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An integrated model of acute exercise on memory function

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ABSTRACT

Memory is a complex cognition that plays a critical role in daily functioning. This review discusses the dynamic effects of acute exercise on memory function, via a hypothesized exercise-memory interaction model, taking into consideration multiple memory systems and exercise parameters.

Introduction

Adequate cognitive function is of critical importance for quality and quantity of life [1]. Memory function is an essential cognitive function that defines the temporal aspects of our cognitive processes. Among the several types of cognitive parameters, such as memory, planning, and executive function, this review focuses on memory function, given its critical role in daily functioning and its ability to be modulated with acute exercise.

Although not an exhaustive list [2–24], several research groups have made considerable progress in our understanding of how exercise may subserve human memory function. Details regarding the effects of chronic exercise on cognition, including memory function, have been discussed in prior work [9,10,13,25–36]. Herein, and unless stated otherwise, I focus on the role of acute exercise (single bout of exercise) on memory function, including multiple memory types, as further discussed herein. I briefly introduce research for varying populations (e.g., healthy and diseased) across the lifespan, given the notable age- and disease-associated effects on memory function [37]. This is a growing area of research, and as noted herein, is dynamic and may be influenced by a multitude of proximal and distal factors. This is not an exhaustive review of the literature, but rather, the purpose of this succinct review is to highlight recent research within the context of a hypothesized exercise-memory interaction model (Fig. 1). As further developed herein, this hypothesized model suggests a complex interrelationship between acute exercise and memory. This model may also serve as a guide for future empirical work (among adult human studies) on this topic. Such work may have important implications in increasing an individual's perception of their ability to control their memory [38], as well as maintaining and improving societal trends of memory function [39].

Model overview

The direct effect of exercise on memory is somewhat mixed. In a meta-analysis, 48% of studies demonstrated that acute exercise improved short-term memory, whereas 58% of acute exercise studies improved long-term memory [12]. This variation may be a result of several factors, such as exercise modality, exercise intensity, or memory type evaluated. As such, I discuss these factors in more detail hereafter.

As shown in Fig. 1, I hypothesize that acute exercise indirectly influences memory function via several pathways, including alterations in executive function, mood, and long-term potentiation (LTP). This effect may be influenced by several factors, including the timing of exercise (temporality), duration of exercise, intensity of exercise, modality of exercise (including open vs. closed skilled exercises), pattern of exercise (e.g., intermittent vs. continuous), actual vs. imagined exercise, and the population assessed (e.g., young adults, diseased individuals), including exclusionary characteristics (e.g., handedness) of the population. The effect of acute exercise on memory may also depend on the memory type, including explicit, emotional, false memory, implicit, prospective, procedural, working memory, or memory interference. In addition to acute exercise potentially enhancing memory function, the hypothesis-driven model (Fig. 1) also suggests that exercise may help to attenuate memory impairment, which may occur from various influences, such as psychosocial stress. Lastly, as depicted in the model, exercise and memory may be bi-directionally related.

The narrative that follows will highlight recent research delineated by the pathways shown in the model (Fig. 1). These discussions are intended to be brief, with references provided to studies that have discussed these relationships in more detail, including proposed underlying mechanisms. Thus, the primary aim of this review is to introduce this complex, hypothesis-driven model that suggests a dynamic effect of acute exercise on memory function.

