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Acute physical exercise promotes the consolidation of emotional material

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ABSTRACT

Physical exercise can improve cognitive functions and promote learning and memory, especially when performed in close temporal proximity to the encoding of information. This benefit may occur due to circulating stress hormones released in response to acute exercise. When administered after encoding, acute stress typically enhances the consolidation of emotional stimuli. However, whether acute exercise also selectively modulates emotional memories remains to be explored. Likewise, the potential role of sex in moderating these effects has not been addressed so far. Here, we tested whether a single bout of aerobic exercise after learning boosts the consolidation and thus long-term memory for emotional versus neutral visuospatial stimuli. Healthy men and women learned an object-location task and subsequently were exposed to a vigorous-treadmill running task or control intervention. Memory was assessed 24 h later. Acute exercise significantly increased heart rate and salivary cortisol in both sexes and selectively facilitated the consolidation of emotional stimuli. In particular, we found improved memory for negative items in women and better recall of positive items in men following exercise exposure. This memory benefit was positively related to the increase in heart rate and cortisol in both men and women, suggesting that the favorable effects of acute exercise on emotional memory may be mediated via a co-activation of the sympathetic nervous system and the hypothalamus-pituitary-adrenocortical axis. Our findings thereby provide first evidence for the improvement of emotional memory consolidation by acute physical exercise that appears to rely on similar neuroendocrine mechanisms as psychosocial stressors. Given that exercise is healthy, cost-effective and practical in nature, it constitutes an ideal behavioral intervention strategy for boosting memory in clinical and educational settings alike.

1. Introduction

Physical exercise is associated with improved attention, executive control and memory (Chang, Labban, Gapin, & Etnier, 2012). Accumulating evidence suggests that already a single bout of exercise facilitates the acquisition and retention of new information (Roig, Nordbrandt, Geertsen, & Nielsen, 2013). However, these effects appear to depend critically on the timing of exercise relative to the encoding of the to-remembered material. Accordingly, acute exercise performed immediately before or after learning mostly enhanced long-term memory recall (Loprinzi, Blough, et al., 2019), whereas exercise directly preceding memory retrieval tended to have no or even detrimental effects on task performance (Roig et al., 2013; 2016), probably due to exercise-induced fatigue (Moore, Romine, O'Connor, & Tomporowski, 2012) or arousal (Park, 2005).

One potential mechanism through which acute exercise might improve long-term memory is by triggering cardiovascular and neuroendocrine changes (Hackney, 2006; Keyan & Bryant, 2019) known to be involved in regulating memory consolidation (McGaugh & Roozendaal, 2002). Studies comparing physiological responses to psychosocial and physical stressors (Hummel et al., 2018; Skoluda et al., 2015) revealed that acute exercise can indeed activate both, the sympathetic nervous system (SNS), leading to a rapid release of (nor) adrenaline and heart rate (HR) elevations, and the hypothalamus-pituitary-adrenocortical (HPA) axis, resulting in the secretion of glucocorticoids (GCs, in humans cortisol; Joëls & Baram, 2009). Similar to the exercise effects reported above, stress hormones are known to exert memory-phase-dependent effects, with typically enhancing effects on memory consolidation (Roozendaal, 2002; Schwabe, Wolf, & Oitzl, 2010; Wolf, 2017).

Evidence from both animal and human work furthermore suggests that this effect is especially pronounced for emotionally arousing material (Cahill, Gorski, & Le, 2003; Wolf, 2008), mediated by an interaction between GCs and noradrenergic activity in the basolateral amygdala (BLA) and hippocampus (Roozendaal & McGaugh, 2011). Consistently, elevations in SNS-related alpha-amylase and HR as well as cortisol have been shown to positively correlate with the amount of emotional information remembered following stress exposure (Larra

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et al., 2014; Smeets, Otgaar, Candel, & Wolf, 2008). Given that exercise elicits comparable physiological responses as psychosocial stressors, it is thus reasonable to predict that a single bout of physical exercise after memory encoding would also improve delayed emotional memory retrieval (Loprinzi, Frith, & Edwards, 2019).

