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Characterizing the Influence of Perturbations in Global State on Working Memory

Author

Garrett, Jordan

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Characterizing the Influence of Perturbations in Global State on Working Memory

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by

Jordan Graham Garrett

Committee in charge:
Professor Barry Giesbrecht, Chair
Professor Scott Grafton
Professor Michael Miller
Professor Thomas Sprague

June 2024

The dissertation of Jordan Graham Garrett is approved.

Scott Grafton

Michael Miller

Thomas Sprague

Barry Giesbrecht, Committee Chair

May 2024

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VITA OF JORDAN GRAHAM GARRETT

May 2024

EDUCATION

Doctor of Philosophy in Psychological & Brain Sciences, University of California, Santa Barbara June 2024 (expected)

Bachelor of Arts in Psychology, California State Polytechnic University, Pomona, June 2018

PUBLICATIONS

https://scholar.google.com/citations?user=ltZLROgAAAAJ&hl=en

Peer-Reviewed

1. **Garrett, J.,** Chak, C., Bullock, T., & Giesbrecht, B. (Under Review). Acute Physical Activity has Selective Effects on Cognition in Young-Adults. *Nature Communications Psychology*.
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Book Chapters

1. Giesbrecht B., & **Garrett, J.** (2024). Electroencephalography. *Encyclopedia of the Human Brain* (2nd Edition).

Manuscripts in preparation

1. **Garrett, J.,** & Giesbrecht, B. The Influence of Aerobic Exercise on Cognitive Control and Working Memory.
2. **Garrett, J.,** Thayer, D., Sprague, T., & Giesbrecht, B. Probing the Prioritization of Multiple Spatial Locations Held Within Working Memory.
3. Dundon, N., Bullock, T., **Garrett, J.,** Stuber, A., Giesbrecht, B., & Grafton, S. Postural Adaptation to Allocentric Task Demands in a Modified Basketball Paradigm

CONFERENCE PRESENTATIONS

*Talks denoted by a **

1. **Garrett J.,** Thayer, D., Sprague, T., & Giesbrecht, B., "*Probing the prioritization of multiple spatial locations held within working memory.*"
   - Vision Sciences Society Annual Meeting May 2023
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- Virtual Working Memory Symposium* — May 2020
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- Vision Sciences Society Annual Meeting — May 2019

3. **Garrett, J., & Blumenfeld, R.,** "*The Functional Coactivation Network of the Prefrontal Cortex"*
    - Western Psychological Association Convention — April 2018
    - 31st Annual California State University Research Competition* — April 2017
    - 5th Annual CPP Student RCSA Conference* — March 2017
    - Cognitive Neuroscience Society Annual Meeting — March 2017

AWARDS

UCSB Graduate Research Mentorship Fellowship	2022-2023
UCSB Graduate Opportunity Fellowship	2020-2021
UCSB Regents Fellowship	2018-2019
Kavli Summer Institute in Cognitive Neuroscience Fellow	2019
Center for Neural Science Summer Undergraduate Research Program, NYU	2017
Frederick Meeker Endowed Scholarship, Cal Poly Pomona	2017
5th Annual CPP Student RSCSA Conference Awardee	2017
Ronald E. McNair Scholar, Cal Poly Pomona	2016-Present

TEACHING EXPERIENCE

Graduate

PSY 221B: Design & Measurement	W2022
PSY 594TS: Models of Working Memory	F2019

Undergraduate

PSY 163BG: Active Brain	W2024
PSY 118L: Attention Laboratory	W2020/F2023
PSY 10B: Statistical Methods in Psychology	S2020

ABSTRACT

Characterizing the Influence of Perturbations in Global State on Working Memory

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When accomplishing goal-directed behavior in naturalistic settings our global physiological state can vary dramatically, oscillating between periods of wakefulness, emotional stress, and physical activity. Fluctuations in global state, in turn, induce a cascade of neuromodulatory changes that affect how the brain processes sensory information from the external environment. Despite the inextricable link between global state and brain function, goal-directed behavior has predominantly been studied when the body is stationary and at rest. Thus, it is unclear as to whether perturbations in global state modulate cognitive processes dependent on this sensory information, such as working memory (WM). The current body of work aims to determine how changes in global state induced by an acute bout of aerobic exercise modulate WM and its underlying neural correlates. Study 1 investigated the relationship between acute exercise and cognition, which revealed that aerobic exercise induces a small enhancement in general task-performance. Moderator analyses indicated that time-dependent measures of cognition were especially improved by exercise-induced perturbations in global state. Importantly, executive functions, such as inhibitory control and WM, were influenced by engaging in physical activity. Building on these meta-analytic results, Study 2 investigated whether the fidelity of spatial WM representations is impacted during an instance of aerobic exercise. Participants completed a delayed change detection task both at rest and during a bout of low-intensity cycling while neural activity was concurrently recorded using electroencephalography (EEG). An inverted encoding modeling technique was employed to estimate location-selective channel response functions from topographical patterns of alpha-band (8-12 Hz) activity. Importantly, robust spatially selective responses were reconstructed both at rest and during exercise throughout the stimulus encoding and retention period, demonstrating for the first time that the fidelity of spatial WM representations could be tracked in a physiologically active state. The selectivity of these responses was degraded during exercise relative to rest, suggesting that the fidelity of location representations may be diminished. Study 3 further investigated the impact of exercise on WM encoding and maintenance abilities. Participants completed a delayed change detection task that consisted of varying set sizes. Importantly, on some of the trials participants were required to encode target stimuli while simultaneously ignoring distractors, thus enabling the evaluation of WM filtering efficiency. Analyses of an event-related potential known as contralateral delay activity (CDA), which tracks the number of items stored in WM, indicated that there was no difference in WM load between rest and exercise conditions. Decoding analyses revealed that patterns of voltage potentials across the scalp tracked WM load both at rest and during exercise. These results suggest that WM filtering efficiency and the number of items that can be actively stored are robust to perturbations in global state caused by light intensity exercise. Together, this collection of studies illuminates the selective impact of exercise on WM processes, and highlights the importance of considering global state when developing theoretical frameworks of cognition.

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Chapter I: Introduction

Throughout our daily routine our global physiological state fluctuates, going from being relaxed to stressed, energized to fatigued, or sedentary to physically active. These fluctuations induce a cascade of neuromodulatory changes that, in turn, perturb multiple brain systems. However, theoretical accounts of human cognition and its neural correlates fail to consider the influence of global state given that they are predominantly based on experiments conducted in standard laboratory conditions. It is possible that these frameworks only represent a snapshot of brain function that evolves along a trajectory within a high-dimensional space, where each dimension corresponds to an aspect of global state (McCormick et al., 2020). Bearing this in mind, the goal of the present body of work is to determine the impact of global state on cognitive processes and their underlying neural mechanisms. A manipulation of global state is achieved through the use of physical activity, which was chosen since many of our daily tasks require engaging the body (e.g., walking to class or in a grocery store, playing sports, etc.). Visuospatial working memory (WM) serves as the aspect of cognition tested, given that it integrates information across multiple sensory modalities and is a platform for goal-directed behavior.

Theoretical Background

Effect of State on Brain and Behavior

Global states can be organized in a hierarchical manner, where the top-level of the hierarchy consists of a distinction between sleep and wakefulness. Nested within these states are sub-states that either change discretely or along a continuum (McCormick, Nestvogel, &

He, 2020). For instance, sleep is typically divided into two discrete states, rapid eye movement (REM) and non-REM (NREM). REM sleep is characterized by the body entering a form of paralysis (muscle atonia) with periods of twitching, low-voltage and fast-frequency cortical activity that resembles wakefulness, prominent hippocampal theta oscillations, and decreased internal heat production (Blumberg et al., 2020; Mukai & Yamanaka, 2023; Peever & Fuller, 2017). This sleep state is thought to be critical for memory consolidation and development, a notion that is supported by the reactivation of brain regions engaged during learning periods (Mukai & Yamanaka, 2023). NREM sleep, on the other hand, is conventionally binned into three stages along a continuum of increasing relative depth. Stage 1 represents the period when an organism first falls asleep and is most prone to being disturbed. Stage 2 is defined by the presence of two distinct neural features, transient bursts of cortical activity between 11-15 Hz (i.e., sleep spindles) and sharp biphasic waveforms known as K-complexes. A hallmark of stage 3 are delta oscillations (i.e., slow waves) that mediate homeostatic processes, can be used as an index of sleep need, and also play a role in memory consolidation (Bellesi et al., 2014; Carskadon & Dement, 2005; Purcell et al., 2017). Taken together, neural activity and their functional roles can differ amongst sub-states, even when the organism engages in a relatively passive behavior.

Contrary to sleep, sub-states of wakefulness are not as clearly defined and have a considerable degree of overlap. One framework is a change in state along dimensions representative of mood, stress, and arousal. A core component of mood/emotion is valence (e.g., happy, angry, fearful), which can vary in its intensity and influence behavior in a nonlinear fashion (e.g., fear leading to fight or flight) (R. Lapate & Schackman, 2018). The neural circuitry that mediates the regulation and production of emotions are distributed throughout the brain, with core regions including the amygdala, striatum, insula, and frontal cortices (Underwood et al., 2021). Contemporary theories of emotional processing emphasize a reciprocal relationship between the amygdala, ventral medial prefrontal cortex (vmPFC) and orbitofrontal cortex (OBFC), where the amygdala ascribes valence to an experience while vmPFC and OBFC regulate behavioral reactions and decision making (Salzman & Fusi, 2010; Šimić et al., 2021). For example, Lapate et al., (2022) observed a decrease in reaction time (RT) on a modified Go/No-Go task when participants viewed happy versus fearful faces and an increase in inhibitory control for fearful faces. A joint representation of emotion and action was found in the lateral frontal pole that positively correlated with task performance, indicating that the emotional context in which information is processed impacts the execution of behavioral goals. This influence can persist long after the emotional state has been experienced. Memory research has shown that percepts formed during an emotional event are augmented with feelings of excitation or agitation that are often paired with a physiological response (e.g., increased heart rate, sweating), leading to robust representations that are easier to retrieve (Kensinger & Ford, 2020; J. Wang et al., 2022). Indeed, the precision of visuospatial WM representations is increased in a negative relative to positive or neutral emotional state (Xie & Zhang, 2016). In contrast, threat-induced anxiety has been found to disrupt the accuracy of visuospatial WM, but have no impact on verbal WM (Shackman et al., 2006). The key takeaway is that cognition is sensitive to both perceived and experienced emotions, and these effects can have a lasting impact on behavior.

The neural mechanisms of stress have been well documented. Two central systems that respond to physical, chemical, and psychological stressors are the sympatho-adrenomedullary (SAM) and hypothalamic-pituitary-adrenal (HPA) axes. Early and transient physiological reactions to a stressor are engendered by the SAM, which secretes the catecholamines epinephrine (E) and norepinephrine (NE) into the bloodstream. These neurochemicals bind to adrenergic receptors present in the central nervous system, smooth muscles, and organs, promoting the canonical “fight or flight” response. A primary output of the HPA is the endogenous glucocorticoid cortisol, an anticipatory hormone that is secreted by the adrenal glands. Once released, cortisol is circulated throughout the body, leading to the modulation of metabolic, cardiovascular, and immunological systems. Physiological responses to stress are regulated by cortisol, which inhibits HPA activity through a negative feedback loop. Relative to the SAM, this system is slower and produces a more sustained response, with peak cortisol typically occurring 15-20 minutes post stress onset (Lightman, 2008). Acute physiological changes produced by both of these systems modulate the circuitry of multiple brain networks (Russell & Lightman, 2019). NE release promotes communication between neurons by decreasing the threshold for actional potential generation and facilitating the transmission of action potential trains (O’Donnell et al., 2012). Cortisol increases corticospinal excitability, leading to motor evoked potentials with increased amplitude (Milani et al., 2010). Cortisol can also modify the synaptic plasticity and excitatory synaptic responses of pyramidal neurons in the hippocampus and prefrontal cortex (PFC) (Chaouloff & Groc, 2011; Dos-Santos et al., 2023). These neuromodulatory effects, in turn, impact cognitive function. There is evidence for an enhancement of memory consolidation during a stressful event, and decrements in memory retrieval and working memory (Barsegyan et al., 2010; Birnbaum et al., 1999; de Quervain et al., 2009). Threats and stressors have been shown to stimulate the locus coeruleus, a major producer of NE and central node in both attention and reward processing networks (Aston-Jones & Cohen, 2005; L. S. Morris et al., 2020; Y. Zhang et al., 2023). Lastly, acute stress influences decision making by biasing choices in risk-seekers toward riskier options and promoting a more conservative behavior in those that are risk averse (Morgado et al., 2015).

Most of the findings discussed thus far stem from studies that induced relatively small perturbations of global state. More extreme manipulations provide insights into brain function and cognition well outside standard operating conditions (i.e., homeostasis). For example, Kramer, Coyne, & Strayer (1993) tested cognitive processing in mountain climbers before ascending the West Buttress route on Mount Denali to determine the effects of high altitude. Relative to matched controls at sea-level, climbers displayed a deficit in learning on pattern comparison and code substitution tasks, and decreased reaction time (RT) on a memory retrieval task. These deficits did not correlate with symptoms of acute mountain sickness, suggesting that the physiological effects of being at high-altitude impact cognitive performance even after acclimatization. Bullock et al., (2021) interrogated how these physiological effects in turn modulate neural activity. Global state was manipulated by changing the levels of arterial blood gases to induce hypercapnia, hypocapnia, and normoxia, while electroencephalography (EEG) was recorded during the completion of a sustained attention task under each of these states. Importantly, task-related parieto-occipital alpha power was modulated as a function of state, with an increase during hypocapnia and a decrease during hypercapnia. P3 amplitude and theta power were also attenuated during hypocapnia, suggesting that attention and executive control are sensitive to the levels of oxygen and carbon dioxide present in the bloodstream. Similar to changes in altitude, changes in barometric pressure can drastically influence our brains. For example, when going below the depth of 120 meters divers can experience high-pressure neurological syndrome.

Symptoms of this condition include headache, vertigo, shivering/tremors, neuropsychiatric disturbances, and changes in EEG (Jain, 1994; Opatz & Gunga, 2021). Examination of 156 saturation divers (diving between 65-1,000 feet) revealed the presence of focal slow waves in temporal regions, and a decrease in P1 latency as the age of the diver increased (Todnem et al., 1991). Professional saturation divers serve as a unique population for studying the long-term effects of barometric pressure on cognition, since they often have to remain at these depths for extensive durations (e.g., months) due to the amount of time it takes to decompress. Interestingly, it is unclear if there exists an extreme change in global state that would augment neural activity and cognition.

Arousal is often operationalized as the level of wakefulness that an organism displays, or the amount of attention/awareness it allocates toward processing information within its environment. In the current work, arousal is instead used to represent the degree an organism engages its body in gross motor movements, such as physical activity. The influence of this state on neural activity and behavior is discussed in the next section.

Impact of Exercise on Neurochemical Levels

Engaging in physical activity causes widespread changes in numerous cells, tissues, and organs in response to meeting the metabolic demands of contracting skeletal muscles (Hawley et al., 2014). Cardiovascular adjustments during exercise are mediated by three autonomic signaling pathways. The first is a feedforward signal to activate areas of the brainstem responsible for regulating heart rate, blood pressure, and respiration. The second is feedback from thinly (un)myelinated type III and IV afferents in contracting muscles that increase sympathetic drive. The final signal is generated by baroreceptors in the carotid sinus and aortic arch that notify centers of the brainstem of changes in blood pressure. In contrast to the redistribution of blood flow away from visceral organs toward activated skeletal muscles, blood flow to the central nervous system remains relatively unchanged during exercise. Critically, muscles are endocrine glands that secrete myokines and exerkines, which are cytokines, peptides, and nucleic acids that exert either autocrine, paracrine, or endocrine effects (Severinsen & Pedersen, 2020). One major myokine that crosses the blood-brain barrier (BBB) is the protein cathepsin-B (CTSB). Across multiple species, CTSB levels have been shown to increase during physical activity, and found to enhance the expression of both doublecortin and brain-derived neurotrophic factor (BDNF) in hippocampal progenitor cells of adult mice (Moon et al., 2016). Another myokine whose secretion levels are increased during exercise is irisin, which similarly stimulates the expression of BDNF in mouse hippocampus (Wrann et al., 2013). A major metabolic pathway that fuels motor movements during exercise is aerobic glycolysis, which produces the byproduct lactate. For many years lactate was considered a metabolic waste product, but relatively recent research has recognized that it is able to cross the BBB, can serve as an alternative energy source in cerebral glycolysis, and modulates neural activity, calcium signaling, axonal myelination and angiogenesis (Basso & Suzuki, 2017; Delezie & Handschin, 2018; Hargreaves & Spriet, 2020; Schurr, 2014). Note, muscles secrete hundreds of peptides during physical activity, and biological function has been identified for only 5% of them (Severinsen & Pedersen, 2020), suggesting that there remains much to be discovered on the modulatory effects that muscles exert on the brain.

Exercise also impacts neurotransmission across multiple cortical networks. Dopaminergic neurons are critical for the control of motor movements, and rodent studies suggest that the rate of dopamine (DA) synthesis and metabolism increases subsequent to a single bout of exercise (Chaouloff, 1989). Using *in vivo* microdialysis, Meeusen et al., (1997) observed an increase in extracellular levels of DA, NE, and glutamate in rat striatum during a 60 minute session of treadmill running, regardless of whether or not the animal had undergone exercise training for 6 weeks. Similarly, Hattori, Naoi, & Nishino (1994) observed an increase in striatal DA turnover during running and that this increase was dependent on running speed with a threshold of 300-600 cm/min, suggesting that DA is modulated in an intensity dependent fashion. Chaouloff et al., (1987) also detected an increase in DA levels within rat hippocampus, midbrain and hypothalamus, but observed no change in DA levels within the frontal cortex or striatum. This implies that exercise impacts the neurotransmitter levels in selective brain regions (Basso & Suzuki, 2017). Indeed, there is evidence for an increase in 5-HT in rat cerebellum, midbrain, and frontal cortex following an 8-week treadmill program relative to sedentary controls, along with elevated NE levels in the midbrain and frontal cortex (Bailey et al., 1992; Brown et al., 1979). By surgically removing rat brains after a bout of 30 minute treadmill running, Otuska et al., (2016) investigated the impact of acute exercise on serotonergic and corticotropin-releasing factor neurons in the dorsal raphe and hypothalamic paraventricular nucleus, respectively. Running at a low (15m/min) compared to high (25m/min) speed was found to elicit an increase in c-Fos, a transcription factor and functional marker of neuronal activity, expression by 5-HT neurons. Few studies have also observed increases in central levels of acetylcholine in the extracellular space of the parietal lobe and hippocampus (Kurosawa et al., 1993; Nakajima et al., 2003). An important caveat to consider when interpreting acute effects of exercise in rodents is that many of the studies involved a training period that can last up to weeks, making it possible that these effects are confounded by long-term physiological changes (but see Meesuen et al., 1997).