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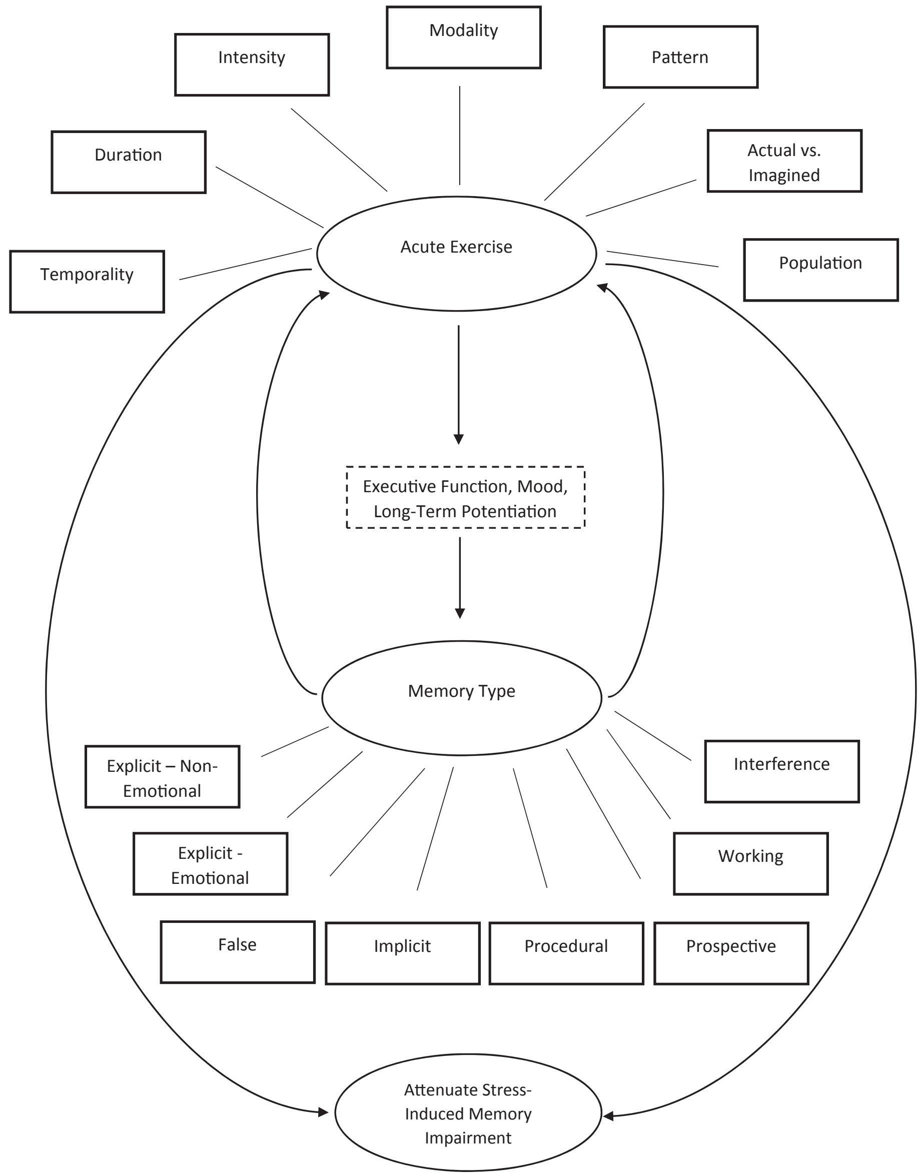

Fig. 1. Hypothesized model depicting the dynamic effects of acute exercise on memory function. Circles represent outcomes, solid rectangles represent moderators, and dashed rectangles represent mediators.

Effects of exercise on memory

Timing of exercise

The temporal coupling (i.e., when the exercise occurs in relation to the memory task) of exercise and memory encoding appears to play a crucial role in the effects of exercise on memory function (Fig. 2). This has been thoroughly discussed elsewhere [11]. Mechanistically, when exercise occurs prior to encoding, it may subserve memory function through the facilitation of long-term potentiation [40,41], via associativity and tag-and-capturing mechanisms [42]. Further, depending on the intensity, modality, and duration of exercise, acute exercise may facilitate memory encoding via enhanced attentional processing. Acute exercise, during the consolidation stage of memory function, may enhance the consolidation of the memory trace via exercise-induced alterations in neurotrophins that stabilize the memory trace. However, depending on the intensity exercise, exercise that occurs during memory encoding may have detrimental effects on memory via a transient redistribution of neuronal resources away from key memory-related brain structures (e.g., prefrontal cortex) [43].

Labban & Etnier provided initial [3] and more recent [44] evidence that acute exercise, occurring shortly before the memory task, is advantageous in enhancing long-term memory. In a free-living experiment, Pontifex et al. [6] demonstrated that physical activity during the period of 1–2 h following memory encoding was detrimental to the maintenance of memory, whereas physical activity occurring 1-hour prior to memory retrieval was associated with greater memory performance. We have also demonstrated the importance of exercise timing on memory function. In a between-subject design [45], we showed that acute moderate-intensity walking shortly before the memory task was advantageous in facilitating memory function, when compared to other temporal periods. We then replicated this finding in two separate within-subject design studies, one including a 15-min moderate-intensity exercise protocol [46] and the other including a 20-min moderate-intensity exercise protocol [47]. We also replicated this temporal effect (acute exercise shortly before the memory task being advantageous) with a high-intensity exercise protocol [48]. Collectively, these findings suggest that when acute exercise occurs shortly before episodic memory encoding, memory function may be enhanced. In alignment with the work of others [16], we have also shown that when acute