Women typically show enhanced subjective, behavioral, and physiological reactivity to emotional stimuli (Bradley, Codispoti, Sabatinelli, & Lang, 2001; Lithari et al., 2010) and have been found to exhibit better emotional memory recall than men (Bloise & Johnson, 2007; Canli, Desmond, Zhao, & Gabrieli, 2002). Moreover, sex-dependent stress hormone effects on emotional learning and memory are well documented (Merz & Wolf, 2017; ter Horst, de Kloet, Schächinger, & Oitzl, 2012). However, whether sex also modulates the effects of exercise on emotional memory consolidation has not been investigated yet.

The present study therefore aimed to test the impact of post-learning acute exercise on memory for emotional and neutral visuospatial stimuli and the potential role of sex in moderating these effects. Healthy men and women learned an object-location task and were subsequently exposed to an acute exercise or control intervention. Memory retention was tested 24 h later. Based on previous research from the stress and exercise literature (Hackney, 2006; Roig et al., 2013; Schwabe et al., 2010), we hypothesized that first HR and cortisol would increase following the exercise relative to the control intervention and second that the exercise group would show improved memory recall for emotional stimuli on the following day (Loprinzi, Frith, et al., 2019). Since stress-induced cortisol and autonomic arousal has been linked to enhanced emotional long-term memory (Larra et al., 2014; Smeets et al., 2008), we further predicted that increases in HR and cortisol would be positively correlated with emotional memory recall.

2. Materials and methods

2.1. Participants

The required sample size was determined using G*Power 3.1 (Faul, Erdfelder, Buchner, & Lang, 2009), assuming a moderate-sized effect ($d = 0.52$) of acute cardiovascular exercise on long-term memory as reported in a *meta*-analysis by Roig et al. (2013). With $\alpha = 0.05$ and an assumed correlation of $r = 0.5$ for repeated measurements, 40 participants were required in order to detect a significant group × memory valence interaction with a power of 1-$\beta \geq 0.95$. Since we additionally aimed to explore the potential interplay between exercise and sex on emotional long-term memory, we also calculated the required sample size for detecting a three-way interaction between exercise, memory valence and sex with a probability of at least 1-$\beta \geq 0.90$. This analysis revealed a required sample size of n = 48.

We thus tested 48 healthy males (n = 22) and females (n = 26) aged between 18 and 35 years ($M = 23.38$, $SD = 2.86$) with a normal BMI ranging between 19–27 kg/m^2 ($M = 23.04$, $SD = 2.07$). They were randomly assigned to either the exercise (n = 25) or control group (n = 23). The mean number of days exercising per week ranged from 1 to 6 days ($M = 3.17$, $SD = 1.49$) and did not differ between the exercise and control group ($t_{(46)} = 1.75$, $p > .05$). Likewise, groups did not differ with regard to sleep duration on both testing days ($t_{(45)} = 0.42$, $p = .68$ and $t_{(46)} = 0.84$, $p = .41$). Prior to participation, all participants were required to fill out the Physical Activity Readiness Questionnaire (PAR-Q; Chisholm et al., 1978), evaluating their health status in regard to exercise. Exclusion criteria comprised chronic or acute illnesses, history of psychiatric or neurological treatment, drug use including smoking, regular medication or alcohol consumption. Female participants were not on hormonal birth control and not tested during their menses or pregnancy (Kirschbaum, Kudielka, Gaab, Schommer, & Hellhammer, 1999). Upon recruitment, they were asked to refrain from physical exercise and consumption of food and drinks except water two hours prior to testing. All participants provided written informed consent and were either paid an allowance of 25€ or received course credit.