Despite the extensive evidence for exercise-induced changes in central neurotransmitter levels in animal models, relatively little research has tested for an equivalent effect in humans, given the invasive nature of techniques used to monitor their synthesis and metabolism. Only one study has investigated the dynamics of human striatal DA levels subsequent a 30 minute instance of treadmill running using positron emission tomography, and observed no change relative to a baseline period (Wang et al., 2000). Though this appears to conflict with findings from animal studies, it is possible that the exercise intensity was too low to elicit changes, especially since participants had a history of engaging in regular exercise. Research on the modulation of neurochemicals as a function of exercise in humans is predominantly based on peripheral levels, with samples being collected from either bloodwork or saliva. For example, Zimmer et al (2016) conducted a large-scale randomized controlled trial to determine the impact of low (45% heart rate max (HR_{max})), moderate (65% HR_{max}), and high intensity (85% HR_{max}) cycling on serum 5-HT and performance on the Stroop color word task. Relative to a control group, serum 5-HT only significantly increased post high intensity exercise. This increase was correlated with a decrease in RT when naming words printed in incongruent ink, suggesting an improvement of selective attention. Recently, Parthimos et al., (2022) tested for a correlation between changes in plasma amino acid neurotransmitter levels and cognitive performance in professional athletes after completing three simulated high-intensity basketball games. Glutamate, tyrosine, alanine, phenylalanine, and glycine concentrations were significantly higher post exercise. In regards to behavior, only participants who had engaged in exercise displayed an increase in accuracy on the Digit

Span Backward task, and a decrease in the amount of time taken to complete version B of the Trail Making Test. Peripheral levels of neurotrophic factors such as BDNF, VEGF, and IGF-1 have also been shown to be modulated by exercise (Basso & Suzuki, 2017; Cotman et al., 2007). Furthermore, it is well established that peripheral concentrations of NE and E increase when skeletal muscles are engaged in physical work (Christensen & Galbo, 1983; Gray & Beetham, 1957; Raab, 1943; Zouhal et al., 2008). Thus, exercise has a similar impact on neurochemical levels in humans as it does animals. However, a limitation with analyzing peripheral concentrations is that they may not accurately reflect central levels (Basso & Suzuki, 2017).

Exercise Modulates Neural Population Dynamics

Widespread exercise-induced changes in neurochemical levels in turn modulate neuronal tuning. Using a novel experimental setup, Niell & Stryker (2010) investigated the tuning response of neurons in the primary visual cortex (V1) and thalamic lateral geniculate nucleus (LGN) of awake mice while they ran on a freely rotating spherical treadmill. Local field potential recordings revealed a suppression in low-frequency power (~10-30 Hz) and a dramatic increase in high-frequency power (~50-70 Hz) during periods of locomotion relative to when the mouse was stationary. Critically, single-unit recordings of narrow- and broad-spiking V1 neurons demonstrated a multiplicative gain in orientation tuning during locomotion. In contrast, LGN neurons were not modulated by changes in behavioral state, reflecting the selective impact of physical activity on neuronal tuning. Corroborating these findings, Ayaz et al., (2013) observed that locomotion decreased the strength of surround suppression in V1 neurons, allowing them to integrate over larger regions of visual space. To determine the cortical circuitry responsible for these modulations in V1 neural tuning properties, Fu et al., (2014) utilized two-photon imaging to record the *in vivo* calcium signals of vasoactive intestinal peptide (VIP)-positive GABAergic neurons during locomotion. Locomotion was found to increase the calcium response of VIP-positive neurons, independent of visual stimulation, through nicotinic inputs from the basal forebrain. Optogenetic activation of VIP neurons during stationary periods were found to induce an increase in the activity of excitatory neurons similar to what is observed during locomotion, suggesting that they play a critical role in physical activity induced changes in visual neural response properties. Such changes in neuronal responses as a function of locomotion have also been observed in other animal models (Chiappe et al., 2010; Maimon et al., 2010; Rother et al., 2023; Turner et al., 2022), and extend to other sensory modalities (Henschke et al., 2021; Schildberger et al., 1988; Vivaldo et al., 2023).

Electrophysiological studies of humans engaged in exercise have reported similar alterations in sensory related neural activity. To investigate the impact of exercise on visual processing, Bullock, Cecotti, & Giesbrecht (2015) recorded EEG while participants completed a three-stimulus visual-oddball task under three conditions: rest, low, and high intensity cycling. P1, an event related potential (ERP) component that reflects the allocation of attention at early stages of visual processing, mean amplitude evoked by standard stimuli was greater during low intensity exercise relative to rest. Occipital and parietal-occipital P1 peak latency for target stimuli was decreased during low intensity cycling compared to both rest and high intensity cycling, suggesting that the modulation of visual processing speed is intensity dependent. P3a peak latency, an index of stimulus classification speed, evoked by distractor stimuli was significantly decreased in both exercise conditions relative to rest.

Hence, the activity of neuronal populations underlying multiple stages of visual processing is modulated during an exercised state. Indeed, Bullock et al., (2017) applied an inverted encoding model (IEM) to reconstruct orientation selective responses from steady state visual evoked potentials (SSVEPs) recorded during rest and both low and high intensity cycling. Low intensity cycling was found to induce a multiplicative gain in orientation selectivity relative to both rest and high intensity exercise, corroborating animal studies that observed changes in feature-selective responses during locomotion. Furthermore, Cao & Händel (2019) assessed visual processing of stimuli presented in the periphery compared to the central fovea while standing and walking. Participants were shown a central flickering grating at varying levels of background contrasts and instructed to report the presence of a briefly presented target. SSVEP power evoked by the flickering grating decreased as background contrast increased during walking but not standing, suggesting an increase in peripheral processing. In a follow up behavioral experiment, relative target detection threshold was found to decrease as eccentricities from fixation increased during locomotion. Together, these empirical results establish the notion that multiple stages of sensory processing are modulated by an acute bout of physical exercise.

Non-sensory evoked neural population level responses are also impacted while in an exercised state. Functional near-infrared spectroscopy (fNIRS) imaging studies provide evidence for an effect of acute exercise on hemodynamic activation patterns in prefrontal cortices (Herold et al., 2018). Yanagisawa et al., (2010) applied fNIRS to participants that completed a Stroop task post a moderate (50% $VO2_{peak}$) bout of cycling to examine exercise-induced effects on task-related activity. The Stroop interference effect significantly decreased post-exercise, and this effect coincided with an increase in left dorsolateral prefrontal cortex

(DLPFC) activation. Increases of Stroop-interference related activation in left DLPFC have also been reported post low intensity (30% $VO2_{peak}$) cycling (Byun et al., 2014) and high intensity interval training (HIIT) (Kujach et al., 2018), indicating that processing in cortices that subserve executive function may be enhanced after acute exercise. In contrast, during exercise such processing may be diminished. Pontifex & Hillman (2007) recorded EEG while participants concurrently completed a flanker task and cycled at a moderate intensity (60% HR_{max}). Response accuracy on incongruent trials was decreased relative during exercise relative to rest. Although frontal P3 amplitude was increased during exercise, its latency was also increased, suggesting a decrease in the efficiency of attentional control. Such a differential impact of exercise on the neural substrates of executive process during versus post-cessation led to the development of the transient hypofrontality hypothesis (Dietrich, 2006). This theory posits that the demand on finite metabolic resources to support continuous neural activation of cortices responsible for sustaining movement, integrating sensory information, and regulating autonomic processes during exercise results in a transient decrease in resources available for frontal cortices. Following exercise, the PFC is believed to receive an influx of oxygenated blood, engendering enhanced activation. Contrary to this hypothesis, fNIRS imaging has shown that oxygenated hemoglobin levels in the lateral PFC remain unchanged when exercising at various intensities (Tempest & Reiss, 2019). Nevertheless, neural population activity underlying multiple cognitive functions is selectively impacted by perturbations in global state caused by physical activity.

Exercise and Cognition

Acute exercise alters performance across a range of cognitive domains. Hippocampal dependent processes such as memory and learning have been shown to benefit from acute physical activity. Coles & Tomporowski (2008) probed both short- and long-term memory performance on the Brown-Peterson task and a free-recall test, respectively, before and after a 40 minute bout of moderate cycling. No change was observed in short-term memory accuracy. In regard to long-term memory, participants recalled significantly more words from both the start and end of a list compared to control conditions, suggesting that exercise impacts both the primacy and recency effect. Winter et al., (2007) assessed the influence of low-impact aerobic and high-impact anaerobic running on vocabulary learning speed, which was operationalized as the number of correctly identified picture and German word pairs from the first to last block of the task. Intense anaerobic running increased learning speed by 20% relative to low-impact running and a resting condition, and this effect was associated with increases in peripheral BDNF. Thus, it is possible that BDNF is a mechanism of exercise-induced enhancements of learning and memory, and that this effect is dependent on intensity. To test this notion, Etnier et al., (2016) examined performance on the Rey Auditory Verbal Learning Test (RAVLT) after participants completed a 30 minute bout of treadmill running at their $VO2_{max}$ and +/- 20% of their ventilatory threshold (VT). Word recall 30 minutes after encoding, short-term memory, and learning did not differ as a function of exercise intensity. However, word recall 24 hours post-encoding was significantly higher after exercising at one's $VO2_{max}$ relative to 20% below VT. Although serum BDNF significantly increased post-exercise, this increase did not differ as a function of intensity nor was it correlated with memory performance. Interestingly, increases in peripheral levels of BDNF after high-intensity cycling are accompanied by improvements in face-name recognition memory (Griffin et al., 2011), portraying the difficulty with establishing the molecular substrates of enhancements engendered by acute exercise in humans. Recently, changes in long term potentiation (LTP) have been proposed to drive the effect of exercise on memory (D. Moore & Loprinzi, 2020). Meta-analytic synthesis of behavioral results indicate that acute aerobic exercise has a moderate positive effect on long-term memory (Roig et al., 2013), yet this relationship is likely to be much more nuanced. Long-term memory performance may be differentially impacted contingent on if the body is engaged in exercise prior to encoding, during encoding, or during consolidation (Schmidt-Kassow et al., 2014; Sng et al., 2018; van Dongen et al., 2016).

A majority of research on exercise and cognition has been dedicated to understanding the impact on executive function, in particular inhibitory control. Meta-analytic modeling has demonstrated that exercise has a small positive influence on time-dependent measures of inhibition, and that this relationship is moderated by participant age and exercise intensity, with high intensity activities eliciting larger effects (Oberste et al., 2019). Indeed, there is extensive evidence for a reduction in response time on the Stroop, Eriksen Flanker, and Go/No-Go tasks due to exercise (Cantelon & Giles, 2021; Levin et al., 2021; Yanagisawa et al., 2010). Tia, Mou, & Qiu (2021) investigated both the immediate and sustained effects of a single bout of HIIT and moderate treadmill running on flanker task performance, and found that RT on incongruent trials was reduced post-HIIT for up to 90 minutes. Post-exercise improvements in RT have been associated with enhanced DLPFC activation (Yanagisawa et al., 2010), while EEG studies have reported increased P3 and decreased N450 amplitude (Y.-K. Chang et al., 2017; Hsieh et al., 2018) and decreased N2 latency (Chueh et al., 2023). Relatively less research has focused on the sensitivity of other executive functions to exercise, such as cognitive flexibility, planning, and decision making. There is evidence that moderate and vigorous exercise reduces the RT cost when switching between global and local target features of visual compound stimuli, and this effect is sensitive to age and sports-related cognitive expertise (Pesce et al., 2003, 2007; Pesce & Audiffren, 2011). In a large sample size study of 110 participants, Mou et al., (2023) investigated how 20 minutes of moderate intensity treadmill running or HIIT influenced set switching in the more-odd shifting task. Briefly, this task requires participants to make differing responses contingent on the color, value, and parity of a presented number. Participants were median split into low- and high-performers based on baseline measurements of cognitive flexibility to test an a priori hypothesis that exercise induced effects are moderated by baseline cognitive performance. Indeed, individuals with lower baseline scores experienced a reduction in RT on switch trials after both moderate exercise and HIIT, while individuals with higher baseline scores only experienced a reduction post-HIIT. In contrast, accuracy remained unchanged, regardless of baseline score. Meta-analytic modeling suggests that overall exercise has a small positive influence on set switching, and this relationship is moderated by exercise intensity with low-intensity exercise inducing the largest benefits (Oberste et al., 2021). A commonly used assessment of planning capabilities is the Tower of London task, and after a 30 minute bout of moderate cycling both planning efficiency (i.e., total move score) and response inhibition (i.e., total initial times) are enhanced for up to 60 minutes (Hung et al., 2013). In regards to the influence of exercise on decision making, a recent study applied a drift-diffusion model to behavioral performance on a perceptual discrimination task completed both during and after high intensity intermittent cycling (Karen et al., 2023). Relative to performance pre-exercise, the drift rate and boundary parameters of the model significantly increased while the non-decision time parameter decreased post-exercise, suggesting that participants adopted a more conservative decision making strategy. No change in model parameters were observed during cycling, though RT decreased in the last relative to the first exercise block. Overall, acute exercise selectively impacts the processing speed of aspects of executive function.

Attention is a nonunitary cognitive ability with aspects that are sensitive to changes in global state caused by physical activity. During moderate intensity cycling with a variable load RT on the sustained attention to response task (SART) has been shown to decrease without compromising accuracy (Radel et al., 2018). This enhancement co-occurred with an increase in saliva α-amylase concentration, an indirect indicator of norepinephrine levels, and DLPFC activation. Huertas et al., (2011) explored how components of the attention networks task were impacted during moderate and high intensity cycling relative to a resting condition in highly experienced cyclists. RT on no-cue trials was significantly reduced during moderate intensity exercise, indicating an enhancement of the alerting component. Additionally, there is evidence for a facilitation of target detection speed on odd-ball tasks during moderate (Yagi et al., 1999) and high intensity exercise (Bullock et al., 2015). Hence, the speed of attentional processing is enhanced when in a physically active state. A similar effect has been shown to occur after exercise. Chang et al., (2015) tested performance on the attention networks task post an instance of moderate intensity cycling in high-fit amateur basketball players. Compared to a control group, RT on incongruent trials was significantly reduced after exercise, signifying an improvement in executive control. Larger P3 amplitude across frontal, central, and parietal electrodes associated with the alerting and executive control components were also observed as a result of exercise. It is worth mentioning that selective attention is a critical component in many of the tasks used to probe executive function (e.g., Stroop, flanker tasks, switching tasks), which may implicate induced modulations of attention as the driver for enhancements of executive processes.

Working Memory

Sensory information is temporarily stored in WM, where it is integrated into either a single or multiple malleable percepts that are used to guide future actions. A distinguishing trait of this memory system is that it is capacity limited, irrespective of the sampled sensory system. Extensive research has been dedicated towards understanding these capacity limits and determining how visual information is stored, giving rise to two competing theoretical frameworks. The first is the notion that percepts are maintained with a fixed and equivalent resolution in WM within discrete slots (Luck & Vogel, 1997). In the event that the number of observed sensory stimuli exceeds the number of slots, which is typically estimated to be between three to four, this theory assumes that no information is stored for excess stimuli (Luck & Vogel, 2013; W. Zhang & Luck, 2008). Evidence in favor of this account stems largely from performance on the ubiquitous change detection task (Rouder et al., 2011) and sustained delay period activity, a classic hallmark of actively maintaining memoranda in mind, that scales with WM set size (Riggall & Postle, 2012; Song & Jiang, 2006; Todd & Marois, 2005). ERP studies have repeatedly shown that when subjects are cued to memorize stimuli on one side of a presented bilateral array, a sustained negative potential emerges during the delay period that correlates to individual WM capacity. This neural signal is known as contralateral delay activity (CDA), given that it is a difference wave between activity at posterior electrodes ipsilateral to the cued stimuli from those that are contralateral, and its amplitude increases as set size increases with an asymptote at three to four stimuli (Adam et al., 2018; Luria et al., 2016; Vogel & Machizawa, 2004). Notably, this property can be used to determine how efficiently goal-relevant information is encoded into WM and distractors are ignored (Vogel et al., 2005). In contrast to the slots account, continuous resource models posit that visuospatial WM capacity can be flexibly divided amongst all observed stimuli at the expense of resolution (Bays & Husain, 2008). This notion stems from the observation that relatively small deviations in probe stimulus features from sample stimulus features (e.g., small location displacement) results in poor change detection even at low sample sizes. Further, the precision of encoded representations decreases as the number of items increase, even at supra-capacity set sizes (Bays et al., 2009; Keshvari et al., 2013; Ma et al., 2014; Wilken & Ma, 2004). Evidence in favor of both theoretical frameworks can be seen in the memory error distributions of continuous response tasks. When applying a mixture model to these distributions, it has been shown that guess rate (i.e., height of fitted uniform distribution) increases while precision (i.e., standard deviation of fitted von-mises distribution) decreases as set size gets larger (Adam et al., 2017; W. Zhang & Luck, 2008). Critically, guess rate drastically increases while precision remains unchanged from sub- to supra-capacity set sizes, suggesting that a fusion of slots and resource models capture the fidelity of WM representations and the capacity of this storage system. Note, this remains an area of active research, and this debate has evolved to the matter of whether information is encoded into WM as discrete-representations or with variable precision across trials and stimuli (Ma et al., 2014; Ngiam, 2023).