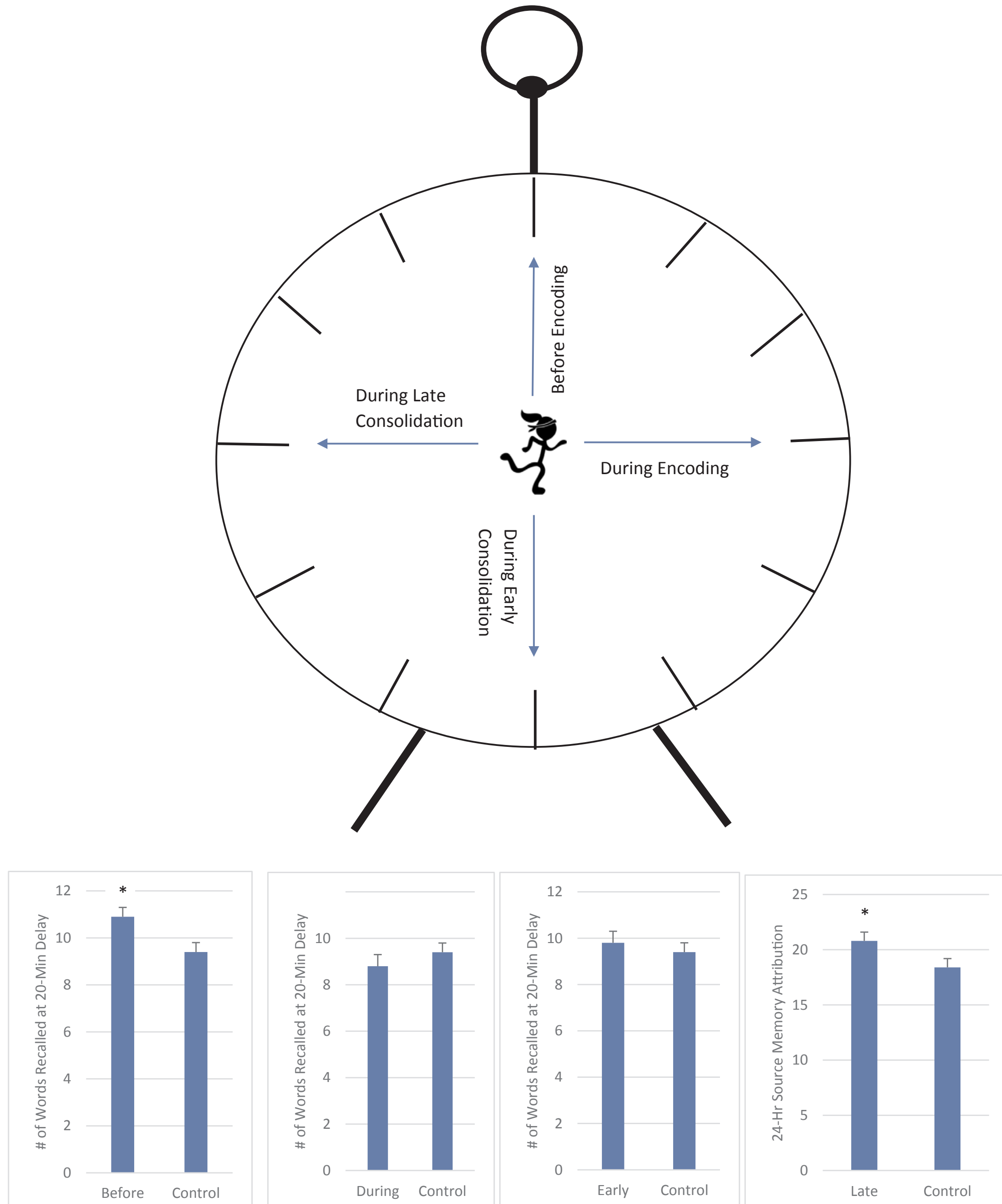

Fig. 2. Time-dependent effects of acute exercise on episodic memory function. Data from the first three graphs (before, during, and early) come from Frith et al. [113]; data from the last graph (late) comes from Delancey et al. [49].

exercise occurs several hours (i.e., 4) into the memory consolidation stage, long-term memory may be enhanced [49]. Related findings in animal models have also been observed [50]. Interestingly, other animal work, utilizing a chronic training protocol, indicates that when the exercise occurs (e.g., morning, day, evening) may influence the effects of exercise on memory function [51]. Further, not only does the timing of exercise during the day have an effect on memory, but, in animal work, the timing of exercise across developmental ages has been shown to influence the effects of exercise on memory and neuroplasticity [52].