2.2. Exercise and control intervention

A 20 min running task served as the acute exercise intervention carried out on a treadmill with a 10% incline. It started with a 1 min warm-up at walking pace, after which a stepwise increase of speed by 0.5 m/s was introduced every 30 s until the target heart rate (HR_{target}) was reached. On average, participants took 4–5 min to reach their HR_{target}. They then trained for 15 min at their HR_{target} and concluded the exercise with a 1 min cool-down at walking pace. Accumulating evidence suggests that a certain intensity threshold needs to be exceeded in order to reliably activate the HPA-axis (Heijnen, Hommel, Kibele, & Colzato, 2016; Hill et al., 2008; Jacks, Sowash, Anning, McGloughlin, & Andres, 2002). Moreover, it has been shown that particularly moderate- to high-intensity exercise facilitated memory consolidation (Etnier et al., 2016; Hötting, Schickert, Kaiser, Röder, & Schmidt-Kassow, 2016; Winter et al., 2007). The exercise group was therefore required to engage in a vigorous-intensity training, individually defined as 85% of the participants' heart rate reserve (HRR). To determine HRR and HR_{target} the following formula was applied: $HR_{target} = [(HR_{max}–HR_{rest}) \times 85\%] + HR_{rest}$, with the maximum age-predicted HR (HR_{max}) calculated as 220–participant's age (HRR method; American College for Sports Medicine, 2013).

Similar to previous studies (Coles & Tomporowski, 2008; Frith, Sng, & Loprinzi, 2017), the resting control intervention requested participants to sit quietly for 20 min while watching two documentaries showing instructions how to manufacture wooden objects. Participants rated each video regarding valence and arousal on a 9-point scale ranging from 1 = negative/calm to 9 = positive/aroused. As expected, both videos were experienced as emotionally neutral ($M = 6.70$, $SD = 1.43$ and $M = 6.39$, $SD = 1.80$) and not arousing ($M = 2.04$, $SD = 1.02$ and $M = 1.70$, $SD = 0.93$).

2.3. Cardiovascular and neuroendocrine measures

2.3.1. Heart rate

HR was recorded using a wireless HR transmitter, consisting of an elastic chest strap (Polar *H*10 Heart Rate Sensor, Polar® Electro, Finland) and a wrist monitor (Polar V800, Polar® Electro, Finland) providing a sampling rate of 1000 Hz. Recordings were obtained during a 5 min resting period (HR_{rest}), the 20 min exercise or control intervention, and a 5 min post-intervention period on day 1. After data acquisition, device specific software (Polar Flow ; Polar® Electro, Finland) was used to export the raw beat-to-beat data for further processing with Kubios HRV 3.1.0 (Tarvainen, Niskanen, Lipponen, Ranta-Aho, & Karjalainen, 2014) according to the guidelines of the Task Force of the European Society of Cardiology and the North American Society of Pacing and Electrophysiology (1996). Recorded data was detrended (smoothn priors: λ = 500), visually inspected for abnormal or biologically implausible beats and corrected with a threshold based artifact correction algorithm using cubic spline interpolation that was adjusted individually for every participant. HR was then calculated for each period.

2.3.2. Salivary cortisol

Saliva samples were collected using Salivette sampling devices (Sarstedt, Nümbrecht, Germany) at multiple time points across day 1 and stored at −20 °C until assayed. Samples were taken prior to memory encoding (baseline), −2min before the onset as well as +1 min, +10 min, +25 min and +40 min after cessation of the exercise or control intervention. Free cortisol concentrations were determined using commercially available chemiluminescence immunoassay (CLIA; IBL, Hamburg, Germany). Intra-assay and inter-assay coefficients of variations were below 10%.

2.4. Memory task

Visuo-spatial memory was probed using a computerized version of the well-known card game "Memory" using a version implemented by Schwabe and Wolf (2009). In this task, participants were presented with a configuration of 15 card pairs showing colored pictures varying in valence (5 neutral, 5 positive, and 5 negative) taken from the International Affective Picture System (Lang, Bradley, & Cuthbert, 2008). At the beginning, all cards were laid face down and participants chose two cards turning them face up. If the two cards showed the same picture, participants turned the next two cards. If they were different, the second card was turned face down again and participants had to continue searching for the correct match. Participants were instructed to find all matching picture cards as fast as possible while keeping errors minimal.