There exists a large corpus of work implicating the frontoparietal network as a storage system for WM representations. In a classic study, Funahashi, Bruce & Goldman-

Rakic (1989) recorded single unit activity in the principal sulcus (PS) and frontal eye fields (FEF) of the prefrontal cortex of macaques during the completion of an oculomotor delayed-response task. A critical manipulation in this task was requiring monkeys to remain fixated on a central stimulus throughout the cue and delay periods, allowing for the dissociation between neural activity corresponding to the execution of motor movements and activity reflecting WM maintenance. Neurons within both regions displayed increased excitatory or inhibitory activity during the delay period relative to an intertrial interval, as well as directional tuning toward memorized locations, signifying that lateral PFC supports WM processes (Sreenivasan & DEsposito, 2019). Extending these findings, Chafee & Golman-Rakic (1998) recorded single-unit activity in prefrontal area 8a and parietal area 7ip during the same task, and observed neurons in both cortical areas that exhibited sustained delay period activity and similar spatial tuning profiles. Human neuroimaging studies have also reported WM related activation within frontal and parietal areas using univariate measures of population-level activity such as the blood-oxygenated-level-dependent (BOLD) signal with functional magnetic resonance imaging (fMRI) (D’Esposito et al., 2000; Postle et al., 2004; Riggall & Postle, 2012) and both spectral power (Jensen & Tesche, 2002; Sauseng et al., 2010) and ERP amplitude (Vogel & Machizawa, 2004; Vogel, McCollough, Machizawa, 2005; Adam et al., 2018) in EEG. Note, the role of the PFC in the storage of WM stimulus representations remains contested, and it is argued to instead support the representation of abstract task rules (Serences, 2016; Sreenivasan & DEsposito, 2019). Relatively recent use of multivariate techniques has revealed that WM representations are also stored in sensory cortices. Harrison and Tong (2009) used fMRI to monitor neural activity during an orientation discrimination task in which participants were first presented with a sequence of two oriented gratings, and after a brief delay were retro-cued to use either the first or second stimulus as a reference against a rotated test grating. Despite the absence of a sustained elevation in the BOLD response during the delay period, successful orientation decoding accuracy was observed throughout the trial period using activity from areas V1-V4. Classifiers trained on neural activity recorded when oriented gratings were passively viewed in a follow-up experiment successfully generalized to activity during the WM task, suggesting that WM representations have a format similar to sensory percepts. Indeed, decoding of feature-selective WM representations from activity generated by sensory cortices has been successfully replicated across many fMRI studies (Ester et al., 2009, 2015; Serences, 2016; Serences et al., 2009). These findings led to a reigniting of the sensory recruitment hypothesis, which proposes that visual WM representations are stored in the same visual cortical areas used to encode stimulus features (Adam et al., 2022; but see Bettencourt & Xu, 2016). Critically, these representations are stored in a "sensory-like" format. Altogether, univariate measures of neural activity can be used to index the capacity limits of visuospatial WM (e.g., CDA), while multivariate modeling can be used to capture the structure of these feature-selective representations.

Exercise and Working Memory

Similar to other executive functions, WM is sensitive to exercise-induced changes in global state. Tempest et al., (2017) investigated performance on the 2-back task during 60 minute bouts of light and vigorous intensity cycling, and observed a significant decline in memory sensitivity (i.e., d-prime) over time in the latter exercise condition. This decrement corresponded to a significant increase in blood lactate concentration over time and enhanced activation in the PFC. In contrast, Zheng et al., (2022) observed no change in 2-back accuracy during moderate intensity cycling relative to rest. Rather, exercise significantly decreased both RT and oxygenated hemoglobin levels in the bilateral frontal polar area, DLPFC, and right premotor and supplementary motor cortex. Quelhas Martins et al., (2013) found evidence for an increase in the number of correct responses on the paced serial addition test (PASAT) during moderate intensity cycling relative to a resting condition. Further, response latency slopes were reduced on the Sternberg task during low and moderate intensity cycling compared to a control condition. After engaging in exercise, WM processing speed has been shown to be enhanced (Loprinzi, 2018). For example, RT on a spatial 2-back task was reduced after a 20 minute instance of HIIT in highly fit participants, and after both a 10 minute instance of HIIT and 20 minutes of moderate intensity running in low fit participants (Mou et al., 2023). RT was also reduced on a modified Sterberg task for up to 30 minutes post moderate intensity running (Pontifex et al., 2009). Hence, during exercise the speed and accuracy of WM may be differentially influenced depending on exercise intensity and type, while after exercise WM performance may be enhanced (Loprinzi, 2018; Cantelon & Giles, 2021).

Outstanding Questions

The ameliorating influence of exercise on cognition is not consistent. For all of the studies recounted so far reporting significant positive effects, there exist an equivalent number of studies that have observed either a negative or null effect. Heterogeneity in empirical results is thought to reflect the moderation of exercise-induced effects by participant traits (e.g., age, baseline cognitive performance, fitness level) and exercised protocol characteristics (e.g., intensity, type, duration) (Basso & Suzuki, 2017; Cantelon & Giles, 2021; Chang et al., 2012). Numerous meta-analyses have been conducted over the years to extract a cohesive and statistically based understanding of the relationship between acute exercise and cognition, however they have largely focused only on executive function, older adults, and adolescents (Chang et al., 2012; Ishihara et al., 2021; Liu et al., 2020; Moreau & Chou, 2019). Further they only have used the frequentist approach, which can fail to accurately capture heterogeneity both with and between studies and does not characterize the relative probabilistic evidence in favor of exercise modulating behavioral task performance. In addition, despite the extensive evidence in favor of altered neural tuning and sensory processing during a physically active state, it is unclear how the neural correlates of cognitive functions dependent on this sensory information may be impacted in turn. More specifically, the neural processes supporting WM encoding and maintenance may be modulated by exercise, especially since activity in regions of the frontoparietal-occipital network is changed during exercise relative to a sedentary state.

The current dissertation aims to investigate these outstanding questions and is organized as follows. Chapter II details a Bayesian meta-analytic investigation of the impact of physical activity on cognitive task performance with the intention of characterizing the relative evidence in favor of acute exercise modulating cognition[1]. Chapter III applies a multivariate technique to EEG recorded during exercise to compare the fidelity of spatial

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[1] These data are currently being considered for publication: Garrett, J., Chak, C., Bullock, T., & Giesbrecht, B. (Under Review). Acute Physical Activity has Selective Effects on Cognition in Young-Adults. *Nature Communications Psychology*.

WM representations in a physically active state relative to a sedentary state.[2] Chapter IV investigates how exercise impacts the ability to selectively encode information into WM encoding and the amount of information that can be stored. Chapter V synthesizes presented results with current frameworks of global state and brain function and discusses remaining gaps in the literature.

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[2] These data have been published: Garrett, J., Bullock, T., & Giesbrecht, B. (2021). Tracking the contents of spatial working memory during an acute bout of aerobic exercise. *Journal of Cognitive Neuroscience*, *33*(7), 1271-1286. https://doi.org/10.1162/jocn_a_01714

Chapter II: Acute Physical Activity has Selective Effects on Cognition in Young-Adults

INTRODUCTION

A single bout of exercise induces a cascade of neuromodulatory changes that influences multiple brain systems (Basso & Suzuki, 2017; Hillman et al., 2008). This includes an increase in the synthesis of neurotransmitters (e.g., acetylcholine, dopamine, GABA, glutamate) and neurotrophic factors (e.g., BDNF), which can occur in a brain-region specific manner (see Basso & Suzuki, 2017 for review). Given these impacts on the brain, it would be reasonable to hypothesize that single brief bouts of exercise are associated with changes in performance across a range of cognitive domains. Consistent with this hypothesis, there is abundant evidence that attention (Alves et al., 2014; Chang et al., 2015; Davranche & Audiffren, 2004; Lambourne et al., 2010), working memory (Chen et al., 2016; S. C. Kao et al., 2020; Quelhas Martins et al., 2013; Roig et al., 2013; Schaefer et al., 2010), decision making (Kamijo et al., 2004; Kamijo & Takeda, 2009), and cognitive control (Hillman et al., 2009; Kamijo et al., 2007) are facilitated by brief bouts of physical exercise. However, there is also evidence suggesting that exercise has little, or no, effect on cognitive task performance. For instance, Komiyama et al. (2016) observed no difference in accuracy on a spatial delayed response task between exercise and rest conditions. Further, Lambourne et al. (2010) found no change in working memory performance either during or after a single bout of exercise. The discrepant pattern of results in the literature investigating the link between exercise and performance on cognitive tasks is surprising given the consistent and robust physiological effects of even brief bouts of physical activity. However, it is unclear whether this limited impact of exercise on performance reflects the true state of affairs or whether the apparent lack of robust influence is due to vast empirical discrepancies across studies in the literature. Studying the impact of single exercise sessions on cognition can provide insight into how changes in our body's physiological state impacts behavior. This understanding can then guide the creation of more effective longer-term exercise interventions, which essentially involve regularly repeating brief exercise sessions over an extended period.

Meta-analytic techniques are a set of powerful tools that can expose dominant trends within a methodologically heterogeneous literature. There is a consensus amongst narrative reviews and previous meta-analyses that an acute bout of exercise has a small positive influence on behavioral performance (Basso & Suzuki, 2017; Cantelon & Giles, 2021; Chang et al., 2012; Haverkamp et al., 2020; Lambourne & Tomporowski, 2010; McMorris et al., 2011; Moreau & Chou, 2019; Oberste et al., 2019). The nature of this effect is moderated by exercise protocol, cognitive task, and participant characteristics. For instance, Lambourne & Tomporowski (2010) observed that task performance during exercise was dependent on exercise modality, the type of cognitive task and when it was completed relative to exercise onset. Similarly, post-exercise performance was moderated by exercise modality and the type of cognitive task. Chang et al. (2012) reported that post-exercise cognitive performance was influenced by exercise intensity duration, and the time of cognitive test relative to exercise cessation. Interestingly, the authors found that study sample age was a significant moderator, where larger positive effects were found for high school (14-17 years), adult (31-60 years), and older adult (>60 years) samples compared to elementary (6-13 years) and young adult (18-30 years) samples. Multiple meta-analyses have observed that the effect of exercise is dependent on cognitive domain, with measures of executive function, attention, crystallized intelligence, and information processing speed showing the largest gains (Chang et al., 2012; Haverkamp et al., 2020; Ishihara et al., 2021; Logan et al., 2023; Ludyga et al., 2016). Further, there is evidence that exercise has a differential influence on the speed and accuracy of cognitive processes. McMorris et al. (2011) observed that acute, intermediate exercise facilitated response times on working memory tasks, while accuracy was compromised. In contrast, exercise has been shown to boost both the accuracy and speed of cognitive control (Oberste et al., 2019). Altogether, it is important to consider cognitive task, participant, and physical activity characteristics to develop a holistic model of the relationship between exercise and cognition.

While these earlier meta-analyses have provided unique insights into understanding the relationship between acute exercise and cognition, they have two major limitations. First, the most recent holistic quantitative synthesis of the extant literature was published over a decade ago (Chang et al., 2012). Meanwhile, the exercise and cognition literature has grown drastically. According to the electronic database Web of Science, almost 6,000 articles associated with the search term “exercise and cognition” have been published since this last holistic meta-analysis. In addition, more recent meta-analyses have primarily focused on executive processes (Haverkamp et al., 2020; Ludyga et al., 2016; Moreau & Chou, 2019; Oberste et al., 2021). Thus, previous models may provide an outdated and limited account of exercise-induced influences on other aspects of cognition, such as perception, long-term memory, and learning. Second, previous meta-analytic approaches employed frequentist statistical methods, which are based on a decision threshold rather than a characterization of the relevant evidence. As a result, it is possible that acute exercise and moderator variables are deemed to have a significant influence on task performance despite the fact that there may only be a small degree of probabilistic evidence in favor of this notion. In addition, relying on a decision threshold prevents these models from conveying the likelihood that an exercise protocol elicits a change in cognitive task performance. Past frequentist meta-analytic models also treated heterogeneity parameters as a fixed quantity and utilize only a point estimate, which can lead to an underestimation of the variability either between or within studies (Borenstein et al., 2010; Hackenberger, 2020; Sutton et al., 2000; Sutton & Abrams, 2001). This is especially true when the number of modeled studies is low (Chung et al., 2013; Kontopantelis et al., 2013; Sidik & Jonkman, 2007). When considered together, there is a clear need for an updated meta-analysis using an approach that addresses these limitations.

The current study addressed these limitations in two ways. First, a comprehensive literature search was conducted spanning the years 1995-2023. To quantify the influence of exercise on cognition in young healthy adults, the search was limited to non-clinical studies whose subjects were between 18-45 years old. The analysis focused on subjects within this age range considering that exercise research has predominantly been dedicated toward studying the effects in children and older adults (Erickson et al., 2019; Stillman et al., 2020). Studies were required to be experimental in nature, and consist of both an acute exercise manipulation and cognitive task measurements. A broad range of cognitive domains encompassing tasks probing perception to executive function were included in the meta-analysis. Similarly, a wide range of exercise types and testing contexts were included. For example, traditional laboratory exposures to exercise (e.g., cycling, running) and sport activities in real-world settings were viable candidates for analysis. By casting a wide net, the current study provides a large scope and updated summary of the current state of the exercise and cognition literature.

Second, the current study uses a Bayesian meta-analytic approach to synthesize studies across the acute exercise and cognition literature. The Bayesian approach affords a flexible modeling framework that uses reported effect sizes to characterize the relative evidence in favor of a modulatory account. Inherently, a random effects meta-analytic model is hierarchical in nature, making it well suited for Bayesian methods. When utilized within this statistical framework, priors are placed on parameters at the highest level of the model such as the estimated pooled effect size and measures of heterogeneity. This approach has several advantages compared its frequentist counterpart. First, the use of priors on heterogeneity parameters can attenuate the underestimation of variation both between and within studies (Thompson & Sharp, 1999; Williams et al., 2018), leading to a clearer understanding of sources of heterogeneity and an increased precision when estimating the pooled effect size (Kruschke & Liddell, 2018). Furthermore, priors provide additional constraints on low-level parameter estimates and a greater degree of “shrinkage” of outliers towards the overall pooled effect size or mode(s) of grouping variables (Kruschke, 2014; Kruschke & Liddell, 2018). Therefore, a Bayesian meta-analysis is more robust to outliers and can be more conservative when proper priors are employed. Second, the method yields a posterior distribution for all parameter estimates. This grants the capability of directly modeling the degree of uncertainty in heterogeneity estimates (Thompson & Sharp, 1999). Posterior distributions can be used to compute the probability that an exercise protocol elicits a change in task performance of a given magnitude (e.g., large effect size). Compared to the approximation of *p*-values and confidence intervals, which require additional assumptions for hierarchical models, calculating the high-density interval (HDI), which indicates the most credible outcomes in the posterior distribution, for complex hierarchical models is seamless (Kruschke & Liddell, 2018). Third, it is possible to incorporate knowledge from previous meta-analyses when constructing prior distributions. This affords the ability to quantitatively compare the observed data to the predictions of previous models.

Considering the results of past meta-analyses, exercise was expected to have a small positive influence on cognition. Cognitive task and exercise characteristics were anticipated to moderate this relationship, as evidenced by nonzero parameter estimates, reflecting the selective nature of exercise-induced effects. Model comparisons were conducted to evaluate how moderator inclusion improved predictive performance, and robustness of parameter estimates were determined by employing multiple priors and likelihood functions.

METHODS

Literature Search

Studies investigating the impact of an acute bout of exercise on cognition were obtained through searches of the electronic databases PsychInfo and Google Scholar according to the PRISMA guidelines (Moher et al., 2015). On 09 September 2023, databases were queried using a search string that combined the following physical activity and cognitive domain keywords: [“exercise” OR “physical activity” OR “physical exertion” OR “physical fatigue”] AND [“perception” OR “attention” OR “working memory” OR “executive function” OR “memory” OR “decision making” OR “motor skill” OR “skill acquisition” OR “language” OR “reasoning”]. For the PsychInfo search, the filters “journal article”, “English”, “empirical study”, “human”, and “peer reviewed” were applied. Search results were limited to studies published between 1995-2023 and whose subjects were between 18-45 years of age.

Eligibility Criteria

Studies were deemed eligible for inclusion in the meta-analysis if they met all of the following criteria: assessed the influence of an acute bout of exercise on cognition, compared the effects of exercise with an active and/or passive control group(s), utilized cognitive tasks that measured reaction time (RT) and/or accuracy, tested cognition either during, pre-, or post- exercise and consisted of cognitively normal subjects. Note, an acute bout was defined as an instance of physical activity that occurred within a single 24-hour period (Chang et al., 2012). Two researchers independently screened records based on their title, abstract, and full-text. In the case of discrepancies, a third researcher resolved them by reading the full-text.

Data Extraction and Coding

Information concerning experimental design and procedures, exercise details (i.e., type, intensity, duration), and sample characteristics were extracted from the final list of studies by a single researcher. Means and standard deviations of accuracy and/or RT measures on all cognitive tasks were inserted into an electronic spreadsheet for the calculation of effect sizes. The primary outcome measures for each domain were inserted separately if a task assessed multiple cognitive domains. Regarding studies that probed cognition at multiple time points during or post-exercise, measures for each time point were also recorded separately. If the statistics necessary for calculating effect sizes were not reported in the full-text of the article, the authors were contacted and asked to provide them.

All effect sizes were categorized into one of seven cognitive domains that were generally based on the DSM-5 (Sachdev et al., 2014): executive function, information processing, perception, attention, learning, motor skills, and memory. The classification criteria used for categorizing a cognitive task into a domain is provided in the **Supplementary Material**. To account for variability in the metric used to measure exercise intensity across studies (e.g., ventilatory threshold, heart rate), each intensity was labeled as either light, moderate, or vigorous according to the American College of Sports Medicine guidelines (Garber et al., 2011). Exercise durations were grouped into one of five time bins: ≤ 16 minutes, 20-27 minutes, 30-35 minutes, 40-45 minutes, ≥ 60 minutes. In the event that a study did not provide the exercise duration, its time bin was labeled as "undefined". Exercise types were based on the modality reported in each study, yielding the following categorizations: cycling, high intensity interval training (HIIT), running, walking, circuit training, resistance exercise, and sports activity. The latter category encompassed studies that used sports-related exercises that did not fit into the other labels, such as rock climbing or soccer. The time at which cognitive task performance was evaluated relative to exercise was categorized as either during exercise or 0, 15, 20-75, and ≥ 180 minutes after cessation. Lastly, effect sizes were coded according to task performance dependent measures (i.e., RT vs accuracy). Note, the levels of each categorical moderator were chosen with the intention of achieving a balance between specificity and statistical power to yield reliable estimates that can inform the design of future exercise studies.

Calculating Effect Sizes

Cohen's *d* effect sizes were calculated for studies that tested cognition pre-/post-exercise without a control condition by dividing the mean change in performance by the standard deviation of the pre-test. If the study included a control group (e.g., rest), the mean change of the control condition was subtracted from the mean change of the exercise condition and divided by the pooled standard deviation of pretest scores (Hedges & Olkin, 1985; Lambourne & Tomporowski, 2010). For studies that tested cognition during, or only after exercise, the mean of the control condition was subtracted from the mean of the exercise condition and divided by the standard deviation of the control condition (McMorris et al., 2011). All effect sizes were converted into the bias-corrected standardized mean difference, Hedge's g, by multiplying them by the correction factor $\mathrm{J} = 1 - \frac{3}{4df-1}$ where *df* is the degrees of freedom (Borenstein et al., 2021). The sign of effect sizes for response time and error were reversed to reflect a positive influence of exercise on cognitive task performance. Once effect sizes were extracted from each study, inspection of a funnel plot and Egger's regression test were conducted to assess the risk of publication bias.