For human studies, as demonstrated below, the memory type may moderate this effect. As an example, human work has demonstrated that when acute exercise occurs during the very early stages of memory consolidation, procedural memory is enhanced [53]. However, other work shows that procedural learning and situation model memory may be enhanced with exercise, regardless of whether exercise occurs before or after encoding [54]. Lastly, as discussed elsewhere [11], the intensity of exercise may moderate the temporal effects of acute exercise on memory function. For example, an exhaustive bout of exercise prior to memory encoding may impair immediate memory function [55].

Duration of exercise

In a comprehensive *meta*-analysis, Roig et al. [12] evaluated the potential moderation effects of exercise duration on human memory function. They concluded that the effects of acute exercise on short-term memory appeared to be greater when the exercise bout was relatively short (< 20 min) and performed at lower intensities. Similarly, regardless of intensity, shorter and medium duration exercise (vs. longer duration exercise, i.e., > 40 min)) were more favorable in enhancing long-term memory. Although speculative, perhaps longer duration exercise may have a less favorable effect on memory processing and consolidation due to heightened activation of the HPA axis and/or alterations in mental fatigue. We recently provided some suggestive evidence that the exercise bout duration may also interact with the post-exercise recovery period to influence memory function [56]. Young adult participants completed two experimental visits, including a control visit and an exercise visit. For the exercise visit, participants were randomly assigned to an acute bout of moderate-intensity treadmill exercise (10, 20, 30, 45, or 60 min) followed by a period of rest (5, 15, or 30 min). Our results suggested an interaction effect of exercise duration and recovery period on memory. For example, shorter and longer (but not medium) durations, coupled with a short recovery period, were advantageous in enhancing memory function.

Intensity of exercise

In a recent publication of ours [57], we reviewed the literature to examine the extent to which acute exercise intensity may influence human memory function. Results varied based on the timing of exercise and the memory type. Findings were: 1) when acute exercise occurs before the memory task, high-intensity exercise, when compared to lower intensities, may be less favorable for working memory but may favor episodic memory; 2) when acute exercise occurs during the memory task, high-intensity exercise may be less favorable for working memory capacity; and 3) high-intensity exercise may not associate with long-term episodic/working memory function when it occurs shortly after memory encoding.

High-intensity exercise may favor episodic memory function via greater increases in key neurotransmitters (e.g., dopamine and norepinephrine) that activate various intracellular signaling pathways (e.g., PKA) to facilitate CREB transcription, and in turn, augment late-phase long-term potentiation. However, these effects may be less favorable for prefrontal cortex-dependent working memory capacity, as activated D_1- and β-adrenoreceptors may dampen prefrontal cortex neuronal activity via cAMP opening of nearby K + channels [57].

Modality or type of exercise

In their *meta*-analysis, Roig et al. [12] indicated that acute walking was superior for short-term memory, with cycling-based exercise being advantageous for long-term memory. However, few studies were included in these moderation analyses, demonstrating the need for additional work on this topic. Conceptually, this has been discussed elsewhere [58,59], indicating that modality-specific exercise may alter neuroelectrical correlates of memory function. Drawing on animal studies [60–64], which have compared aerobic exercise training to resistance exercise training, both modalities tend to improve memory function, however, they appear to activate unique memory-related intracellular pathways. For example, aerobic training has been shown to increase hippocampal levels of IGF-1, BDNF, TrkB, and β-CaMKII, whereas resistance training has been shown to increase peripheral and hippocampal levels of IGF-1, with concomitant activation of IGF-1 receptor and AKT in the hippocampus [60]. Critically, though, these studies employed chronic exercise protocols, and thus, provide limited information as to whether the modality of exercise moderates the effects (and mechanisms) of acute exercise on memory. Future work should address this gap in the literature.

Related to the modality of exercise, the movement patterns of the stimulus may have unique cortical demands, with more complex movement patterns increasing cortical excitability [65,66]. Behaviorally, research demonstrates that open-skilled exercises (e.g., wrestling) are more effective in enhancing working memory when compared to closed-skilled exercises (e.g., walking) [67–69]. This effect, however, may not occur for procedural memories [70]. In animal work, the type of exercise has been shown to induce neuroplasticity in specific brain regions [71]. Similar to the above assertion, the field is in need of additional work evaluating whether different acute exercise patterns have a unique effect of memory.