During the encoding phase on day 1, they completed two consecutive sessions of the memory task. On the following day, one retention test session was conducted. The cards were randomly arranged across participants but were kept constant within each participant. Memory performance was scored as the percentage of hits (i.e. correct card pair locations without error) for the retention test session on day 2 relative to the hits for the last encoding session on day 1.

2.5. Procedure

Participants were tested on two consecutive days with an interval of 24 h and sessions were scheduled between 1 and 6 pm to keep variations in the diurnal cortisol rhythm minimal (Horrocks et al., 1990; Joëls & Baram, 2009). All study procedures were in accordance with the Declaration of Helsinki and approved by the ethics committee of the Faculty of Psychology of the Ruhr University Bochum. The study protocol is summarized in Fig. 1A.

2.6. Statistical analyses

Statistical analyses were performed using IBM SPSS with $\alpha = 0.05$. Analyses of variance (ANOVA) always included the between-subjects factors group (exercise vs. control) and sex (men vs. women). Greenhouse-Geisser corrected *p*-values were used if assumptions of sphericity were violated and Cohen's *d* were reported as effect size estimations. For cardiovascular and neuroendocrine measures, mixed-design ANOVAs with the repeated-measurement factor time (HR: HR_{rest}, $HR_{intervention}$, HR_{post}; cortisol: baseline, −2min, +1min, +10 min, +25 min, +40 min) were conducted. Memory performance, expressed as percentage of hits was analyzed using mixed-design ANOVAs with emotional valence (neutral vs. positive vs. negative) as the within-subjects factor. Significant results were followed by Bonferroni-adjusted post-hoc *t*-tests. In order to test whether changes in HR or cortisol were related to memory performance, Pearson product-moment correlations were conducted for the entire group as well as for the exercise and control group and men and women separately. Therefore, we first calculated the following exercise increase scores. For HR, we computed ΔHR by subtracting the HR_{rest} from the $HR_{intervention}$ score and for cortisol, the area under the curve with respect to ground (AUC_G) was calculated as a measure of total hormonal output according to the trapezoid formula described in Pruessner, Kirschbaum, Meinlschmid, and Hellhammer (2003)[1]. Data was checked for non-normality using Shapiro-Wilk tests of normality, which showed skewness of cortisol and HR data. These data were thus log-transformed before use in subsequent analyses.

3. Results

3.1. Manipulation check: Exercise and control intervention

3.1.1. Heart rate

Acute exercise significantly increased participants' HR when compared to controls (main effect time: $F_{(2,88)} = 916.59$; $p < .001$; $d = 8.72$, main effect treatment: $F_{(1,44)} = 112.04$; $p < .001$; $d = 3.21$, time × group interaction: $F_{(2,88)} = 1082.97$; $p < .001$; $d = 9.80$). While HR did not differ at rest, participants exhibited significantly higher HR during ($t_{(46)} = 32.76$; $p < .001$; $d = 9.68$) and after ($t_{(46)} = 7.22$; $p < .001$; $d = 2.09$) the exercise relative to the control intervention (see Fig. 1C).

3.1.2. Salivary cortisol

There was a significant main effect of time ($F_{(5,215)} = 8.48$; $p = .002$; $d = 0.91$), group ($F_{(1,43)} = 11.68$; $p = .001$; $d = 1.03$) and time × group interaction ($F_{(5,215)} = 13.89$; $p < .001$; $d = 1.12$), revealing that cortisol concentrations were significantly elevated +10 min ($t_{(46)} = 40.95$; $p < .001$; $d = 1.22$), +25 min ($t_{(46)} = 40.78$; $p < .001$; $d = 1.71$) and +40 min ($t_{(46)} = 40.60$; $p < .001$; $d = 1.64$) after the exercise relative to the control intervention (Fig. 1B). Cortisol levels did not differ between groups at baseline, immediately before or after the exercise manipulation (all $ps > 0.05$).