Bayesian Hierarchical Modeling

The overall effect of exercise on cognition was assessed using a Bayesian hierarchical model (Higgins et al., 2009; Röver, 2020), which was implemented through the R package *brms* (Bürkner, 2018). In the first level of the model, a study's observed effect size(s) $\hat{\theta}_{ik}$ was assumed to be an estimate of the true effect size θ_k. The observed effect(s) $\hat{\theta}_{ik}$ were modeled as being sampled from a normally distributed population underlying study *k* with a mean equivalent to the true effect and a variance of σ_k^2. In the second level of the model, the true effect size θ_k was assumed to have been drawn from an overarching distribution whose mean represented the overall pooled effect μ, and whose variance depicted the degree of between study heterogeneity τ^2. The final level of the model contained weakly informative priors. A standard normal prior was used for the pooled effect, while the prior for τ^2 was a Half-Cauchy distribution with location and scale parameters set to 0 and 0.5, respectively.

Following the main meta-analysis, subgroup analyses were conducted to determine potential moderators of the relationship between exercise and cognitive task performance. More specifically, we analyzed the influence of the following primary moderators: cognitive domain, time of cognitive test relative to exercise, task outcome measure, exercise intensity, duration, and type. The following secondary moderators were also analyzed to determine the influence of study and participant characteristics on the overall pooled effect size: average sample age, body mass index (BMI kg/m^2), height (cm), weight (kg), VO2 max (ml/kg/min), percentage of female participants, within- vs between-study design, and publication year. With the exception of publication year and the percentage of female participants, all secondary moderators were mean centered for interpretability. A standard normal distribution was used as a weakly informative prior for the difference in effect sizes between subgroups. When reporting model parameter estimates, we use the [mode ± standard deviation] and the 89% HDI of posterior distribution.

Statistical Inference

For all estimated effect sizes, Bayes Factors (BFs) were used to determine the degree of evidence in favor of a difference from zero. BFs were approximated using the reciprocal of the Savage-Dickey density ratio, which was implemented using the function *bayesfactor_parameters* from the *bayestestR* package (Makowski et al., 2019). This method involves dividing the height of the prior distribution for the null value by the height of the posterior distribution at the same value, and represents the credibility of the null value for a parameter once the data has been taken into consideration. BFs were also used to ascertain the predictive performance of subgroup models. After each model was compared to a null counterpart (i.e., moderator excluded) using the function *bayesfactor_models*, an inclusion BF (*bayesfactor_inclusion*) was estimated to determine if including a moderator improved predictive power (Hinne et al., 2020). To estimate stable BFs, a large number of sampling iterations (10,000) and warmup samples (2,000) were used for each of four chains when estimating model parameters (Schad et al., 2021). BFs were interpreted following the guidelines proposed by Jeffreys (1961). A BF between 1 and 3 indicates "anecdotal" evidence for the alternative hypothesis, between 3 and 10 indicates "moderate" evidence, between 10 and 30 indicates "strong" evidence, and greater than 30 indicates "very strong" evidence (Dienes, 2016; Kass & Raftery, 1995; Kruschke & Liddell, 2018; Wetzels et al., 2011). The reciprocal of these ranges signifies evidence in favor of the null hypothesis (e.g., 0.33-1 = anecdotal evidence). When conducting subgroup analyses with more than two factors, orthonormal coding was employed to ensure that an identical prior was used for each factor level and that estimated BFs were accurate (Rouder et al., 2012). Parameter estimates were extracted from all models using the R package *emmeans*.

Sensitivity Analysis

A popular criticism of the Bayesian approach is that priors are chosen subjectively, which in turn can bias parameter estimates and their corresponding BFs (Goldstein, 2006; Kruschke, 2014). Although utilizing weakly informative priors mitigates bias, a sensitivity analysis that evaluates the contribution of both priors and the likelihood function must be conducted to determine if the model results are robust (Depaoli et al., 2020; Lambert et al., 2005; McElreath, 2018; Williams et al., 2018). Thus, we replicated the previously described modeling approach with the exception of using two different priors for the overall pooled effect size. The first was a normal distribution with a mean of zero and standard deviation of ½. Since this prior adds greater weight to the probability that exercise has no influence on task performance, we denoted it as the no effect (NE) prior. The second prior was constructed by synthesizing estimates from previous meta-analyses on acute exercise and cognition (Chang et al., 2012; Lambourne & Tomporowski, 2010; McMorris et al., 2011; Moreau & Chou, 2019; Oberste et al., 2019), resulting in a normal distribution with a mean of 0.24 and standard deviation of 0.57. This prior was denoted as the positive effect (PE) prior.

The influence of the likelihood function was assessed by modeling study effect sizes as being sampled from a *t*-distribution. An advantage of using this likelihood function, compared to a normal distribution, is that model parameter estimates are stable with outliers (Kruschke, 2014). The Half-Cauchy prior was used for the scale of the distribution, while a standard normal prior was used for its mean. For its shape (i.e., degree of freedom) an exponential distribution with a rate equal to 1/29 served as a prior. To determine if meta-analytic estimates were robust across the alternative priors and likelihood function, we visually compared the posterior distributions across models for large deviations (Depaoli et al., 2020).

RESULTS

Description of Studies

The literature search yielded 15,900 peer reviewed journal articles, and after removing duplicates 8,295 remained. Subsequent an initial screening based off the titles and abstracts, 805 studies were identified as potential candidates for modeling. 113 of these studies were deemed eligible for inclusion in the meta-analysis according to their full-text contents (**Figure 1**). In total, 642 effect sizes were extracted from these studies, representing data from 4,390 subjects. A majority of the effects measured the influence of exercise on executive function (*k* = 434) and attention (*k* = 109). Fewer effects were measured during exercise (*k* = 82) relative to after the cessation of exercise (*k* = 560). Visual inspection of a funnel plot suggested that the effect sizes were distributed symmetrically (**Figure 2A**), however there was very strong evidence for asymmetry according to Egger's regression intercept (β = 1.18 ± 0.25; HDI = [0.78, 1.58]; BF = 253.24) suggesting the presence of publication bias. This was addressed

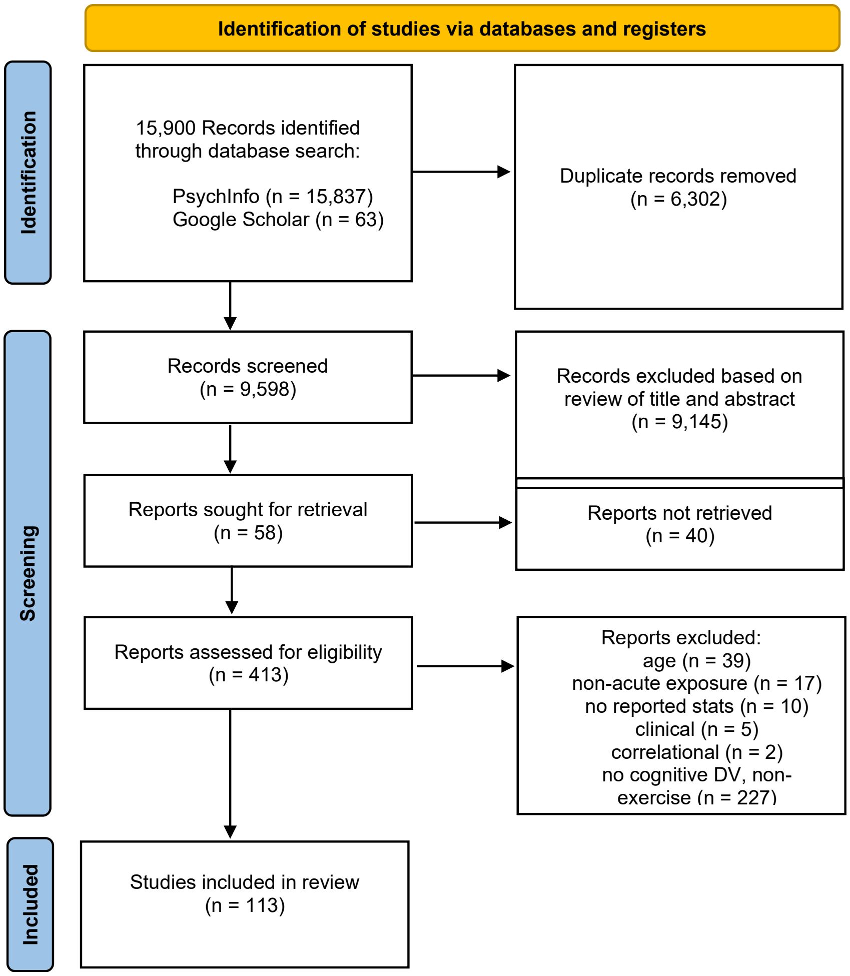

Figure 1. PRISMA flow diagram of literature search and study selection for meta-analytic modeling.

by employing the trim and fill approach, which imputes low-precision effect sizes until the funnel plot is symmetrical (Duval & Tweedie, 2000).

Overall Effect

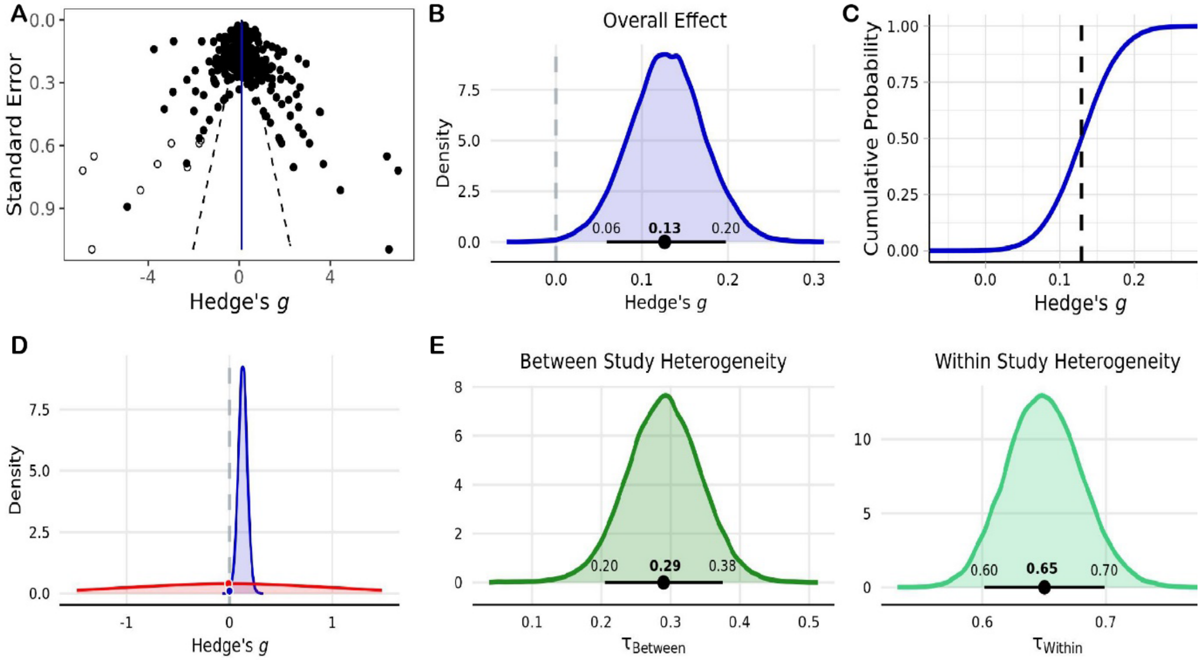

Figure 2. A) Funnel plot of study effect sizes. Imputed effect sizes after using the trim and fill method are represented by the unfilled circles. Vertical blue line indicates the estimated pooled effect sizes, while dashed black lines represent a pseudo 95% confidence limits. B) Posterior distribution of estimated pooled effect. Horizontal black line indicates bounds of 89% HDI. C) Empirical cumulative density function of distribution in B, where the dashed black line indicates the pooled effect. D) Representation of using the Savage-Dickey ratio to calculate BFs. The density of the null value in the prior distribution (red) is divided by its density in the posterior distribution (blue) to yield probabilistic evidence in favor of the alternative hypothesis. E) Posterior distributions of between and within study heterogeneity.

The meta-analysis indicated that there was moderate evidence for an acute bout of exercise to have a small positive influence on overall performance across cognitive domains ($g = 0.13 \pm 0.04$; HDI = [0.06, 0.20]; BF = 3.67) (**Figure 2B & 2D**). According to the posterior distribution, there was a low probability that the estimated pooled effect was less than or equal to zero ($p = 0.01$) and an 80% chance that the effect size fell between the range of 0 to 0.2 (**Figure 2C**).

Table 1.

Study description and estimated effect sizes

Study	*N*	Experimental Design	Exercise Type	Exercise Intensity	Duration (min)	Cognitive Domain	Test Time	*N Effects*	*g*	89% HDI
Hogervorst et al., 1996	15	Within	Cycling	Vigorous	60	Inhibition	Pre-Post	1	0.03	-0.39, 0.47
McMorris & Graydon, 1996	20	Within	Cycling	Moderate Vigorous	2	Executive Function	During	6	0.11	-0.19, 0.45
Brisswalter et al., 1997	20	Within	Cycling	Vigorous	40	Information Processing	Pre-Post	4	0	-0.36, 0.35
Arcelin & Delignieres, 1998	22	Within	Cycling	Moderate	10	Information Processing	During	2	0.03	-0.35, 0.44
McMorris et al., 1999	9	Within	Cycling	Moderate Vigorous	Task Completion	Executive Function	During	4	0.01	-0.34, 0.38
Collardeau et al., 2001	11	Within	Running	Vigorous	90	Perception	Pre-Post	2	-0.05	-0.47, 0.34
Deuster et al., 2002	13	Within	Running	Vigorous	Volitional Exhaustion	Attention Learning Executive Function	Pre-Post	24	0.16	-0.05, 0.39
Hillman et al., 2003	19	Within	Running	Vigorous	30	Executive Function	Post	2	-0.08	-0.44, 0.35
Pesce et al., 2003	16	Within	Cycling	Moderate	Task Completion	Attention	During	2	0.25	-0.15, 0.70
Davranche et al., 2005a	7	Within	Cycling	Maximal	Volitional Exhaustion	Perception	Pre-Post	2	0.08	-0.32, 0.49

Davranche & Pichon, 2005b	12	Within	Cycling	Maximal	Volitional Exhaustion	Perception	During	1	0.06	-0.37, 0.49
Pesce et al., 2007	48	Within	Cycling	Vigorous	Task Duration	Attention	During	2	0.14	-0.24, 0.57
Vickers & Williams, 2007	10	Within	Cycling	Moderate Vigorous	2	Motor Skills	Pre-Post	4	-0.05	-0.43, 0.29
Lo Bue-Estes et al., 2008	26	Between	Running	Vigorous	20	Executive Function Memory	Pre-Post	8	0.01	-0.28, 0.32
Coles & Tomporowski, 2008	18	Within	Cycling	Moderate	40	Executive Function	Pre-Post	1	0	-0.41, 0.44
Fontana et al., 2009	32	Within	Running	Light Moderate Vigorous	4	Executive Function	During	6	0.07	-0.23, 0.40
Luft et al., 2009	30	Within	Running	Vigorous	20	Attention Information Processing Memory	Pre-Post	10	-0.11	-0.39, 0.16
Pontifex et al., 2009	21	Within	Running Resistance	Vigorous	30	Executive Function	Pre-Post	4	-0.31	-0.69, 0.05
Srygley et al., 2009	52	Within	Walking	Light	Task Completion	Executive Function	During	2	0.03	-0.4, 0.39
Thomson et al., 2009	163	Within	Treadmill	Vigorous	27	Executive Function	Pre-Post	2	0.1	-0.3, 0.49
Lambourne et al., 2010	19	Within	Cycling	Moderate	40	Executive Function	Pre, During, Post	4	-0.36	-0.76, 0

Norling et al., 2010	121	Between	Running	Light Moderate Vigorous	30	Attention	Pre-Post	3	0.08	-0.28, 0.46
Young et al., 2010	27	Within	Running	Moderate	7	Motor Skills	Pre-Post	1	-0.02	-0.47, 0.39
Chang et al., 2011	42	Between	Cycling	Vigorous	30	Executive Function	Pre-Post	3	-0.02	-0.37, 0.35
Green & Helton, 2011	12	Within	Climbing	Moderate	3	Memory	During	1	-0.2	-0.71, 0.20
Ohlinger et al., 2011	50	Within	Walking	Light	Task Completion	Attention Executive Function	During	3	-0.01	-0.38, 0.35
Hope et al., 2012	52	Between	Punching	Vigorous	Volitional Exhaustion	Memory	Post	3	-0.42	-0.83, -0.02
Lambourne, 2012	16	Within	Cycling	Vigorous	35	Executive Function	Pre-Post	1	-0.01	-0.46, 0.39
Moore et al., 2012	30	Between	Cycling	Moderate	6-54	Perception Executive Function Attention	Pre-Post	5	-0.12	-0.43, 0.23
Quelhas Martins et al., 2013	24	Between	Cycling	Moderate	8	Executive Function	During	1	0.1	-0.33, 0.53
Roberts & Cole, 2013	40	Within	Circuit	Light Moderate	1-5	Executive Function	Pre-Post	8	-0.05	-0.34, 0.25
Bullock & Giesbrecht, 2014	26	Between	Cycling	Moderate	136	Perception	Pre, Post	8	-0.14	-0.44, 0.15

Byun et al., 2014	25	Within	Cycling	Light	10	Executive Function	Pre-Post	2	0.17	-0.23, 0.58
Darling & Helton, 2014	12	Within	Climbing	Moderate	5	Memory	During	2	-0.1	-0.51, 0.29
Nibbeling et al., 2014	22	Between	Running	Vigorous	10	Motor Skills Executive Function Memory Attention	Post	5	-0.08	-0.43, 0.24
Pontifex et al., 2015	34	Within	Running	Moderate	20	Attention	Pre-Post	2	0	-0.39, 0.4
Schmidt-Kassow et al., 2014	18; 31	Within	Walking	Light	30	Memory	During	2	0.05	-0.36, 0.43
Tsai et al., 2014	60	Between	Resistance	Moderate Vigorous	45	Executive Function	Pre-Post	4	0.02	-0.33, 0.36
Bantoft et al., 2016	45	Within	Walking	Light	< 60	Executive Function Attention Information Processing	During	4	-0.1	-0.39, 0.17
Larson et al., 2015	69	Between	Walking	Light	60	Executive Function	During	2	-0.03	-0.43, 0.35
Osgood, 2015	86	Between	Sport Activity	Light	2	Attention	Post	1	-0.06	-0.47, 0.37
Perciavalle et al., 2015	30	Within	Cycling	Vigorous	Volitional Exhaustion	Executive Function	Pre-Post	4	0.22	-0.11, 0.61