Pattern of exercise

As we have discussed elsewhere [67], and although considered in the context of exercise-related affect [72], limited research has evaluated whether the pattern of exercise, for an acute bout of exercise, may influence memory function. In an animal model, and for chronic training, intermittent voluntary wheel running (vs. voluntary continuous wheel running) was more effective in enhancing hippocampal neurogenesis and spatial memory [73]. Other animal work [74] evaluated whether neurogenesis and spatial memory were different between regular running, irregular duration running, and irregular time-of-day running, and showed that regular running (i.e., running at the same time of day for the same speed and duration) was most effective in enhancing neurogenesis and spatial memory. Future work evaluating this paradigm among humans is needed. That is, it would be useful to determine whether intermittent vs. continuous acute exercise, as well when during the day this occurs, has a unique effect on memory function. Such work should also carefully consider the volume of exercise when considering these different patterns of acute exercise on memory function.

Actual vs. Imagined

Actual physical locomotion has been shown to enhance memory function, and interestingly, imagined locomotion may also increase neuronal activity in key memory-related brain structures [75]. This makes us question whether it is the actual locomotion or, perhaps, the perceived nature of the event that may be influencing neuroelectrical correlates of memory. Of course, both scenarios could be contributory, or perhaps, acting synergistically (Fig. 3). Thus, we should consider moving beyond a model of locomotion that involves minimal cognitive engagement. It would be worthwhile to investigate whether actual and imagined locomotion have differential effects on episodic memory. Further, this area of research could be advanced by comparing actual locomotion to locomotive activities that include varying degrees of cognitive engagement (e.g., imagery of locomotion, cognitive resource depletion via inhibitory-based tasks). At this point, it is uncertain as to whether imagined vs. actual movement have differential effects on memory, but this is an area noteworthy of investigation.

Population assessed

In a recent systematic review [76], physically fit children were found to have greater hippocampal volume, enhanced working memory capacity, and improved learning outcomes. Among adults, in a *meta*-analysis by Roig et al. [12], age appeared to moderate the effects of acute exercise on memory function, with effects being larger for younger adults. However, additional work is needed to further our understanding of potential age-moderated effects of acute exercise on memory function. We have demonstrated that, among young adults, approximately 71% [67] of studies demonstrate a beneficial effect of exercise on memory. We have observed these beneficial effects in several of our experimental acute exercise studies [45–49,77,78]. We have also demonstrated that exercise may have memory-enhancing effects for neurological populations, including those with mild cognitive impairment [79], Parkinson's disease [80,81] and Alzheimer's disease [82,83]. However, most of this work has focused on the effects of chronic exercise on memory function among these populations.

Other population-specific recommendations for studies evaluating the effects of acute exercise on memory function have been made [84,85]. Specifically, we need additional studies evaluating whether sex moderates the effects of acute exercise on memory function, as biological sex has a differential effect on episodic memory [84]. Further, we should consider not excluding left-handed individuals when evaluating the effects of acute exercise on memory function [85]. Handedness plays an important role in behavioral measures of episodic memory