3.2. Memory performance

For the percentage of hits, ANOVA revealed a significant valence × group × sex interaction ($F_{(2,82)} = 3.94$; $p = .023$; $d = .06$). Following up on this, separate univariate ANOVAs for each valence category indicated that participants of the exercise group remembered more positive card pairs than controls (main effect treatment: $F_{(1,44)} = 4.90$; $p = .032$; $d = 0.67$; Table 1). This beneficial effect of exercise on memory retention for positive card locations was more pronounced in males (group × sex interaction: $F_{(1,44)} = 4.76$; $p = .034$; $d = 0.67$; main effect treatment in men: $F_{(1,20)} = 8.36$; $p = .009$; $d = 1.31$; Fig. 2). A significant group × sex interaction occurred also for negative card pairs ($F_{(1,43)} = 5.14$; $p = .029$; $d = 0.70$). Women who exercised after memory encoding tended to remember more negative card pairs when compared to controls (main effect treatment in women: $F_{(1,24)} = 4.36$; $p = .055$; $d = 0.84$, Fig. 2). Overall, memory performance tended to be higher for negative than positive card pairs ($F_{(2,82)} = 3.04$; $p = .053$; $d = 0.55$; $p = .055$ for exploratory Bonferroni-corrected post-hoc *t*-tests).

3.3. Relationship between physiological changes and memory performance

For women, both a stronger HR increase ($r = 0.39$; $p = .05$) and cortisol output ($r = 0.49$; $p = .013$) was related to better memory for negative pairs. By contrast, for men, a positive association was found between post-encoding HR increase and memory for positive pairs ($r = 0.56$; $p = .007$) as well as between cortisol output and memory for neutral pairs ($r = 0.49$; $p = .025$). Overall, participants with a higher cortisol output remembered more neutral pairs on day 2 ($r = 0.40$; $p = .006$). Correlational analyses conducted separately for the exercise and control group furthermore indicated that this positive association between cortisol and memory for neutral pairs was evident in the exercise group (overall: $r = 0.49$; $p = .016$) for both men ($r = 0.61$; $p = .048$) and women ($r = 0.56$; $p = .045$), but only for women ($r = 0.67$; $p = .024$) in the control group (overall: $r = 0.16$; $p = .49$). Similarly, higher cortisol levels in the exercise group were positively

[1] The AUC_G was computed by summarizing the trapezoids that are calculated with **(a)** the cortisol values themselves (i.e. baseline, −2min, +1min, +10min, +25min, +40min) and **(b)** the time distance between these measurements. The formula thus takes into account both the difference between the single measurements from each other (i.e. the change over time) and the distance of these measures from the ground (i.e. the level at which the changes over time occur).