Shia et al., 2015	17	Within	Cycling	Vigorous	45	Attention	Pre-Post	1	-0.11	-0.55, 0.3
Stevens et al., 2015	35; 34	Between	Cycling	Light Moderate	15	Learning	During	4	0.04	-0.31, 0.4
Weng et al., 2015	26	Within	Cycling	Moderate	30	Executive Function	Pre-Post	4	0.29	-0.07, 0.67
Alloway et al., 2016	72	Within	Running	Light	8	Executive Function	Pre-Post	1	-0.01	-0.43, 0.42
Ando et al., 2012	14	Within	Cycling	Moderate Vigorous	6	Perception	During	2	-0.08	-0.48, 0.31
Brush et al., 2016	28	Within	Resistance	Light Vigorous	45	Executive Function	Post	60	-0.1	-0.26, 0.04
Connell et al., 2016	24	Between	Cycling	Moderate	180	Attention	Pre-Post	4	-0.21	-0.6, 0.12
Hsieh et al., 2016a	20	Within	Resistance	Moderate Vigorous	30	Executive Function	Pre-Post	1	0.04	-0.39, 0.46
Hsieh et al., 2016b	18	Within	Resistance	Moderate	30	Executive Function	Post	1	0.03	-0.39, 0.47
Komiyama et al., 2016	10	Within	Cycling	Moderate	30	Executive Function	During	3	0.04	-0.33, 0.42
Lowe et al., 2016	51	Within	Walking	Light Moderate	20	Executive Function	Pre-Post	4	0.01	-0.34, 0.35
Torbeyns et al., 2016	23	Within	Cycling	Light	30	Memory Executive	During	6	-0.1	-0.42, 0.22

						Function Attention				
Tsukamoto et al., 2016	12	Within	Cycling	Moderate Vigorous	40	Executive Function	Pre-Post	16	-0.19	-0.45, 0.07
Zach & Shalom, 2016	20	Within	Running Volleyball Resistance	Vigorous	15; Game duration	Executive Function	Pre-Post	6	0.37	0.02, 0.7
Chang et al., 2017	30	Within	Cycling	Vigorous	30	Executive Function	Post	1	0.35	-0.07, 0.9
Crush & Loprinzi, 2017	352	Between	Running	Moderate	10; 20; 30; 45; 60	Executive Function Attention	Post	75	-0.14	-0.28, 0.0
González Fernández et al., 2017	18	Within	Cycling	Light	45	Attention	During	1	0.02	-0.39, 0.45
Lindheimer et al., 2017	60	Between	Cycling	Light	25	Executive Function	Pre-Post	16	-0.12	-0.35, 0.12
Lowe et al., 2017	28	Within	Walking	Light Moderate	20	Executive Function	Pre-Post	4	-0.31	-0.68, 0.06
Luu & Hall, 2017	31	Within	Yoga	Light	25	Executive Function	Pre-Post	2	-0.19	-0.62, 0.19
Randolph & O'Connor, 2017	18	Within	Walking	Light	10	Attention Executive Function Information Processing	Pre-Post	28	-0.06	-0.25, 0.14

Slutsky et al., 2017	24	Between	Cycling	Light	15	Attention Executive Function	Pre-Post	7	-0.18	-0.47, 0.14
Sudo et al., 2017	32	Between	Cycling	Vigorous	Volitional Exhaustion	Executive Function	Pre-Post	3	0.28	-0.07, 0.7
Cuttler et al., 2017	120	Between	Resistance Walking	Light Moderate	30	Memory Attention	Pre-Post	6	-0.61	-0.98, -0.25
Daikoku et al., 2018	44	Between	Cycling	Light	3	Memory	During	1	-0.04	-0.5, 0.35
Elkana et al., 2018	69	Between	Cycling	Moderate	15	Executive Function	Pre-Post	1	-0.03	-0.5, 0.35
Fenesi et al., 2018	77	Between	Calisthenics	Light	13	Learning Memory	Post	2	0.16	-0.24, 0.55
Kendall, 2018	60	Between	HIIT	Vigorous	20	Information Processing Learning Cognitive Control	Post	8	0.82	0.42, 1.16
Legrand et al., 2018	101	Between	Running	Moderate	15	Attention Executive Function	Pre-Post	2	0.05	-0.34, 0.44
Samani & Heath, 2018	14	Within	Cycling	Vigorous	10	Executive Function	Pre-Post	1	0.08	-0.34, 0.52
Siddiqui & Loprinzi, 2018	20	Within	Walking	Moderate	20	Memory Executive Function	Pre, During, Post	4	0.02	-0.31, 0.4
Sng et al., 2018	80	Between	Walking	Light	15	Memory	During, Post	4	-0.25	-0.62, 0.1

Wade & Loprinzi, 2018	34	Between	Walking	Moderate	15	Memory	Post	1	-0.13	-0.56, 0.3
Yamazaki et al., 2018	30	Within	Cycling	Light Moderate	10	Attention Executive Function	Pre-Post	16	0.07	-0.16, 0.32
Baker et al., 2019	19	Within	Cycling	Light	120	Attention Executive Function	During	3	-0.06	-0.44, 0.31
Du Rietz et al., 2019	26	Within	Cycling	Vigorous	20	Attention Executive Function	Pre-Post	4	-0.06	-0.42, 0.28
Engeroff et al., 2019	26	Within	Resistance	Moderate Vigorous Maximal	60	Executive Function	Pre-Post	4	0.1	-0.26, 0.45
Haynes et al., 2019	24	Within	Walking	Light	15	Memory	During, Post	9	-0.04	-0.32, 0.24
Johnson & Loprinzi, 2019	40	Within	Walking	Moderate Vigorous	15	Memory	Post	2	-0.01	-0.04, 0.38
McGowan et al., 2019	58	Within	Running	Moderate	20	Executive Function	Pre-Post	2	-0.02	-0.39, 0.39
Mehren et al., 2019	31; 32	Within	Cycling	Vigorous	30	Executive Function	Post	8	0.15	-0.14, 0.45
Schmidt et al., 2019	15; 19	Within	Running	Vigorous	38	Attention	Pre-Post	6	-0.24	-0.57, 0.09
Stenling et al., 2019	32	Within	Walking	Moderate	3	Executive Function Attention	Post	8	0	-0.29, 0.29

Wu et al., 2019	35	Within	Cycling Resistance	Light Vigorous	30	Executive Function	Post	8	0.28	-0.03, 0.59
Zhou & Qin, 2019	72	Between	Cycling	Light	25	Executive Function	Pre-Post	2	-0.05	-0.42, 0.37
Aly & Kojima, 2020	40	Between	Cycling	Light	20	Executive Function	Pre-Post	2	0.07	-0.32, 0.47
Chacko et al., 2020	15	Within	Cycling	Vigorous	30	Executive Function	Pre-Post	2	0.06	-0.32, 0.49
Kao et al., 2020	23	Within	Walking	Light	20	Executive Function	Post	4	0.24	-0.10, 0.63
Morris et al., 2020	14	Within	Cycling	Moderate	30	Attention Executive Function	Pre-Post	6	-0.01	-0.33, 0.3
Walsh et al., 2020	15; 13	Within	Walking	Moderate	20	Executive Function Attention	Pre-Post	8	0.01	-0.31, 0.29
Kao et al., 2021	36	Within	HIIT Walking	Moderate	16	Executive Function	Post	2	0.32	-0.06, 0.78
Kim et al., 2021	16	Within	Walking	Vigorous	10	Executive Function	Pre-Post	2	-0.03	-0.38, 0.41
Klatt & Smeeton, 2021	27	Within	Cycling	Vigorous	Task Completion	Memory	During	4	-0.15	-0.5, 0.21
Kuhne et al., 2021	50	Between	Cycling	Moderate	40-55	Memory	Post	2	-0.09	-0.49, 0.29
Manocchio & Lowe, 2021	22	Within	Walking	Light Moderate	20	Attention Executive Function	Pre-Post	8	-0.06	-0.34, 0.25

Miyashiro et al., 2021	17	Within	Push-Ups	Vigorous	20	Executive Function	Post	1	0	-0.45, 0.41
Trammell & Aguilar, 2020	28	Within	Running	Vigorous	20	Memory Executive Function	Pre-Post	5	-0.11	-0.47, 0.2
Zhu et al., 2021	16	Within	Cycling Running	Moderate Vigorous	40	Executive Function	Pre-Post	16	0.1	-0.14, 0.34
Aguirre-Loaiza et al., 2022	19	Between	Cycling	Vigorous	20	Executive Function	Pre-Post	4	-0.06	-0.41, 0.3
Drollette & Meadows, 2022	22	Within	HIIT	Vigorous	9	Executive Function	Post	6	0.06	-0.24, 0.39
Engeroff et al., 2022	26	Within	Resistance	Moderate Vigorous	60	Attention	Pre-Post	16	-0.17	-0.39, 0.08
Frith et al., 2022	45	Within	Running	Moderate	15	Executive Function	During	1	0.06	-0.4, 0.46
Kao et al., 2022	27	Within	Running	Moderate	24	Attention Executive Function	Pre-Post	5	-0.04	-0.35, 0.31
LaCount et al., 2022	18	Within	HIIT	Vigorous	16	Attention Executive Function Information Processing	Post	3	-0.09	-0.46, 0.28
Loprinzi & Storm, 2023	180; 225; 158	Between	Treadmill	Moderate Vigorous	25	Memory	Post	6	-0.02	-0.33, 0.3
Shirzad et al., 2022	28	Within	Cycling	Light	26	Executive Function	Pre-Post	2	-0.23	-0.64, 0.17

Zheng et al., 2022	27	Within	Cycling	Moderate	15	Executive Function	During	2	0.27	-0.11, 0.72
Chueh et al., 2023	30	Within	Step Exercise	Vigorous	20	Attention Executive Function	Pre-Post	8	0.15	-0.15, 0.44
Yamada et al., 2023	85	Within	Recumbent Bike	Vigorous	20	Executive Function	Pre-Post	4	0.02	-0.31, 0.38
B. Zhang et al., 2023	18	Within	Cycling	Moderate	25	Perception	Post	4	0.29	-0.09, 0.65
D. Zhang et al., 2023	76	Within	Cycling	Light	20	Attention	Pre-Post	4	0.03	-0.33, 0.36

There was a large amount of heterogeneity within (τ_{within}= 0.65 ± 0.03; HDI = [0.60, 0.70]; I^2_{within}= 81.19%) and moderate amount between ($\tau_{between}$= 0.29 ± 0.05; HDI = [0.20, 0.38]; $I^2_{between}$ = 15.9%) studies (**Figure 2E**).

Subgroup Analyses

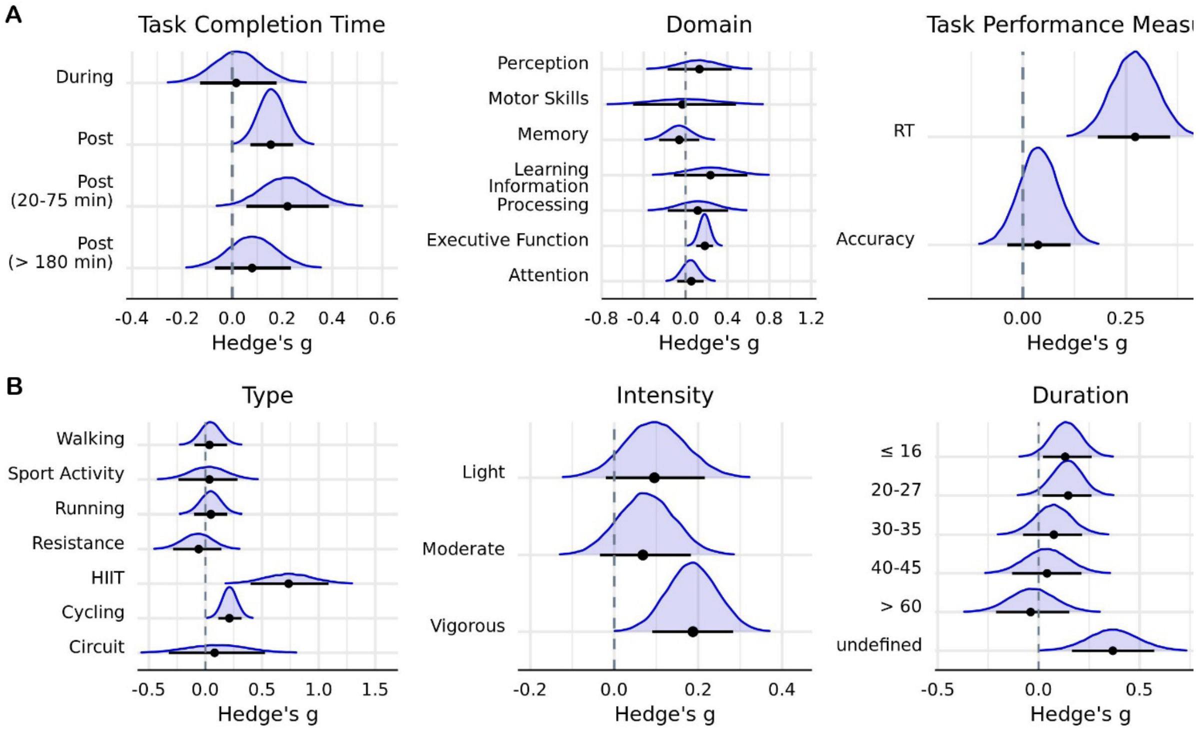

Figure 3. Posterior distributions of A) cognitive and B) exercise moderators. The horizontal black line indicates the 89% HDI interval, while the black dot represents the mode of the posterior distribution.

Primary subgroup analyses revealed that acute exercise reduced RT on cognitive tasks (*g* = 0.27; HDI = [0.18, 0.36]; BF $= 6.71 \times 10^{3}$) but had no impact on accuracy (*g* = 0.04; HDI = [-0.04, 0.12]; BF $= 6.15 \times 10^{-2}$) (**Table 2**) (**Figure 3A**). Engaging in either cycling (*g* = 0.21; HDI = [0.11, 0.32]; BF = 14.74) or HIIT (*g* = 0.73; HDI = [0.40, 1.09]; BF = 26.05) was found to have an enhancing effect on performance in cognitive tasks (**Figure 3B**). In regard to cognitive domain, there was evidence that acute exercise has a positive influence on

Table 2.

Primary Moderator Estimates

Exercise Moderator Variable	*N*	*g*	89% HDI	BF_{10}	Cognitive Moderator Variable	*N*	*g*	89% HDI	BF_{10}
Intensity					Domain				
Light	167	0.10	-0.02, 0.22	0.13	Attention	109	0.06	-0.08, 0.17	0.08
Moderate	222	0.07	-0.03, 0.18	0.09	Executive Function	434	0.18	0.10, 0.27	36.97
Vigorous	253	0.19	0.09, 0.28	5.03	Information Processing	15	0.12	-0.17, 0.41	0.14
					Learning	12	0.24	-0.11, 0.59	0.25
Duration (minutes)					Memory	44	-0.06	-0.25, 0.13	0.08
≤ 16	161	0.14	0.02, 0.26	0.30	Motor Skills	6	-0.03	-0.51, 0.49	0.20
20-27	152	0.15	0.02, 0.26	0.32	Perception	22	0.13	-0.17, 0.44	0.15
30-35	93	0.08	-0.08, 0.22	0.09					
40-45	113	0.04	-0.13, 0.21	0.09					
> 60	48	-0.03	-0.21, 0.15	0.08	Task Outcome				
Not provided	75	0.37	0.17, 0.57	6.21	Accuracy	377	0.04	-0.04, 0.12	6.15e-2
					Reaction Time	265	0.27	0.18, 0.36	6.71e3
Type									
Circuit	8	0.08	-0.33, 0.53	0.26					
Cycling	204	0.21	0.11, 0.32	14.74	Task Completion Time (relative to exercise)				
HIIT	18	0.73	0.40, 1.09	26.05	During	82	0.02	-0.18, 0.13	0.09
Resistance	97	-0.06	-0.29, 0.14	0.11	Immediately After	315	0.16	0.11, 0.30	4.03
Running	172	0.05	-0.10, 0.19	0.08	20-75 min post	94	0.22	0.13, 0.44	0.76
Sport Activity	26	0.04	-0.23, 0.29	0.11	> 180 min post	151	0.08	-0.03, 0.28	0.10
Walking	117	0.04	-0.10, 0.19	0.07					

Table 3.

Secondary Moderator Estimates

Moderator Variable	*N*	*g*	89% HDI	BF$_{10}$
Publication Year	642	0.13	0.06, 0.20	3.25
Exp. Design				
Between	193	0.03	-0.11, 0.16	0.07
Within	449	0.17	0.08, 0.24	12.18
Age (Years) ($\mu = 22.49$)	599	0.14	0.06, 0.21	3.13
% Female	577	0.12	0.05, 0.20	4.23
BMI (kg/m^2) ($\mu = 24.02$)	378	0.20	0.08, 0.30	1.28
VO2 max (ml/kg/min) ($\mu = 43.22$)	299	0.19	0.05, 0.34	1.08
Height (cm) ($\mu = 158.55$)	275	0.21	0.09, 0.33	2.90
Weight (kg) ($\mu = 65.02$)	283	0.21	0.08, 0.33	4.28

executive processes (*g* = 0.18; HDI = [0.10, 0.27]; BF = 36.97). Furthermore, behavioral performance was found to improve immediately after exercise cessation (*g* = 0.16; HDI = [0.11, 0.30]; BF = 4.03) and in response to vigorous intensity exercises (*g* = 0.19; HDI = [0.09, 0.28]; BF = 5.03). Lastly, at least moderate evidence in favor of non-zero parameter estimates were observed for the secondary moderators publication year, within-subjects design, age, percentage of female participants, and weight (**Table 3**). To test for the possible contribution of a learning effect to the estimated overall pooled effect size, a separate meta-analysis was conducted on effects from studies employing

Table 4.

Subgroup model comparisons

Model	**BF$_{\text{Inclusion}}$**
No Moderators	1
Exercise Intensity	2.16e-4
Exercise Duration	9.35e-4
Exercise Type	2.00e-2
Cognitive Domain	4.97e-3
Task Outcome	357.10
Task Completion Time	5.52e-4
Publication Date	9.05e-4
Experimental Design	0.04
Age	0
% Female	4.53e-3
BMI	0.04
VO2	8.40e-3
Height	2.89e-3
Weight	0.01

a pre-/post-test design (N effect sizes = 298). Despite the estimated pooled effect size for this subset of data being nominally similar to the estimate for the entire dataset, there was anecdotal evidence in favor of the null hypothesis (g = 0.15 ± 0.06; HDI = [0.04, 0.24]; BF =0.95). Moderator analyses indicated that this effect did not differ as a function of whether or not a control group was included in the study (BFInclusion =0.12"; w/ control: g "=0.18 ±0.10"; HDI"="[" 0.03,0.33"]; BF"=0.51"; w/o control: g"=0.11 ±0.13"; HDI"=[-0.03,0.26]"; BF"=0.18" "), suggesting that the estimated influence of exercise on general cognitive performance is not driven by a learning effect.