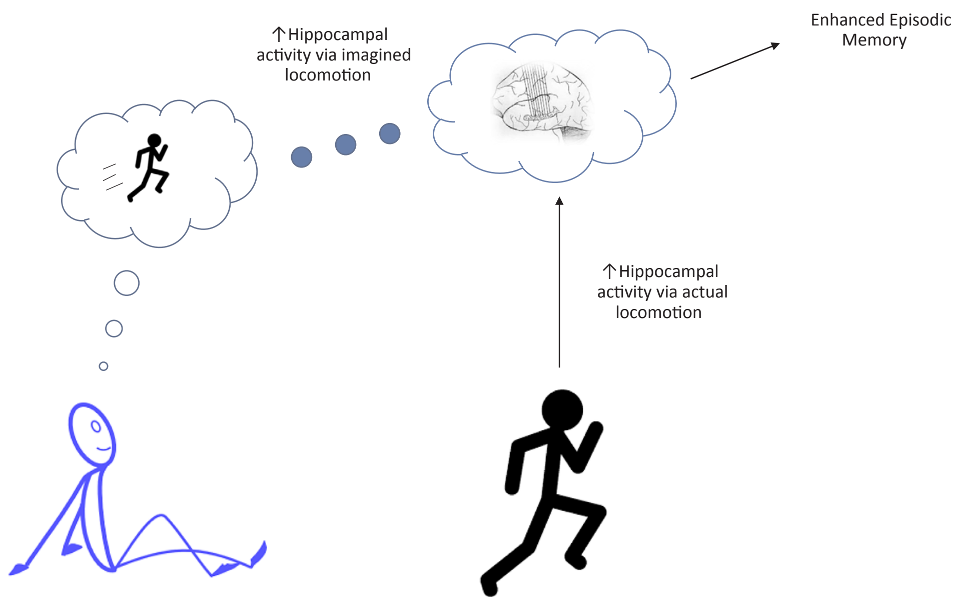

Fig. 3. The potential role of actual and imagined locomotion on hippocampal-dependent episodic memory.

function (e.g., mixed-handed individuals tend to outperform their counterparts on various memory tasks) [85]. It would be worthwhile to investigate whether handedness moderates the effects of acute exercise on memory function.

Although not all studies demonstrate a mediating effect of neurotrophins (e.g., BDNF) on the effects of exercise on memory [86], future work on this topic should take into consideration BDNF val66 genotype. Lastly, recent work from our laboratory indicates that baseline cognitive function may moderate the effects of acute exercise on cognition, in that individuals with lower baseline cognitive function performance demonstrate greater exercise-induced cognitive improvements [56]. This aligns with other recent work from other laboratories [87,88]. Thus, future work should consider evaluating individual differences regarding the effects of acute exercise on memory.

Moderation effects of memory type

Explicit memory

Explicit memories, or consciously encoded memories, are often subdivided into episodic and semantic memories. Episodic memories are spatiotemporal memories consisting of "what", "where", and "when" aspects of a memory, whereas semantic memories consist of non-contextual facts. Few exercise-related experimental studies have evaluated each of the constituents of an episodic memory (i.e., what, where, and when). Common protocols include using paragraph passages or word-list trials [45,46,48,78]. We have demonstrated that acute exercise may be causally related to (weak-to-modest) improvements in episodic memory [45,46,48,78]. Although under-investigated, we have also discussed the potential role that exercise may play in subserving semantic memory, via induced activations of internal representations of semantic memories [89]. These general favorable effects of acute exercise on explicit memory, particularly episodic memory, is support by several review studies [12,13,67]. As we have thoroughly discussed elsewhere [40,42], a likely candidate mechanism through which acute exercise influences episodic memory is through LTP-related mechanisms.

Emotional memories

A form of explicit memory, emotional memories are memories with vivid, or emotionally-charged stimuli, which may help to enhance encoding and consolidation of memories. Potential mechanisms of emotional memory incorporate psychological (e.g., rehearsal, elaboration, attentional encoding), neural (e.g., adrenoreceptor activation) and hormonal systems (e.g., cortisol facilitation of synaptic plasticity) [90]. We recently reviewed the literature regarding the effects of exercise on emotional memory, as well as the underlying mechanisms of this potential relationship [90]. Although this area has not been extensively investigated, accumulating research provides encouraging evidence that exercise may help to subserve emotional memory [90], particularly if the exercise bout occurs during the early consolidation period, as opposed to prior to memory encoding [91].

False memories

Another area that is ripe for additional research is the potential role of acute exercise on false memories. False memories, which we have assessed using the Deese-Roediger-McDermott (DRM) Paradigm [92], involves the presentation of a list of associates (e.g., bed, rest, awake) for 1 non-presented word/lure (e.g., sleep). A false memory occurs if an individual recalls this non-presented lure after being exposed to the list of associate words. We have conducted two separate experiments evaluating the effects of acute exercise of false memory, and both studies provided suggestive evidence (albeit weak) that acute walking may help to minimize a false memory effect [47,77]. Given that paucity of work in this area, explanations for this effect are unclear. Speculatively, and via its influence on the hippocampus and prefrontal cortex [40,93,94], acute exercise may subserve the encoding of contextually specific information (reactivate verbatim memory traces and attenuate the reactivation of gist traces [95]), and in turn, minimize false memory recall. Further, and related to the enhancement of prefrontal cortex functioning, acute exercise may improve executive function [96], which is important for attenuating false memories [97].