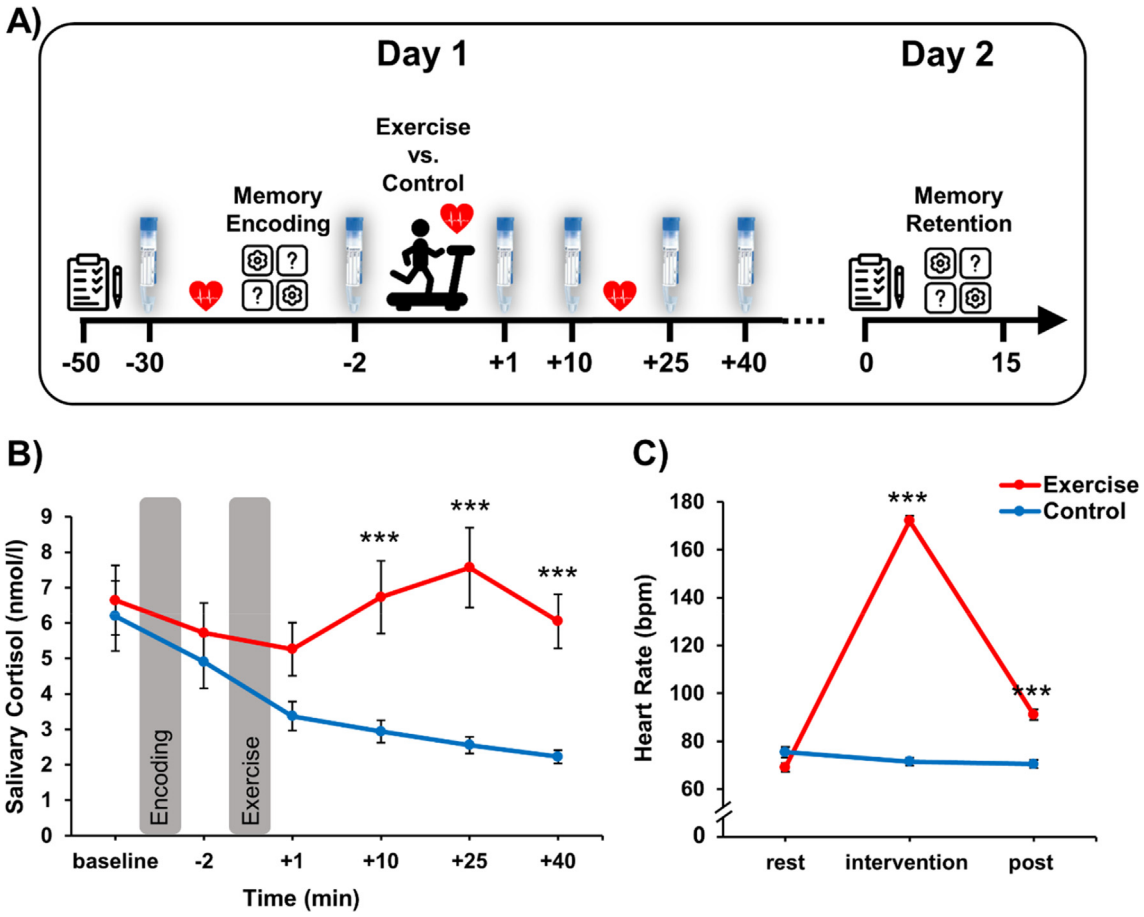

Fig. 1. A) Overview of the study protocol. On day 1, participants performed two sessions of the memory card game (i.e. encoding) and were then exposed to an exercise or control intervention. Memory performance was tested 24 h later in a retention test session. Salivary cortisol (indicated with salivette symbols) was collected before memory encoding, immediately before as well as +1, +10, +25 and +40 min after the exercise or control intervention. Heart rate (indicated with a heart symbol) was measured at rest (before memory encoding), during and after the exercise and control intervention. B) Salivary cortisol concentrations and B) heart rate (HR) responses in the exercise and control groups. Participants in the exercise group showed a significant increase in salivary cortisol and HR, whereas no such increase was found in controls. Data represent means ± SEM. ***$p < .001$.

Table 1
Performance in the exercise and control groups expressed as correct card pair locations across the two encoding sessions on day one (1 and 2) and on the retention test session on day two (3).

	Correct Card Pair Locations								
	neutral			positive			negative		
	1	2	3	1	2	3	1	2	3
	M (SD)	*M (SD)*	*M (SD)*	*M (SD)*	*M (SD)*	*M (SD)*	*M (SD)*	*M (SD)*	*M (SD)*
Exercise	2.32 (1.38)	2.80 (1.29)	2.96 (1.17)	2.36 (1.15)	2.76 (1.20)	2.88 (1.30)	2.68 (1.07)	2.60 (1.22)	3.04 (1.02)
Control	2.00 (1.13)	2.57 (1.12)	2.96 (1.02)	2.26 (1.14)	3.09 (1.08)	2.52 (1.12)	2.35 (1.11)	2.57 (1.12)	2.74 (1.21)

related to memory for negative pairs ($r = 0.46$; $p = .026$), whereas no such correlation was found for the control group ($r = 0.01$; $p = .97$).