Model Comparisons

Model comparisons were performed to determine if including a moderator improved predictive performance. Only a model that included task performance measure as a moderator was more likely when compared to a null counterpart ($BF_{\text{Inclusion}} = 357.10$) (**Table 4**). This is likely due to a number of factors. First, acute exercise had a negligible impact on a majority of the levels in each subgroup. Second, there was a high degree of uncertainty in estimated model coefficients, as evidenced by their wide HDI intervals. Third, Bayesian inference automatically penalizes model complexity and favors more parsimonious models. If a model has many parameters, but a majority of them are nonzero, then a simpler counterpart will be favored.

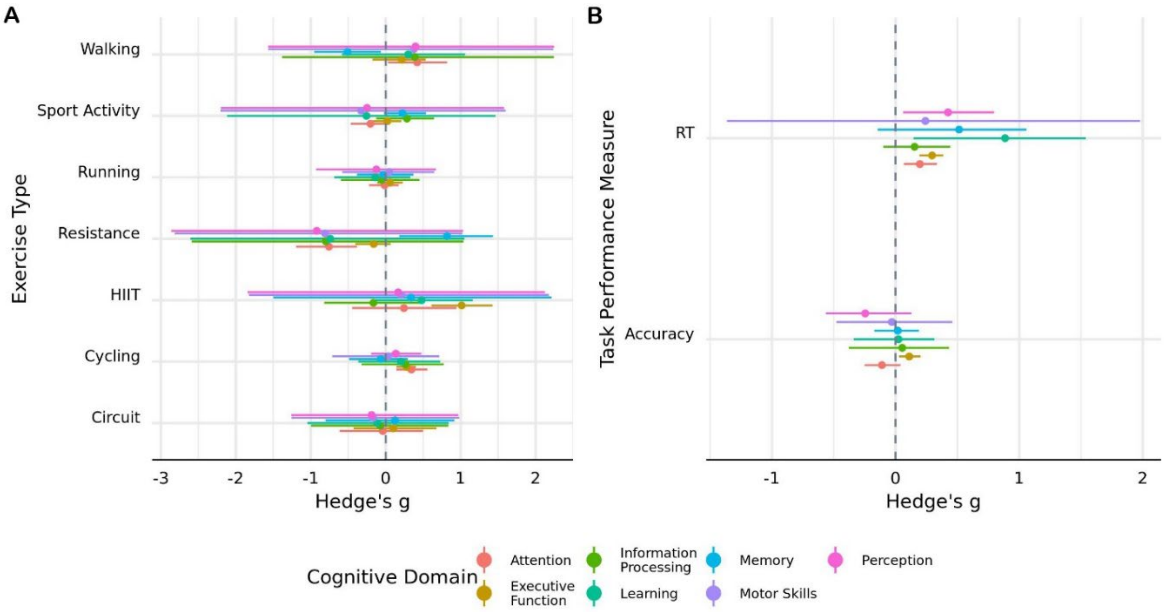

Figure 4. Posterior mode estimates of models including interactions between cognitive domain and A) exercise type and B) task outcome measure. Width of line represents 89% HDI.

Interactions Between Moderators

An exploratory analysis was conducted to determine if the influence of moderator variables was contingent on one another. Due to the computationally intensive nature of Bayesian modeling, analyses were limited to the following pairs of moderators: 1) exercise intensity and type, 2) exercise intensity and duration, 3) exercise type and duration, 4) cognitive domain and exercise type, 5) cognitive domain and exercise intensity, 6) cognitive domain and task performance measure, 7) exercise type and task performance measure. Although none of the pairs of interaction models had more predictive power compared to a null counterpart ($\mathrm{BF}_{\mathrm{Inclusion}} \leq 1$), there were two that had nonzero parameter estimates.

The first model included an interaction between cognitive domain and exercise type ($\mathrm{BF}_{\mathrm{Inclusion}} = 7.30 \times 10^{-4}$). There was evidence in favor of cycling improving performance

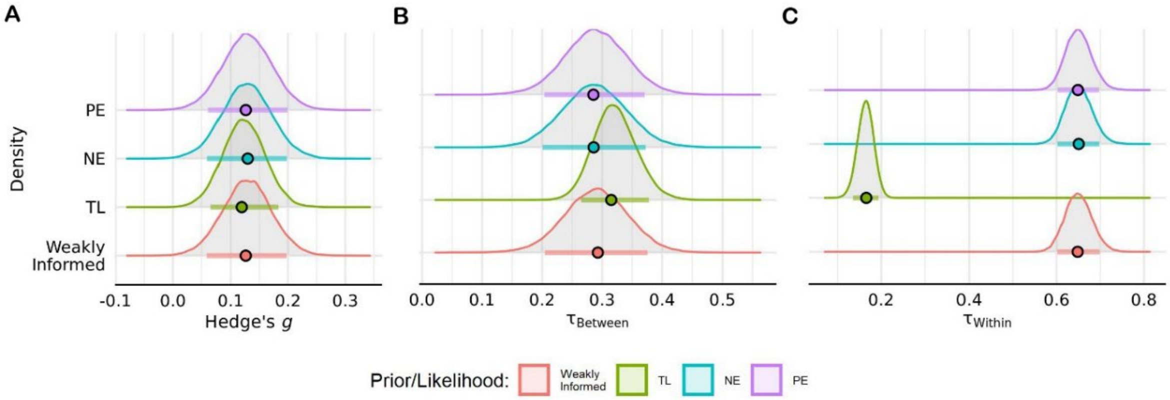

Figure 5. Estimates for the A) overall pooled effect size, B) between- and C) within-study heterogeneity parameters across the t-likelihood function (TL), weakly informed, null effect (NE), and positive effect (PE) priors.

on tasks that probed attention (*g* = 0.34; HDI = [0.14, 0.56]; BF = 3.05) and executive function (*g* = 0.28; HDI = [0.14, 0.40]; BF = 17.83). HIIT exercises were found to bolster executive function (*g* = 1.01; HDI = [0.61, 1.43]; BF = 155.33), while resistance exercises had an aversive impact on attentional performance (*g* = -0.76; HDI = [-1.20, -0.38]; BF = 18.07) (**Figure 4A**). The second model included an interaction between cognitive domain and task performance measure ($\text{BF}_{\text{Inclusion}} = 7.56 \times 10^{-3}$) and indicated that time-dependent measures of executive function are improved (*g* = 0.30; HDI = [0.19, 0.39]; BF = 1.10×10^{3}) (**Figure 4B**).

Sensitivity Analyses

The estimated overall effect of acute exercise on cognition was consistent across the NE prior (*g* = 0.13 ± 0.04; HDI = [0.06, 0.20]; BF = 6.52), PE prior (*g* = 0.12 ± 0.04; HDI = [0.06, 0.19]; BF = 6.51), and *t* likelihood function (*g* = 0.12 ± 0.04; HDI = [0.06, 0.18]; BF = 8.77) (**Figure 5A**). Interestingly, there was anecdotal-to-moderate evidence in favor of the synthesized estimate from previous meta-analyses (i.e., *g* = 0.24) across the PE (BF = 3.19), NE (BF $= 2.78$), and standard normal (BF $= 5.27$) priors. Estimates of between study heterogeneity were also robust across the NE prior ($\tau_{between}$= 0.29 ± 0.05; HDI = [0.20, 0.37]), the PE prior ($\tau_{between}$= 0.29 ± 0.05; HDI = [0.21, 0.37]), and *t* likelihood function ($\tau_{between}$= 0.31 ± 0.03; HDI = [0.26, 0.38]) (**Figure 5B**). In contrast, within study heterogeneity was estimated to be lower when using the *t* likelihood function (τ_{within}= 0.17 ± 0.02; HDI = [0.13, 0.19]) relative to the NE (τ_{within}= 0.65 ± 0.03; HDI = [0.61, 0.70]) and PE (τ_{within}= 0.65 ± 0.02; HDI = [0.60, 0.70]) priors (**Figure 5C**). Note, this reduction reflects the diminished influence of outliers on variance estimates by the inclusion of the shape parameter for the *t* distribution (v = 1.52 ± 0.14; HDI = [1.30; 1.73]). In addition to testing the robustness of parameter estimates, a model comparison was conducted to determine if either the null or positive effect prior was more probable given the data. The *t*-likelihood function was not included in this comparison since it would only indicate if effect sizes were more likely to have been drawn from either a normal or *t*-distribution. When compared to a standard normal prior, there was anecdotal evidence in favor of both the PE (BF $= 2.56$) and NE (BF $= 1.48$) priors. Relative to the PE prior, there was anecdotal evidence against the NE prior (BF $= 0.73$). Altogether, parameter estimates were not biased by the prior or likelihood function.

Executive Function Meta-Analysis

Considering that the majority of the effect sizes were from tasks that probed executive function, and that this cognitive domain encompasses multiple sub-domains, a separate meta-analysis and set of meta-regressions were conducted on this subset of data. Categorization criteria from previous meta-analyses and systematic reviews (Ludyga et al., 2016, Ishihara et al., 2021, Cantelon & Giles, 2021) were used to classify effect sizes into the following sub-domains of executive function: working memory, cognitive control, decision making, planning, and inhibition. For completeness, the primary moderators used in the main meta-analysis were also tested.

The results were similar to the main meta-analysis. There was very strong evidence in favor of exercise having a small positive influence on overall task performance (g = 0.20 ± 0.06; HDI = [0.12, 0.30]; BF $= 29.57$), and a moderate degree of heterogeneity both within (τ_{within}= 0.51 ± 0.03; HDI = [0.47, 0.57]) and between studies ($\tau_{between}$= 0.40 ± 0.06; HDI = [0.30, 0.48]). Subgroup analyses indicated that a model including the moderator task outcome measure was had more predictive power relative to a null counterpart (BF $= 48.43$). Paralleling the main meta-analysis, there was very strong evidence that acute exercise

Table 5.

Executive Function Moderator Estimates

Exercise Moderator Variable	*N*	*g*	89% HDI	BF_{10}	Cognitive Moderator Variable	*N*	*g*	89% HDI	BF_{10}
Intensity					Sub-Domain				
Light	107	0.23	0.08, 0.37	1.71	Cognitive Control	55	0.23	0.06, 0.39	0.73
Moderate	151	0.15	0.01, 0.28	0.30	Decision Making	28	0.10	-0.16, 0.39	0.14
Vigorous	175	0.24	0.12, 0.36	13.49	Inhibition	153	0.21	0.09, 0.33	3.14
					Planning	18	0.14	-0.12, 0.38	0.15
Duration (minutes)					Working Memory	179	0.22	0.11, 0.34	6.89
≤ 16	93	0.25	0.09, 0.40	1.76					
20-27	99	0.13	-0.02, 0.27	0.19	Task Outcome				
30-35	68	0.19	0.03, 0.36	0.44	Accuracy	253	0.13	0.04, 0.23	0.63
40-45	100	0.13	-0.06, 0.32	0.16	Reaction Time	180	0.32	0.21, 0.42	749.18
> 60	25	0.11	-0.12, 0.32	0.13					
Not provided	48	0.53	0.29, 0.83	24.40	Type				
					Circuit	8	0.15	-0.31, 0.65	0.31
Task Completion Time (relative to exercise)					Cycling	133	0.28	0.15, 0.42	19.58
During	39	0.23	0.004, 0.44	0.45	HIIT	12	0.96	0.56, 1.38	71.23
Immediately After	197	0.21	0.10, 0.31	4.17	Resistance	90	-0.07	-0.33, 0.17	0.12
20-75 min post	72	0.31	0.13, 0.47	4.11	Running	116	0.06	-0.12, 0.25	0.10
> 180 min post	125	0.13	-0.03, 0.29	0.17	Sport Activity	11	0.30	-0.07, 0.68	0.35
					Walking	63	0.14	-0.05, 0.34	0.18

improved RT on executive function tasks (*g* = 0.32; HDI = [0.21, 0.42]; BF = 748.18) but had no effect on accuracy (*g* = 0.13; HDI = [0.04, 0.23]; BF = 0.63) (**Table 5**). Furthermore, there was moderate evidence in favor of a positive impact of exercise on inhibition (*g* = 0.21; HDI = [0.09, 0.33]; BF = 3.14) and working memory (*g* = 0.22; HDI = [0.11, 0.34]; BF = 6.89) (**Figure 6**). Yet, a model including executive function sub-domain as a moderator did not improve model performance ($BF_{\text{Inclusion}} = 7.52 \times 10^{-4}$), nor did models including any interactions between moderators.

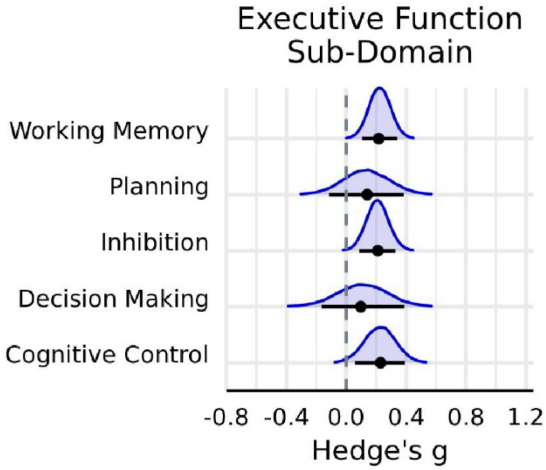

Figure 6. Posterior distributions for executive function sub-domain. Horizontal black line indicates the 89% HDI interval, while the black dot represents the mode of the posterior distribution.

DISCUSSION

A large corpus of empirical work has examined how a single bout of acute exercise modulates activity within multiple brain systems that underly cognition. Despite inconsistencies in results across empirical studies, there is consensus amongst previous reviews and meta-analyses that acute exercise impacts behavioral performance (Chang et al., 2012; Lambourne & Tomporowski, 2010; Moreau & Chou, 2019) and that this relationship is moderated by both exercise protocol and behavioral task characteristics. The goal of the present work was to address two key limitations of previous meta-analyses. First, recent meta-analyses have a narrower focus, often limited to a single cognitive domain or a specific subset of domains. In contrast, the current meta-analysis presents an updated synthesis of the literature spanning a much wider range of cognitive domains. Second, in contrast to previous frequentist approaches, a Bayesian framework was adopted allowing for the quantification of the degree of evidence in favor of the hypothesis that acute exercise influences cognition in young healthy adults. The current meta-analysis observed that acute exercise has a small positive influence on overall cognitive task performance, and sensitivity analyses indicated that the alternative hypothesis was 6.51-8.77 times more likely than the null across multiple priors and likelihood functions. The magnitude and directionality of this effect were consistent with the results of previous meta-analyses on acute exercise and cognition (Chang et al., 2012; Etnier et al., 1997; McMorris et al., 2011; Moreau & Chou, 2019). Subgroup analyses suggested that this relationship is moderated by task performance measure, cognitive domain, exercise type and intensity, and the time of task completion relative to exercise cessation. Model comparison results indicated that accounting for variations amongst moderator levels did not improve predictive performance. Given our eligibility criteria, these results are limited to healthy individuals between the ages of 18-45 years old.

Similar to McMorris & Hale (2012), acute exercise was found to improve RT but have no influence on accuracy. A possible explanation for this differential impact on task outcome measures is that exercise modulates primary motor cortex (M1) excitability (Neva et al., 2021). There is accumulating evidence that acute exercise increases M1 intracortical facilitation (Lulic et al., 2017; Neva et al., 2017; Singh et al., 2014; Yamazaki et al., 2019) and inhibition (Mooney et al., 2016; Smith et al., 2014). Yamazaki et al. (2019) observed that the intracortical circuits of both exercised (i.e., legs) and non-exercised (i.e., hand) effectors are modulated by an acute bout of low intensity pedaling. Thus, alterations in the activity of excitatory or inhibitory circuits of non-exercised cortical representations may promote faster

RT on cognitive tasks. However, the lack of concurrent changes in corticospinal excitability or motor evoked potentials suggests that this explanation is not a viable account of a mechanism that engenders faster RTs. An alternative explanation is that exercise increases peripheral and central concentrations of catecholamines, such as norepinephrine, epinephrine, and dopamine, which in turn improves the speed of cognition (Basso & Suzuki, 2017; McMorris et al., 2009; McMorris & Hale, 2015). Indeed, acute exercise has been found to improve RT on choice reaction time, decision making, and interference tasks (Chang et al., 2012; Tomporowski, 2003). Yet, it is unclear as to why changes in neurochemical levels would facilitate reaction time but have no impact on accuracy. Considering that physical activity modulates population-level tuning in the sensory areas of nonhuman animals and invertebrates (Ayaz et al., 2013; Fu et al., 2014; Kaneko et al., 2017; Keller et al., 2012; Maimon et al., 2010; Niell & Stryker, 2010; Polack et al., 2013), along with sensory responses in humans (Bullock et al., 2015, 2017; Cao & Händel, 2019), it stands to reason that the fidelity of stimulus representations would also be impacted, resulting in changes in accuracy. Changes in the fidelity of feature selective stimulus representations can be determined by applying encoding models to recorded neural activity (Brouwer & Heeger, 2009; Bullock et al., 2017, 2023; Foster et al., 2016; MacLean et al., 2019; Samaha et al., 2016; Sprague et al., 2015). For instance, Garrett et al. (2021) applied an inverted encoding model to topographical patterns of alpha band activity, recorded at the scalp, while subjects completed a spatial working memory task both at rest and during a bout of moderate intensity cycling. Notably, it was possible to reconstruct spatially selective responses during exercise, and the selectivity of these responses decreased during exercise relative to rest. Therefore, encoding models can be a powerful tool for future research to demystify how the accuracy of task-relevant representations is influenced by exercise. It is also important to keep in mind that many psychological tasks are relatively simple to do, which can lead to ceiling effects that may mask the influence of exercise on accuracy measures. Lastly, the differential impact of exercise on accuracy and RT may be due to the relative sensitivities of these dependent measures to modulations of different stages of information processing. For example, there is evidence that in near-threshold tasks accuracy is sensitive to perceptual manipulations, whereas in supra-threshold (i.e., perceptually easy tasks, including many of those used in the studies in this meta-analysis) RT is sensitive to modulations in both perceptual and post-perceptual processes (Mordkoff & Egeth, 1993; Santee & Egeth, 1982). Indeed, Davranche et al., (2023) utilized a drift diffusion model to determine which aspects of decision-making are modulated by HIIT. Importantly, drift rate and decision response boundary size increased significantly after exercise relative to before, while non-decision time decreased. This suggests there was an improvement in perceptual discrimination, the efficiency of non-decisional processes (e.g., motor execution), and the adoption of a more conservative criterion. Future research employing computational models of response time and representational fidelity is needed to develop a comprehensive understanding of the selective influence exercise on information processing speed and accuracy.