Implicit memory

Implicit memories are memories not under conscious encoding. We recently reviewed the evidence linking exercise with implicit memories [98]. Relatively few human experimental studies have investigated the effects of exercise on implicit memories, with the majority of these studies conducted in animal models. Among the few human studies on this topic, findings are mixed [98], underscoring the importance of additional work on this topic. Notably, however, it is conceivable that acute exercise could enhance implicit memory, as there are shared molecular mechanisms (e.g., LTP) subserving both explicit and implicit memory [99,100]. Relatedly, research demonstrates that unconscious relational encoding may be influenced by the hippocampus [101–103], which is a critical memory-related brain structure that is influenced (increased neuronal activity) by acute exercise [104].

Procedural memory

Procedural memory, or gains in motor memory, have been observed when acute exercise occurs during the early stages of memory consolidation [105]. Although exercise type does not appear to influence this effect [70], exercise intensity does [106], with higher intensities favoring greater gains in procedural memory. Mechanisms of these effects may be related to alterations in corticospinal excitability [107] and LTP [17].

Prospective memory

Prospective memories involve the execution of an intended behavior. Our recent review paper discusses the plausibility through which exercise may positively influence prospective memory [108]. For example, exercise may alter several psychological and cognitive parameters (e.g., emotional state, executive function) that may influence the initiation and execution of prospective memories [108]. However, in five separate experiments that we have conducted [45,46,48,49,77], we have failed to demonstrate any convincing evidence that acute exercise influences prospective memory. Unlike our five published experiments which focused on aerobic exercise, a recent study provided suggestive evidence that resistance exercise may help to improve prospective memory [109]. Notably, as we have detailed elsewhere [110], the effects of resistance exercise on memory in general, is an emerging area of research.

Working memory

Working memory performance involves the temporary storage of information to be later recalled. This occurs while concurrently processing other information. Per Baddely's model [111], working memory capacity is multidimensional, involving central executive function and two independent subsystems (phonological loop and visual-spatial sketchpad). As reviewed elsewhere [112], chronic exercise is effective in enhancing working memory capacity, whereas the effect of acute exercise on working memory is less consistent. Additional work investigating the effects of acute exercise on working memory is needed.

Memory interference

As a component of working memory, memory interference is often classified as proactive or retroactive memory interference (Fig. 4). Proactive interference involves a preceding stimulus interfering with the recall of a subsequent, target stimuli. Retroactive interference involves a subsequent competing stimulus interfering with the recall of a previously encoded target stimuli. We have published three experiments on acute exercise and memory interference [113–115], with all three experiments providing some, but not necessarily convincing evidence, that acute exercise may minimize a proactive and retroactive memory interference effect. However, given the few studies specifically evaluating the effects of acute exercise on memory interference, additional work in this area is needed. If future research demonstrates robust effects of acute exercise on attenuating memory interference, then follow-up work will need to identify the candidate mechanisms of this effect. I anticipate that exercise-induced regulation of the medial prefrontal cortex will likely play a mechanistic role, via facilitating inhibitory effects during encoding (e.g., competing pattern separation in the hippocampus) and retrieval (e.g., differential activation of the target and interfering engrams).

Attenuation effects of exercise on stress-induced memory impairment

As demonstrated, acute exercise may help to subserve various memory types, including episodic and emotional memory. As we have detailed elsewhere [116], psychophysiological stress may influence memory function, and exercise may help to attenuate this potential stress-induced memory impairment effect. For example, exercise may help attenuate chronic stress-induced memory impairment via reduction of HPA axis activity, oxidative stress suppression, production of new neurons, and regulation of mineralocorticoid and glucocorticoid receptor expression [117]. However, this body of research has almost exclusively been conducted in animal models employing a chronic exercise training protocol. Although we have shown that acute exercise can attenuate a stress-induced affective response [118], we are in need of human studies evaluating the effects of acute exercise on potentially attenuating a stress-induced memory impairment effect. In addition to potentially attenuating stress-induced memory impairment, it would be worthwhile to evaluate if acute exercise can still enhance episodic memory function across varying exposure levels of psychological stress. Further, not all forms (e.g., modality and intensity) of exercise induce the same activation of valence and arousal, and thus, future work would benefit by evaluating whether the exercise-induced valence and arousal response moderates the effects of exercise on memory function.