4. Discussion

The present study indicates that performing physical exercise shortly after encoding improved emotional memory retention 24 h later. This exercise-induced consolidation enhancement was specific to negative items in women but positive items in men and positively related to the increase in HR and cortisol in response to exercise. Our findings thereby provide first evidence for a sex-specific modulation of emotional memory consolidation by exercise, which is potentially mediated via interactions between GCs and SNS-related activity.

As expected (Hill et al., 2008; Hummel et al., 2018; Skoluda et al., 2015), our exercise intervention reliably activated the SNS and HPA axis, leading to significant increases in HR and cortisol, respectively. The facilitation of emotional memory consolidation furthermore lines up with previous work showing long-term memory improvements following aerobic exercise (Roig et al., 2013). However, the majority of these studies required participants to exercise before or during learning, theoretically affecting both memory encoding and consolidation. By placing the exercise intervention directly after learning, here we provide direct evidence for a consolidation-enhancing effect, which specifically occurred for emotional stimuli. Our data thereby extend the current exercise literature, indicating that exercise effects may interact with the emotional content of the encoded material rather than

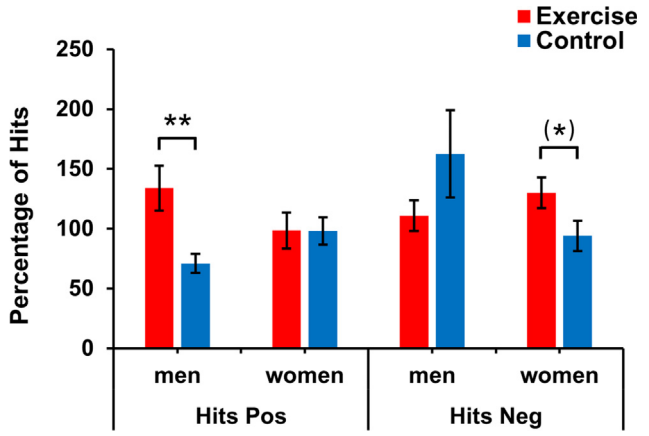

Fig. 2. Percentage of correct card locations on the retention test session relative to the last encoding session 24 h before as a function of group (exercise vs. control) and sex (men vs. women). Post-encoding exercise enhanced memory performance for positive card pairs in men, while it tended to increase memory for negative card pairs in women. Data represent means ± SEM. $^{**}p < .01$, $^{(*)}p = .055$.

proposing a benefit for memory in general. This corroborates with newly emerging evidence suggesting an exercise-induced augmentation of emotional memory (Loprinzi, Frith, et al., 2019). Paralleling these results, there is a large body of work demonstrating that acute stress also selectively enhances emotional memory (Wolf, 2008) and that this effect is mediated by GCs interacting with noradrenergic activity in the BLA to modulate memory consolidation in the hippocampus (Roozendaal & McGaugh, 2011). Consistent with this idea, we could show that post-encoding increases in HR and cortisol were related to improved retention of emotional items. Correspondingly, work in rodents demonstrated that blocking GC synthesis prior to exercise impairs both the acquisition and retention of an arousing spatial learning task (Hajisoltani et al., 2011). Similar associations were found between emotional memory and elevations in HR, alpha-amylase, and cortisol following stress exposure (Larra et al., 2014; Smeets et al., 2008), suggesting that the beneficial effects of acute exercise and stress on emotional memory consolidation rely at least to some extent on similar autonomic-neuroendocrine mechanisms. In the present study however, a stronger cortisol output especially in the exercise group was not only related to better memory for emotional but also for neutral items, indicating that exercise-induced cortisol (but not autonomic arousal) might also facilitate neutral memory recall. Neutral material is usually less well remembered than emotional material, probably due to the lower arousal associated with these stimuli (Cahill & McGaugh, 1998; LaBar & Cabeza, 2006). It could be speculated though that a pronounced post-learning cortisol increase in response to exercise might compensate for this lack of arousal and hence also enhance the memorability of neutral items. Our results therefore may also imply that autonomic arousal and cortisol could be differently involved in the effects of post-learning exercise on memory for neutral and emotionally valent material. Given that the underlying mechanisms of exercise-related memory modulations are still poorly understood, future studies are warranted which systematically explore the different contributions of the SNS and HPA axis in mediating these effects, for example by using pharmacological agents to either activate or block GC or (nor) adrenergic activity during acute exercise. Furthermore, it has to be noted that physical exercise stimulates a complex set of signaling pathways, leading to increases in a variety of different neurochemicals (Keyan & Bryant, 2019), including hormones, neurotransmitters, neurotrophins (e.g. BDNF) or other neuromodulators such as endogenous opioids that might contribute to neuroplasticity and stabilize synaptic networks tagged during consolidation processes (Basso & Suzuki, 2017; Cassilhas, Tufik, & de Mello, 2016). However, the distinct contributions of such neurochemicals on exercise-related memory improvements have yet to be disentangled.