Parameter estimates of a model including exercise modality as a moderator suggested that engaging in cycling or HIIT may beneficially impact cognition, especially on attentional and executive processes. Cycling is a commonly used modality in exercise and cognition research. Numerous empirical studies have found that a bout of cycling benefits inhibition, as measured using either the Stroop or Eriksen Flanker task (Basso et al., 2015; Chang et al., 2014; Davranche et al., 2009; Faulkner et al., 2016; Kamijo et al., 2007; Kunzler & Carpes, 2020; Yanagisawa et al., 2010). Improvements in planning (Basso et al., 2015; Hung et al., 2013), task-switching (Bae & Masaki, 2019; Oberste et al., 2021; Pesce & Audiffren, 2011), and the speed of decision making (McMorris, 2009) have also been reported. In contrast to the ubiquity of cycling, the use of HIIT workouts in exercise and cognition research is a relatively recent practice, hence the small number of effect sizes from studies using this modality compared to other modalities. The number of effect sizes is important because low-level parameters in a hierarchical model are influenced both by the subset of data directly dependent on the low-level parameter, and by high-level parameter estimates that rely on all of the data. This makes low-level parameter estimates indirectly dependent on the entire dataset, and causes shrinkage in estimates at all levels of the model. In other words, the estimated relationship between HIIT and behavioral performance is derived directly from the few representative effect sizes and indirectly from the rest of the data. The observed positive effect of HIIT on cognition corroborates previous findings. For example, Alves et al. (2014) observed that the time to complete a Stroop Task decreased after ten 1-minute bouts of exercising at 80% heart rate reserve relative to a control condition. Improvements in time-dependent measures on interference tasks (i.e., Stroop and flanker) have been correlated with an increase in left dorsolateral prefrontal cortex activity, as measured with functional near infrared spectroscopy (fNIRS), and a decrease in P3 latency measured with EEG (Kao et al., 2018). Furthermore, enhancements have also been shown to coincide with an increase in peripheral levels of neural growth factors and lactate (Kujach et al., 2020). Lastly, a recent meta-analysis on elite athletes observed that HIIT team-based sports had a positive impact on cognitive task performance (Logan et al., 2023). Interestingly, because of the small number of published studies in the literature, it is currently unclear if the type of exercise modality used for HIIT workouts (e.g., cycling, sprinting, resistance) differentially impacts cognition.

Behavioral task performance was found to be improved by engaging in vigorous intensity exercise. These results are surprising, considering that exercise intensity is believed to have an inverted-U relationship with performance; where moderate intensity exercise elicits the greatest enhancements while more intense, fatiguing exercise imposes decrements (Chang et al., 2012; Dietrich & Audiffren, 2011; Etnier et al., 1997; McMorris et al., 2009; McMorris & Hale, 2012; Mehren et al., 2019). This effect could be driven by HIIT workouts but may also depend on multiple cognitive task and exercise protocol characteristics. For instance, Chang et al. (2012) observed that exercise intensity was only a significant moderator when cognition was tested post-exercise. Similarly, Oberste et al. (2019) found that exercise intensity influenced time-dependent measures of interference control but not accuracy. When considering these results, one must also consider that both aforementioned meta-analyses included studies whose subjects were children, adolescents, and older adults. In contrast, the current study was limited to young adults, and there is evidence that the effect of exercise on cognition is comparatively smaller in this age group (Chang et al., 2012; Oberste et al., 2019). Thus, a model containing an interaction between cognitive domain, task outcome measure, and age groups across the lifespan may be required to observe evidence for an effect of intensity. In addition, there was evidence for the enhancing effects of exercise post-cessation, corroborating previous research (Basso et al., 2015; Basso & Suzuki, 2017; Chang et al., 2012). Interestingly, in the current meta-analysis cognition was not found to be impacted during exercise. Prior meta-analytic findings on cognition during exercise are mixed, with some reporting that it is exacerbated (Lambourne & Tomporowski, 2010), while others that find evidence for an enhancement (Chang et al., 2012).

Given that the majority of the effect sizes were from tasks that probed executive function, a separate meta-analysis was conducted on this subset of data. This analysis revealed that exercise has a small positive impact on reaction time measures of executive processes. When looking at model parameters, there was evidence in favor of exercise enhancing inhibition and working memory. Behavioral research has shown that both the accuracy (Quelhas Martins et al., 2013) and speed of working memory (Kao et al., 2021; Rattray & Smee, 2016) are facilitated by an instance of physical activity. What remains to be determined is the neural mechanisms that engender these behavioral effects. Kao et al., (2021) observed that a reduction in RT on the Sternberg task post-HIIT corresponded to an increase in frontal alpha desynchronization during encoding, maintenance, and retrieval periods when working memory load is high. Neuroimaging studies have also found evidence for changes in the activation levels of frontal areas (Li et al., 2014) and their connectivity with the intraparietal sulcus post-exercise (Weng et al., 2017). These changes in neural activity were not accompanied by a change in behavior, suggesting that more research is needed to demystify the neuromodulatory effect of acute exercise on working memory.

Engaging in repeated bouts of acute exercise over a long period of time can have lasting changes on baseline neurochemical levels, cortical volume, and structural/functional connectivity, which can alter cognitive task performance (Baniqued et al., 2018; Basso & Suzuki, 2017; Firth et al., 2018; Voss et al., 2011, 2013). Research investigating the influence of these long-term interventions on cognition has primarily focused on children or older adults. Systematic reviews and meta-analyses suggest that exercise has a small to moderate beneficial impact on general task performance for both of these age groups, with the largest effect sizes observed for measures of executive function, attention, and academic performance (Erickson et al., 2019). Despite the relative paucity of meta-analyses on how exercise interventions impact cognition in healthy young adults, recent work suggests that it may have a similar beneficial effect. Indeed, a recent meta-analysis, conducted by Ludyga et al. (2020), indicated that long-term exercise interventions have a small positive influence on general cognition regardless of age. The magnitude of this effect was dependent on the interaction between intervention length and exercise duration, with longer interventions and sessions producing greater benefits. Integrating these findings with the current meta-analysis, there is support for the notion that the beneficial impact of long-term interventions on cognition may be a product of repeated exposure to acute exercise induced effects.

There are a number of possible explanations as to why exercise induced effects are small. One possible explanation is that cognitive function is at its peak during young adulthood, leaving little room for improvements in task performance. Indeed, previous reviews and meta-analyses have observed that the effect of exercise is moderated by age (Erickson et al., 2019), with the greatest benefits observed for preadolescent children and older adults (Chang et al., 2012; Ludyga et al., 2016; Oberste et al., 2019). Contrary to this account, though, the largest exercise induced effects were observed for executive processes, which are believed to be at peak efficiency during this period in the lifespan (Ferguson et al., 2021; Hartshorne & Germine, 2015). Furthermore, there was moderate evidence that the impact of exercise increased as the average age of sampled young adults also increased. Another explanation may be that cognition is resilient to slight or modest perturbations in overall global state. For example, Bullock et al., (2021) demonstrated there was no change in accuracy or RT on a target detection task during experimentally induced hypoxia, hypercapnia, hypocapnia, and normoxia. Meta-analytic modeling of the influence of acute stress on executive function revealed that stress has a small negative impact on working memory and cognitive flexibility, but no impact on inhibition (Shields et al., 2016). This suggests that cognition is able to selectively adapt to changes in physiological state caused by various types of stressors, including exercise. A final more intriguing and functional explanation for exercise having a small impact on cognition is that experimental protocols do not typically require the engagement of the body to execute the cognitive task, but rather have people engage in a cognitive task while exercising (or shortly thereafter). This experimental design contrasts real-world tasks that require engagement of the body in the service of the cognitive task. When components of the exercise are incorporated into task goals, then larger changes in performance may be observed. Empirical research investigating how exercise influences task performance in embodied settings versus classic laboratory settings (see Gordon et al., 2021 for review) is necessary to test the plausibility of this explanation. In addition, the notion that the integrated action of the body and the mind are required to produce the largest effects of exercise on cognition is consistent with a recent evolutionary account of the link between cognition and exercise (Raichlen & Alexander, 2017a).

The discrepancy in moderator results between the current meta-analysis and previous meta-analyses could be due to differences in the statistical approach. Frequentist methods typically conduct an omnibus test to determine if levels of a moderator are significantly different from one another and as a measure of a model’s goodness of fit. In contrast, the

Bayesian approach determines how likely the observed effect sizes are under a model that includes a moderator and if predictive power is increased. There are a few key advantages to using the Bayesian approach compared to classical frequentist methods. First, it models the uncertainty involved in estimates of between- and within-study heterogeneity and returns a full posterior distribution for both parameters (Raudenbush & Bryk, 2002). With these posterior distributions, one can simulate possible pooled effect sizes across credible levels of heterogeneity and develop an informed hypothesis for a subsequent meta-analysis. Similarly, the posterior distributions of effect size estimates can be used as well-informed prior distributions for new data. Importantly, this facilitates the updating of meta-analyses as new research is published. It should be mentioned that the degree of between-study heterogeneity was numerically similar to previous meta-analyses (Chang et al., 2012; Moreau & Chou, 2019), implying that they did not suffer from an issue of underestimation by assuming heterogeneity to be a fixed quantity. Second, the Bayesian approach permits the inclusion of prior knowledge. Across all tested priors, there was evidence in favor of a pooled effect derived from averaging the reported estimates of previous meta-analyses. When comparing a prior distribution based on this knowledge to a null effect prior, the former was found to be more probable. Lastly, the posterior distribution of parameter estimates can be used to ascertain the likelihood that one will observe an effect size of a given magnitude for an exercise protocol and cognitive task combination. For example, a researcher could compute the probability that the influence of a bout of cycling on cognitive control will fall within the range of large effect sizes, even if that range does not encompass the maximum a posteriori probability estimate. In contrast, the frequentist approach only produces the maximum likelihood estimate and an interval around it based on fictitious repeats of the meta-analysis.

Therefore, the Bayesian approach provides more information for designing future exercise and cognition studies.

Limitations

A potential limitation in the current meta-analysis is the categorization of exercise type using the activity reported in each study. An alternative approach is to categorize exercise based on the theoretical and physiological distinctions between aerobic and anaerobic exercise. We did not adopt this approach here because many activities used in the literature typically include aerobic and anaerobic components, and basing their classification on what authors reported provides insights into the exercise modalities that have been predominantly used in the literature. Another limitation is the schema used to categorize exercise duration. In the event that a study did not report how long participants engaged in exercise, these effects were classified as "not provided", rendering them as uninterpretable. Lastly, sensitivity analyses were not conducted for moderator parameter estimates due to the high degree of computational demands. However, considering that the pooled effect size estimate was robust across multiple priors and likelihood functions, it is likely that moderator parameter estimates are also consistent.

Conclusions

In summary, the current meta-analytic examination has shown that there is moderate evidence for an acute bout of aerobic exercise enhancing overall performance on cognitive tasks, especially on those that probe executive function and measure response time. Incorporating computational models of decision-making processes, such as drift-diffusion or signal detection models, into exercise research may provide useful insights into the nature of speeded executive processes. Furthermore, testing performance in a real-world setting where individuals typically engage in physical activity may amplify exercise-induced effects.

Chapter III: Tracking the Contents of Spatial Working Memory During an Acute Bout of Aerobic Exercise

INTRODUCTION

Non-human animals and invertebrates show robust response gain in sensory processing areas during locomotion when compared to rest (Ayaz, Saleem, Schölvinck, & Carandini, 2013; Fu et al., 2014; Kaneko, Fu, & Stryker, 2017; Keller, Bonhoeffer, & Hübener, 2012; Maimon, Straw, & Dickinson, 2010; Niell & Stryker, 2010; Polack, Friedman, & Golshani, 2013). More recently, EEG studies suggest that a similar enhancement in human sensory responses may occur during bouts of acute physical exercise (Bullock et al., 2015, 2017; Cao & Händel, 2019). If sensory processes are impacted during bouts of acute aerobic exercise, then this raises the possibility that higher-order cognitive functions relying on input from these sensory areas may also be affected. Here, we test whether neural representations of object locations stored in visual working memory (WM) in humans are modulated during a bout of acute exercise.

WM is an essential cognitive process that is critical for maintaining and manipulating information. Serving as the core interface between multiple cognitive systems (e.g., learning, attention, perception, long-term memory), this process provides a platform for guiding goal directed behaviors. Previous research has produced mixed evidence regarding modulations in WM during exercise. For instance, meta-analytic results indicate that information processing speed (i.e., reaction time) in WM tasks is enhanced during cycling, while accuracy is diminished (McMorris, Sproule, Turner, & Hale, 2011). McMorris and colleagues proposed that this pattern does not reflect a speed-accuracy trade off, but rather is due to increased peripheral and serum levels of neurotransmitters, which, in turn, engenders greater levels of neural noise in some cortical regions while facilitating activity in others. Contrary to findings that suggest WM is impaired during exercise, there is evidence that moderate intensity exercise boosts the functioning of WM overall (Martins, Kavussanu, Willoughby, & Ring, 2013). Further, it has been shown that walking at a preferred speed compared to a seated rest condition can result in enhanced performance under high memory loads (Schaefer et al., 2010). Finally, concurrent exercise also has been found to have no impact on WM (Lambourne, Audiffren, & Tomporowski, 2010). Given the multimodal nature of WM (e.g. verbal, visuospatial, auditory), the heterogeneity of these findings may stem from exercise differentially affecting each domain. Indeed, there is evidence for a greater improvement of visuospatial WM compared to verbal-auditory WM as a result of exercise (Roig, Nordbrandt, Geertsen, & Nielsen, 2013). Regardless of the mixed behavioral outcomes, none of these studies provide insight into whether the underlying neural correlates of WM representations are modulated during exercise.

To investigate whether WM representations are modulated during exercise, in the present study participants performed a visuospatial change detection task at rest and during a bout of low-intensity cycling exercise while EEG was recorded at the scalp. Each trial of this task involved remembering the location of a single memorandum presented at pseudorandomized locations on the circumference of an imaginary circle centered on fixation. After a delay period (1750 ms), a test stimulus was presented at the same location or at a different location and the participant indicated whether the location of the test stimulus changed relative to the location of the memorandum presented at the beginning of the trial. Previous studies have shown that patterns of EEG alpha power (~8-12 Hz) measured at the scalp covary with the locations of attended and remembered stimuli (Sauseng et al., 2005; Thut, Nietzel, Brandt, & Pascual-Leone, 2006; Rihs, Michel, & Thut, 2007; MacLean, Bullock, & Giesbrecht, 2019), implicating a key role for this oscillation in spatial attention and working memory. Here, alpha power was modeled using a computational technique known as an inverted encoding model (IEM) to estimate the location-selective representations of the remembered locations from the unique patterns of brain activity recorded during this task. The IEM technique has been applied to fMRI blood oxygen-level dependent (BOLD) activity in visual and parietal cortex (Brouwer & Heeger, 2009, 2011, 2013; Serences & Saproo, 2012; Sprague, Saproo, & Serences, 2015) as well as in scalp-recorded EEG (Garcia, Srinivasan, & Serences, 2013; Samaha, Sprague, & Postle, 2016) to recover feature- or location-selective information from the patterns coded in brain activity. Previous studies have applied this technique to patterns of scalp-recorded oscillatory activity in the alpha frequency band to successfully track the locations of items that are stored and maintained in WM with high temporal precision (Foster, Sutterer, Serences, Vogel, & Awh, 2016; Sutterer, Foster, Serences, Vogel, & Awh, 2019; MacLean, et al., 2019). In addition, previous studies not only demonstrate that EEG is well suited to recording brain activity from physically active human participants (Cheron, 2016, Bullock et al., 2015) , but also that the IEM technique can be applied effectively to the EEG steady state visually evoked response recorded during cycling (Bullock et al., 2017). Here, the IEM technique was used to reconstruct spatially selective response profiles from topographical patterns of alpha-band activity recorded at rest and during exercise. Replicating previous work, the IEM technique revealed evidence for location-specific reconstructions of item locations held in WM coded in alpha activity at rest. Importantly, evidence for location-specific information was also observed during exercise for much of the retention period. Direct comparisons of the IEM reconstructions between rest and exercise revealed evidence for degraded representations during exercise, but only late in the retention interval.

MATERIALS AND METHODS

Participants

Thirty-four (*N* = 34) adult student volunteers from the University of California, Santa Barbara (UCSB) community took part in the study in exchange for financial compensation ($20/h). All participants completed the Physical Activity Readiness Questionnaire (PAR-Q; National Academy of Sports Medicine) to determine their eligibility to participate in aerobic activity. Informed consent was provided before the study began. All participants reported normal or corrected-to-normal vision. The procedures detailed below were approved by the UCSB Human Subjects Committee and the US Army Human Research Protection Office.

Table 6.
Demographic Information.

Demographics	
Measure	Average Score
N	34 (17 females)
Age (years)	21.85 ± 0.55
Height (in)	67.79 ± 0.63
Weight (lb)	152.67 ± 4.47

Visual Stimuli

Participants performed a delayed spatial change detection task (**Figure 7A)** to measure WM performance (Foster et al., 2016; Wilken & Ma, 2004; Zhang & Luck, 2008). A grey target circle (subtending 1.6° visual angle) served as the sample stimulus and appeared centered on a point in an imaginary circle circumventing 4° from a blue fixation dot (subtending 0.2° visual angle). The sample stimulus was presented within one of eight equally spaced 45° location bins relative to fixation [0°, 45°, 90°, 135°, 180°, 225°, 270°, 315°], with stimulus location jittered randomly within each bin between +1-44°. The task consisted of 640 trials (10 blocks of 64 trials per block) and was presented on a 28-in. monitor (ASUS VG278Q, 1920 x 1080) via custom scripts that used functions from Psychophysics ToolBox for MATLAB (Brainard, 1997). The viewing distance was ~100 cm.

Eye-Tracking

Gaze contingent eye-tracking was employed to ensure participants remained fixated throughout the trial period, and to minimize the contamination of ocular artifacts in the EEG signal. Further, this ensured a stable projection of the visual display on the retina. The eye-tracker (Eyelink 1000, SR Research Ltd., Mississauga, Ontario, Canada) was positioned 50-70 cm from both eyes and binocular tracking sampling at 500 Hz was enabled. Pupil area and gaze position were collected throughout the trial period in both conditions. Pupil area was normalized using the following equation: $(x - xmin)/(xmax - xmin)$, where x is the area for a given timepoint.

