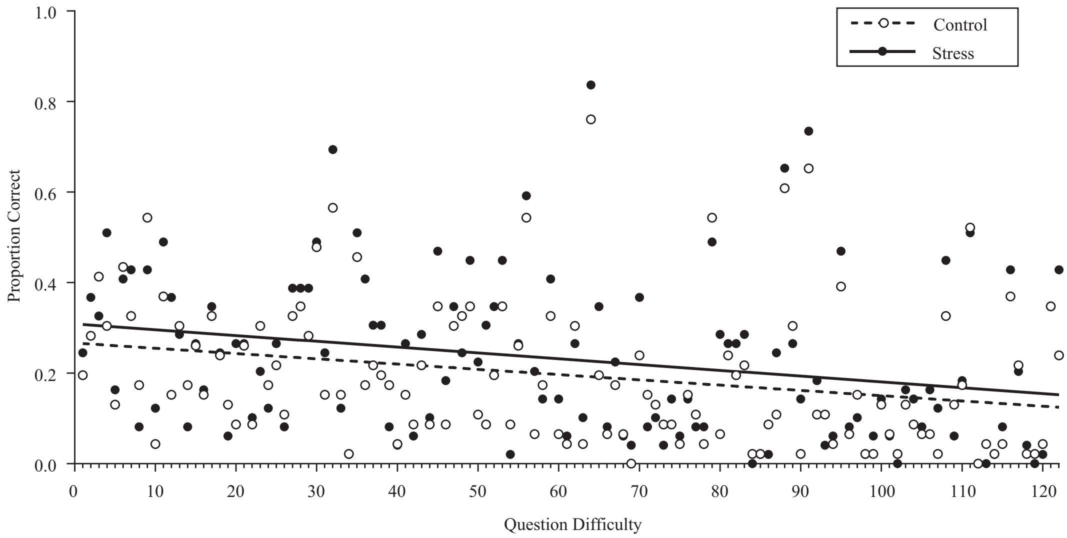

Fig. 2. Average accuracy on each general knowledge question for the stress and control groups, plotted as a function of question difficulty. Question difficulty was ranked from 1 to 122 in order of how likely each item was to be recalled (1 = most likely to be recalled).

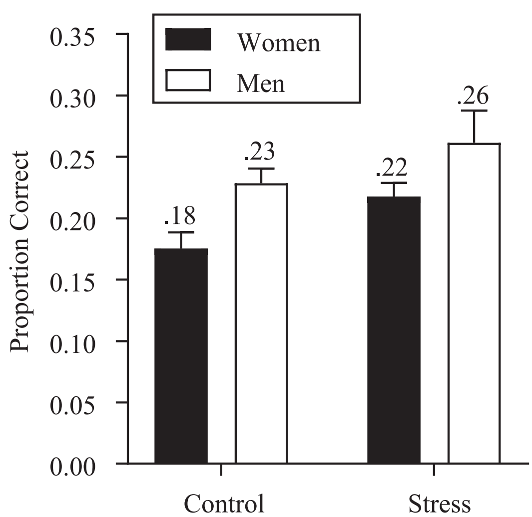

Fig. 3. Average accuracy on the general knowledge test for men and women in the stress and control groups. Error bars represent *SEM*.

Group was not significant, F (1, 88) = 0.09, p = .771.

As is standard practice in experiments examining stress and memory (e.g., Merz et al., 2016; Oei et al., 2006; Schonfeld et al., 2014; Schoofs and Wolf, 2009; Smeets et al., 2008; Wolf et al., 2002), we next examined the relationship between cortisol reactivity to the TSST and memory performance. We conducted a hierarchical linear regression examining the influences of cortisol reactivity (delta cortisol) and gender on average accuracy. Delta cortisol was calculated by subtracting each participant's pre-TSST cortisol concentration from their post-TSST concentration. This model yielded a significant R^2 of 0.12, F (3, 85) = 3.94, p = .011. We found a main effect of delta cortisol, as participants with greater increases from pre- to post-TSST demonstrated higher average accuracy on the general knowledge test (β = 0.008, t = 2.08, p = .040). No other effects were statistically significant. Thus, supporting the finding that stress improved memory accuracy, higher cortisol reactivity to the TSST tasks was associated with higher accuracy on the general knowledge test.

3.3.2. Inaccurate responses

We next examined the influence of TSST Group and Gender on memory *inaccuracy*. Memory inaccuracy for each participant was calculated as the proportion of incorrect responses that participants provided, excluding unanswered questions, out of 122 total questions on the general knowledge test. A 2 (Gender: Male or Female) × 2 (TSST Group: Stress or Control) ANOVA on average inaccurate responses found no significant effects. Thus, although stress increased correct responding, it did not influence the number of incorrect responses that participants offered.