Exercise affected emotional memory in a sex-specific manner. While it improved the retention of negative items in women, the memory benefit for positive items was more pronounced in men. This result pattern corroborates with data showing that post-encoding stress specifically enhanced the consolidation of negative images in women (Felmingham, Tran, Fong, & Bryant, 2012). Interestingly, this effect was related to the amount of cortisol released in response to the stressor, whereas a stronger correlation between cortisol and recall for neutral images were found in men. Similarly, Segal and Cahill (2009) found greater noradrenergic activation and concurrent recall of negative images in women relative to men, suggesting that women have a greater sensitivity to stress hormone effects particularly when processing threat-related information. In the present study, positive correlations between correctly recalled negative pairs and increases in HR and cortisol also occurred especially in women, whereas in men, stronger HR increases were related to memory for positive pairs, and cortisol output to memory for neutral pairs. Given that increases in HR or cortisol in response to our exercise intervention did not differ between sexes, our findings rather suggest that the same neuroendocrine signals triggered by exercise may affect memory consolidation differently in men and women. Furthermore, men and women could have also differed in their emotional response to the pictures presented in the memory game. In support of this idea, sex differences in the processing of emotional stimuli have been frequently reported, with women typically displaying stronger subjective, physiological and neural emotional reactivity, in particular to aversive stimuli (Bradley et al., 2001; Canli et al., 2002; Lithari et al., 2010), whereas responses to pleasant stimulation are sometimes more pronounced in men. For the present study, it could therefore be speculated that exercise boosted memory for pictures that were experienced as particularly arousing. Yet, to directly test such interactions, emotional responses to the to-be-learned material have to be assessed in future studies. Sex-dependent effects of physical exercise have been recently reported for the consolidation of fear extinction memory in rodents (Bouchet et al., 2017). We add up to this line of research by providing first evidence for a sex-specific effect of exercise on the consolidation of emotional memories in humans. Future research is yet needed to allow for a more detailed understanding of how sex hormones may interact with neurochemicals triggered by acute exercise to influence memory consolidation.

There are some limitations of this study. First, we did not use a VO_2max test to assess participants' cardiovascular fitness. Even though self-report measures indicated that groups did not differ in exercise frequency per week, we hence cannot rule out whether the current results were modulated by the fitness level of our participants. Likewise, it remains open if specific cognitive functions or cognitive capacity in general could play a mediating role for exercise to exert its beneficial effects on memory. Future studies should ideally include both a cognitive screening and a standardized fitness test at baseline to gain more insight into potential moderators of exercise-induced memory improvements.

In conclusion, the present study demonstrates that a single bout of physical exercise promotes emotional memory consolidation, resulting in enhanced recall for negative items in women and positive items in men on the following day. This sex-specific effect is potentially mediated via a co-activation of the SNS and HPA-axis, triggering molecular signaling pathways crucial for consolidation processes. Since exercising is healthy, cost-effective and easy to implement in daily life, it constitutes an ideal intervention strategy for boosting memory in clinical and educational settings alike.

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