Bi-directional effects of exercise and memory

Thus far, I have illustrated the complex effects of acute exercise in potentially subserving memory function. Importantly, this relationship is likely not unidirectional, but rather, bi-directional. We have thoroughly discussed this elsewhere [119,120]. Although an acute bout of exercise may, potentially, influence memory function, the memory of the affective response from exercise may play an important role in subsequent exercise behavior. Research demonstrates that the affective response during exercise predicts future exercise behavior [121]. Individuals are likely to avoid exercise if they associate it with displeasure [122]. Identifying and promoting enjoyable activities is a key aspect of lifelong exercise engagement. Thus, the experience, and memory of that experience, plays a critical role in exercise behavior, and by extension, cognitive health. As a result, promoting activities that leave a positive memory should be of high priority in exercise prescription programs.

Conclusion

In conclusion, this brief review highlights the dynamic relationship between acute exercise and memory function. As demonstrated, the effects of acute exercise on memory function may be influenced by the memory type (e.g., episodic, semantic, prospective) and parameters related to the exercise stimulus (e.g., temporality, intensity). Additionally, these aspects (memory type and the exercise stimulus) may interact to influence the effects of acute exercise on memory. Clearly, dedicated research in this area is needed to improve our understanding of how acute exercise may influence memory function. It is not within the scope of this review to discuss all the mechanisms that may be influencing these relationships, as these relationships are very complex and likely result from unique mechanisms based on the memory type and exercise parameter. For example, for episodic memory, acute exercise may exert its effects via alterations in LTP, which we have discussed thoroughly elsewhere [40,42]. Similarly, certain outcomes, such as episodic memory, may be more influenced by exercise-induced changes in hormones [123] or neurotrophins [86]. Conversely, other memory outcomes, which may be more influenced by the functional connectivity of several brain structures, may also be influenced by exercise-induced changes in mood [124]. Relatedly, we

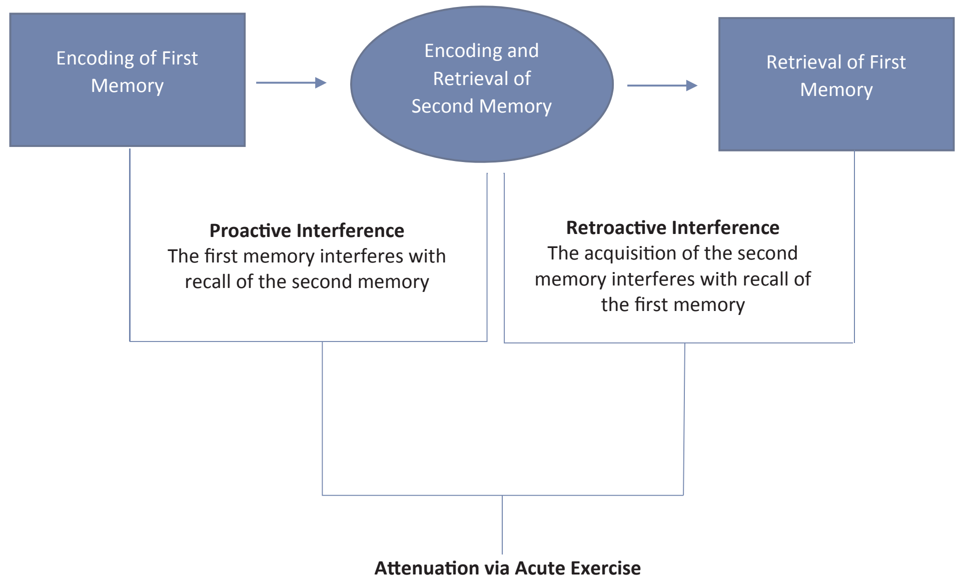

Fig. 4. Memory interference illustration with potential attenuation via acute exercise.

recently demonstrated that physical activity is associated with the functional connectivity of the hippocampal-orbitofrontal pathway [125]. In detail elsewhere [126], we have discussed the unique mechanisms through which exercise may influence various memory outcomes. However, future work should continue to explore the dynamic relationship between acute exercise and memory function, including their unique mechanisms.

As we have started to investigate [127], I believe that a key area that the field also needs to explore is, not only whether acute exercise can enhance memory function, but whether it can also facilitate forgetting. Intentional forgetting may be useful in many contexts, as forgetting outdated or irrelevant information may help to prevent proactive memory interference. Thus, distinguishable from unintentional forgetting, intentional forgetting is a desirable and adaptive memory outcome.

Conflict of interest

None.

Acknowledgment

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