3.3.3. Errors of omission

We last examined whether TSST Group and Gender influenced participants' tendency to leave answers blank on the general knowledge test. Errors of omission were calculated as the proportion of questions that each participant left unanswered out of 122 total questions. In a 2 (Gender: Male or Female) × 2 (TSST Group: Stress or Control) ANOVA on average errors of omission, we found a main effect of Gender, F (1, 88) = 10.80, p = .001, η_p^2 = 0.11, as women (M = 0.16, SEM = 0.02) were more likely than men (M = 0.08, SEM = 0.01) to leave questions unanswered. No other effects were statistically significant. Notably, as with our analysis on memory inaccuracy, stress did not influence participants' tendency to leave questions blank.

4. Discussion

The enhancing effect of acute stress on the retrieval of semantic memories presents a novel finding to the area of research on stress and memory. Prior experiments, which examined the influence of stress on episodic memory retrieval, consistently demonstrated post-stress memory impairment with occasional reports of null findings (see Gagnon and Wagner, 2016; Shields et al., 2017; Smith and Thomas, 2017). Our results demonstrate that the stress response does not impair access to all memories. Instead, the neural networks that are upregulated during stress may also be relevant for general-knowledge retrieval, making this information more accessible under stress. From an evolutionary perspective, this seems more plausible than the presently-held belief that the stressed brain adaptively enhances some cognitive processes (e.g., attention) at the expense of all memory retrieval (Gagnon and Wagner, 2016; Hermans et al., 2014; Shields et al., 2017; Smith and Thomas, 2017).

Our results combine with recent evidence to take a step forward in determining what qualities a memory must possess to resist the negative consequences of stress. In recent research on stress and episodic memory, post-stress memory impairment was eliminated in a paradigm in which the stimuli were particularly well-learned. Specifically, Smith and colleagues (Smith et al., 2016; Smith et al., 2018) used a common episodic memory paradigm in which participants studied a series of words, underwent stress induction, and then took a post-stress memory test for the words. Critically, they manipulated whether words were learned through passive studying or through a highly effective learning paradigm involving a combination of studying and practice testing. Whereas stress did impair memory for words that were learned via passive studying, stress did not impair memory for words that were learned by studying and taking practice tests. Further, in one of these experiments, memory for information learned using the latter paradigm even trended toward being enhanced by stress (Smith et al., 2016). The results of the present study suggest that the practice-test paradigm may have begun to create memories that, like semantic memories, could be retrieved under conditions of reduced hippocampal support. This hypothesis is further supported by research with rodents showing that information that is well-learned (e.g., multiple exposures to stimuli) can be remembered after a hippocampal lesion, but information that is less well-learned (e.g., a single exposure to stimuli) cannot (Lehmann et al., 2009; Lehmann and McNamara, 2011).

Thus, accumulating evidence suggests that, in the context of stress, the accessibility of a given memory may be predicted by its level of dependence on the hippocampus and its level of dependence on extra-hippocampal regions (e.g., neocortex and striatum). Where a memory falls along these dimensions may be inferred by several factors, including how recently the memory was acquired (e.g., Manns et al., 2003; Moscovitch et al., 2005), how many times the memory has been recalled before (e.g., Smith et al., 2016, 2018), and how much the retrieval of the memory depends on retrieval of associated contextual cues (e.g., Rugg et al., 2012). An example of a memory that may be enhanced rather than impaired by stress is a memory of an event that occurred 10 years ago, has been thought of often since then, and can be recalled without effortfully thinking about the exact date, time, and location in which the event took place.

These new findings and theoretical possibilities call for more research on the topic. For instance, further questions about the relationship between stress and semantic memory retrieval stem from research with amnesic patients who have localized damage to the hippocampus. In addition to profound episodic memory impairment, these patients have demonstrated memory deficits for semantic information that was learned in the few years prior to amnesia, but intact retrieval of memories that were acquired early in life (Manns et al., 2003; Moscovitch et al., 2005). These findings suggest that the hippocampus may no longer be involved in semantic retrieval once semantic memories are sufficiently old, well-established, and/or have become independent of any episodic context. One direction for future research is to examine whether stress differentially influences recently-acquired versus older semantic memories. Additionally, the present paradigm did not include a measure of episodic memory, and thus future researchers should consider implementing a paradigm that allows for a direct comparison of stress effects on episodic versus semantic memory.

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Author contributions

All authors contributed to the design of the experiment. A. Smith oversaw data collection. A. Smith and G. Hughes conducted data analysis. A. Smith and G. Hughes wrote the manuscript and all authors helped edit the manuscript.

Open practices statement

The experiment reported in this article was not formally pre-registered. The data and materials have been made available on a permanent third-party archive and can be accessed via DOI 10.17605/OSF.IO/EQ8SY.

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