Stationary bike

The stationary bike was a CycleOps 400 Pro Indoor Cycle (Saris Cycling Group, Madison, WI, USA). T2 + Profile Design Aero Bars (Profile Design, Long Beach, CA, USA) were attached to the handlebars and a Logitech Trackball Mouse (Logitech, Newark, CA, USA) was fixed to the end of the bars (**Figure 7B)**. The addition of aero bars served two important purposes. First, the participant was able to lean their elbows onto the bars leaving their hands free to respond to the task. Second, the bars stabilized the participant and helped reduce head and body movement, which is a critical factor for reducing noise during EEG

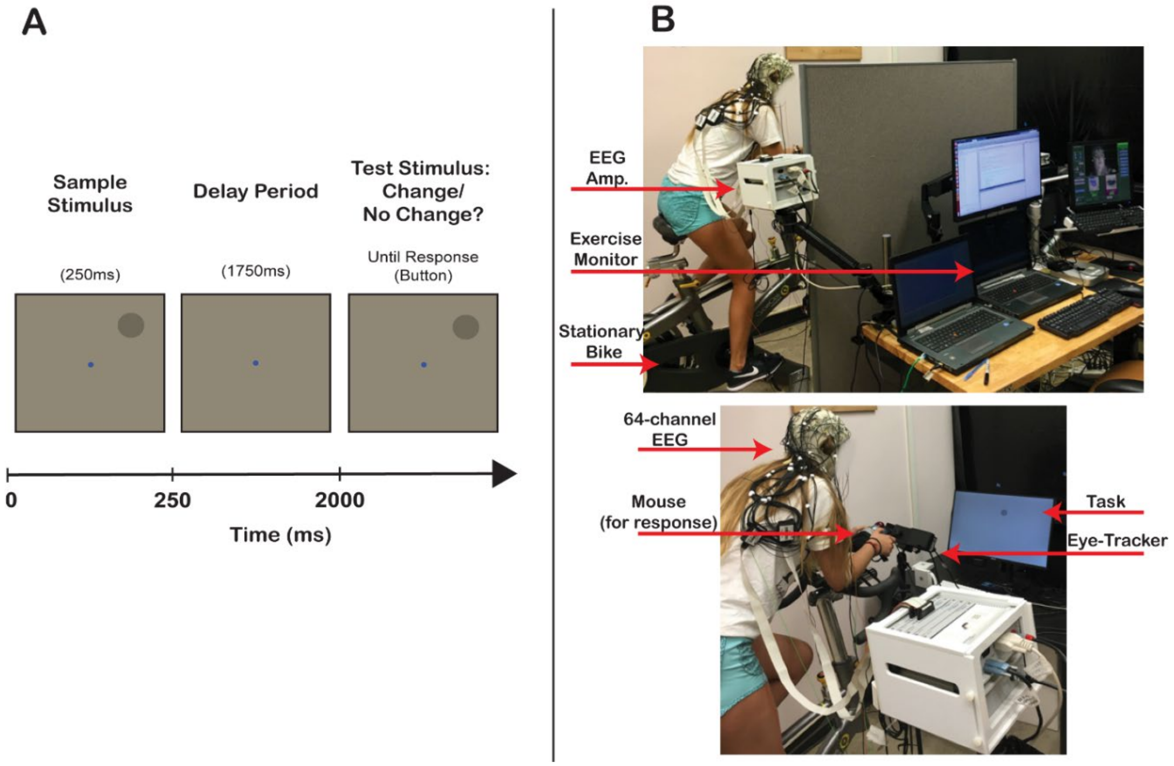

Figure 7. (A) Delayed spatial change detection task. (B) Experimental setup. Note, the task was completed in a dark room for optimal eye-tracking performance.

recording. To minimize discomfort, the bike saddle and handlebar positions were carefully adjusted for each participant. Heart rate was tracked using a CycleOps wireless heart rate monitor, while pedaling resistance and cadence were set and recorded through Trainer Road software (Trainer Road, Reno, NV, USA).

EEG

EEG data were recorded using a Brain Products ActiCHamp system (Brain Vision LLC, Morrisville, NC) consisting of 64 active electrodes arranged in an actiCAP elastic cap and placed in accordance with the 10–20 System. The TP9 and TP10 electrodes were adhered directly to the right and left mastoids. Connections were established between electrodes and the scalp using SuperVisc gel (Brain Products), which is especially viscous, thus mitigating the potential for loss of signal due to gel dispersion as well as the potential for electrodes bridging due to increased sweating during exercise. At the beginning of each investigation, all impedances were reduced to below 15 kΩ. Data were sampled at 1000 Hz and referenced offline to the average mastoid signal.

Procedure

Participants were informed of the study's structure and the intensity at which they would be required to exercise. They then completed a brief set of practice trials while cycling to ensure that they were capable of completing the task and to assess the stability of the eye-tracker. Participants were also familiarized with the Rating of Perceived Exertion (RPE) scale (RPE; Borg, 1970; 1982). RPE is a subjective rating of the intensity of physical sensations experienced during physical activity; the scale ranges from 6 (no exertion) to 20 (maximal exertion).

Prior to mounting the stationary bike, the wireless heart rate monitor and EEG cap were placed on the participant. Once on the bike, the seat position was carefully adjusted to maximize participant comfort. When ready, participants initiated the spatial change detection task. Each trial began with the fixation dot in the center of the screen, along with a green dot (subtending 0.4° visual angle) representing the location of the participant's gaze. The participant aligned their gaze dot with the fixation dot and pressed the mouse button with their right thumb to start the trial. The fixation dot immediately turned grey to indicate that the trial was underway. The sample stimulus was then presented for 250 ms (with onset jittered randomly between 600 ms and 1500 ms after trial initiation). Stimulus offset was followed by a 1750 ms retention interval, where the fixation cross exclusively remained on screen. During the fixation, stimulus presentation, and retention periods, participants were instructed to maintain their gaze at the center of the screen and covertly shift attention to the position of the sample stimulus and remember its location. If gaze position deviated from fixation > 2.4° or eye-blinks occurred during these periods, the trial was aborted and the message “Broken Fixation!” appeared on the screen. Aborted trials were appended to the end of the trial sequence, to ensure that a complete set of trials free from blinks and other eye movements was obtained. At the end of the retention period, a test stimulus (identical in size and color to the sample stimulus) appeared, either in the same location as the sample stimulus (50% of trials) or in a location shifted 20° clockwise or anticlockwise from the sample location (50% of trials). Participants were required to indicate whether the test stimulus appeared at the same location or different location as the sample stimulus by pressing either the left or right mouse button, respectively.

Participants completed this task in both rest and exercise conditions (counter-balanced) while seated on a stationary bike. In the exercise condition, they engaged in low-intensity cycling with a resistance of 50 watts of power and at a pedaling cadence of 50 revolutions per minute (RPM). These resistance and cadence levels were based on the intensity and cadence used in a previous study (Bullock et al., 2017). To ensure that participants maintained this cadence, they were instructed to pedal in time to a metronome set at 100 beats per minute (equaling 50 RPM). Cadence was continuously monitored throughout exercise. In the resting condition, the pedals were removed and replaced with a box positioned under each foot. Using these boxes, participants tapped their feet to a metronome set at the same frequency as described in the exercise condition; totaling to 50 taps per foot per minute (equivalent to cycling cadence of 50 RPM). This manipulation was intended to attenuate possible dual-task differences between conditions that may confound modulations in WM. To mitigate any possible exercise-induced arousal carry-over effects, participants who completed the exercise condition prior to the rest condition were required to sit quietly until their heart rate returned to within 10% of resting activity before beginning the resting condition.

Excluding warm-up and cool-down time, each condition took ~50 minutes to complete. The warm-up consisted of either cycling with the aforementioned cadence/resistance or foot tapping for 3 minutes. Prior to, and following warm-up, the RPE scale was displayed to the participant, who then verbally reported their current level of exertion to the experimenter. Exertion ratings were also collected after every two blocks. Each experimental session took ~3.5 hours, including instrumentation time.

Biases in Eye Position

Considering that the tolerance threshold for deviations from fixation is more lenient than what is typical for studies of visual WM and attention (i.e., > 1°) (Luck, 2014), it is possible that gaze position toward stimulus location may differ between rest and exercise conditions. Such an effect may be the source of differences in spatial selectivity between rest and exercise. To rule out this possibility, eye position bias was quantified by calculating the distance between fixation and stimulus location for each trial using the eye-tracking data. Distances were baseline corrected to the mean of the 200 ms pre-stimulus period. Because distance was computed relative to the stimulus location, more negative values would represent greater deviations towards the stimulus location. For ease of interpretation, the absolute value of the average baselined gaze position was computed and plotted in **Figure 10**.

EEG Preprocessing

Custom scripts in MATLAB (version 2019a, Massachusetts, The MathWorks Inc.) and functions from the EEGLAB toolbox (Delorme & Makeig, 2004) were used for offline processing of the EEG data. The continuous data were referenced to the average mastoid signal and then high- and low-pass filtered between 4 Hz and 30 Hz, respectively (EEGLAB function *pop_eegfiltnew*). The data were then resampled at 250 Hz (EEGLAB function *pop_resample*), to reduce computation time and memory demands, and epoched between -1 and 2.5 s around the onset of the stimulus. Trials that were aborted due to eye-movements and trials where incorrect responses were made were excluded from any analysis. Noisy electrodes were removed via visual inspection (mean electrodes removed [mean ± SEM] = 1 ± 0.39). Electrodes that were excluded from one condition were also excluded from the other condition for each participant in order to avoid introducing bias when comparing EEG results across conditions. Trials exceeding ± 150 µV in remaining electrodes were then excluded (mean trials excluded overall: 4.99 ± 0.79; Rest: 4.71 ± 1.28, Exercise: 5.26 ± 0.95). For computing the degree of alpha lateralization (see *Alpha Lateralization* below) in topographical patterns of activity at the scalp, noisy electrodes were interpolated to facilitate averaging across participants.

Spectral Decomposition

Epoched data were filtered using a 3rd order Butterworth bandpass filter (MATLAB function *butter*) between 8-12 Hz. A Hilbert transformation (MATLAB function *hilbert*) was then applied to the filtered signal in order to extract a measure of instantaneous amplitude and phase. To avoid edge artifacts, all subsequent EEG analyses were then focused on time points between -0.5s to 2s (from 0.5 pre-stimulus onset to the end of the retention period). Prior to modeling, total power was calculated as the square of the absolute value of the Hilbert transformed complex values. Total power reflects continuous oscillatory activity independent of its phase relationship with stimulus onset.

Alpha Lateralization

Numerous studies have reported alpha power to be greatest over posterior electrodes ipsilateral to the cued location when compared to contralateral electrodes—indicating that spatial attention/memory alters the topographical distribution of alpha (Kelly, Lalor, Reilly, & Foxe, 2006; MacLean et al., 2019; Sauseng et al., 2005; Thut et al., 2006; Worden, Foxe, Wang, & Simpson, 2000). Further, exercise has been shown to modulate power across parietal-occipital electrode sites for a range of frequencies (Ciria et al., 2018; Ciria, Perakakis, Luque-Casado, & Sanabria, 2019). Thus, the degree to which exercise influenced the systematic changes in alpha power topography was determined by normalizing (i.e., dividing) the difference in alpha power at contralateral and ipsilateral parietal/occipital electrodes sites (P5/6, P7/8, PO7/8) by the sum of power at contralateral and ipsilateral sites. Normalized alpha power at contralateral and ipsilateral sites was then averaged by condition for the stimulus (0-250 ms) and retention (500-2000 ms) time periods.

P1 Event Related Potential (ERP)

Possible differences in spatial selectivity between conditions may be driven by modulations in the early visual evoked response. Considering this, the impact of exercise on the P1 ERP component was examined. Raw EEG data were first referenced to the average mastoid signal, and then high/low-pass filtered at 1 and 30 Hz, respectively. Note, this high-pass filter was applied to minimize the amount of sweat and movement related artifacts (e.g., cycling cadence was ~0.83 Hz). Afterwards the data was epoched again between -0.5 to 2.5 s (from 0.5 s pre-stimulus onset to the end of the retention period). Trials exceeding ± 150 μV measured at scalp electrodes of interest (P1/2, P3/4, P5/6, PO7/O8, POz/Oz, O1/2) were excluded. Three participants retained fewer than half of their trials after applying this rejection criterion, thus they were excluded only from subsequent ERP analyses. Note, we did not exclude these participants in IEM analyses since they did not yield the same amount of artifact rejected trials when using a more aggressive high-pass filter (4 Hz), and the focus of the IEM is on WM processes rather than sensory-evoked activity. Artifact free trials (mean overall: 494.47 ± 14.91; Rest: 514.10 ± 76.46; Exercise: 474.84 ± 88.12) were baseline corrected between -100-0 ms.

Inverted Encoding Model

Spatially selective neural population ("channel") response functions/profiles (CRFs) were estimated based on the distribution patterns of total alpha power across the scalp (Foster et al., 2016). First, the model was trained to estimate the extent to which the linear combination of *a priori* canonical channel responses (i.e., set of basis functions) capture the underlying structure of the observed data (topographical distribution of induced alpha power), yielding a set of regression weights. Next, these weights were tested on observed data that were excluded during training in order to estimate the channel response. The parameters of these channel response estimates were then used to quantify the spatially selective response. This method has been successfully used to reconstruct feature- and location- selective responses from human fMRI data (Brouwer & Heeger, 2009, 2011, 2013; Ester, Sprague, & Serences, 2015; Naselaris, Kay, Nishimoto, & Gallant, 2011; Serences & Saproo, 2012) and EEG recorded at the scalp (Bullock et al., 2017; Foster et al., 2016; Garcia et al., 2013; Samaha et al., 2016; Sutterer et al., 2019; MacLean et al., 2019).

The IEM was computed for each participant separately using total alpha power. Within each location bin, trials were then randomly subdivided into three samples. Note that since trial-based artifact rejection can result in an uneven numbers of trials per condition, it was necessary to ensure that any comparisons between conditions were not influenced by unequal trial counts. Before entering the data into the IEM, the minimum number of trials per location bin (*n*) was calculated across both conditions for each participant. To ensure equal numbers of trials from each location bin were entered into the model, *n*-1 trials were randomly selected from each bin. After trials were randomly subdivided into samples, these samples were then averaged. Thus, each condition included 24 samples of averaged trials (8 location bins x 3 samples of averaged trials). To ensure the outcome of the model and subsequent analyses were not influenced by an idiosyncratic selection of trials, this process was repeated 10 times, with a randomized selection of trials entered into the IEM for each of the iterations. For each iteration, an independent IEM was computed for each time point over the course of the trial (250 Hz EEG sampling rate x 2.5 s = 625 time points) to model the temporal dynamics of the location-selective response. For each iteration (and time point), the independent IEMs were cross-validated using a k-fold scheme, where $k = 4$. The averaged trials were randomly grouped into four folds, with each fold having one averaged trial per location bin. Training was performed using 3/4 folds. Importantly, the IEM was trained on equivalent numbers of trials from both rest and exercise conditions to estimate a fixed encoding model. This training scheme mitigates the possibility that differences in spatial selectivity between rest and exercise are merely a reflection of differences in the signal-to-noise ratio between conditions (Gardner & Liu, 2019; T. Liu et al., 2018; Sprague et al., 2018, 2019). For each participant and each of the 10 iterations, IEMs were computed using the following algorithm. Let *m* represent the number of EEG electrodes in each dataset (mean electrodes = 63 ± 0.38; equal across rest and exercise conditions within each participant), n_1 represents the number of trials in the training set (3 folds of 8 averaged trials) and n_2 represents the number of trials in the testing set (1 fold of 8 averaged trials). Let *j* be the number of hypothetical location selective channels (C_1, j x n_1), composed of half-sinusoidal functions raised to the seventh power as the basis set. Here, the basis set was comprised of 8 equally spaced locations (i.e. j=8). B_1 (m x n_1) represents the training set and B_2 (m x n_2) the test set. A standard implementation of the general linear model (GLM) was then used to estimate the weight matrix (W, m x j) using the basis set (C_1). More specifically, using the GLM:

$$B_1 = WC_1 \tag{1}$$

Then, the ordinary least-squares estimate of *W* can be computed as:

$$\widehat{W} = B_1 C_1^T (C_1 C_1^T)^{-1} \tag{2}$$

Using the estimated weight matrix ($\widehat{W}$, Equation 2) and the test data (B_2), the channel responses C_2 (j x n_2) can be estimated by:

$$\hat{C}_2 = (\widehat{W}^T\widehat{W})^{-1}\widehat{W}^T B_2 \tag{3}$$

After $\hat{C}_2$ was solved for each location bin, the CRF on each average trial was then circularly shifted to a common stimulus-centered reference frame (degrees of offset from channel's designated location bin), and the centered response functions were averaged across channels. The model was then repeated for each time point. The final centered CRF was computed by averaging over all 10 iterations at each time point.

IEM Generalization

To examine the temporal generalization of patterns of activity underlying spatially selective responses, IEMs were trained at each point in time, and then tested on every other point in time (ensuring independence of training and test sets). To reduce computation time (and the number of statistical comparisons), the data were down sampled to 25 Hz prior to training and testing.

Quantifying Spatially Selective Representations

Estimated channel responses were folded around 0° channel offset, and transformed from [-135˚, -90˚, -45˚, 0˚, 45˚, 90˚, 135˚, 180˚] into [0˚, 45˚, 90˚, 135˚, 180˚] by averaging the response at corresponding offsets (± 45˚, 90˚, and 135˚; 0˚ and 180˚ were not averaged) for quantification. Slope was then computed (MATLAB function *polyfit*) as the linear regression weight of total alpha power across offset and served as our index for the amount of spatial selectivity in patterns of alpha activity underlying channel responses. Larger slope values indicate greater spatial selectivity.

In addition, the IEM procedure was carried out with randomly permuted location bin labels for 250 iterations. In theory, this should generate flat channel response profiles devoid of spatial information. Slopes of these corresponding channel responses (i.e., permuted slopes) were then calculated for each iteration, which served as our null distribution for the statistical analyses of "real" slope values.

Hypothesis Testing

All statistical inference relied on computing Bayes Factors (BFs) using functions from the BayesFactor toolbox for R (Morey, Rounder, & Jamil, 2015), which employs a Cauchy prior. A BF between 1-3 indicates "anecdotal" evidence for the alternative hypothesis, between 3-10 indicates "moderate" evidence, between 10-30 indicates "strong" evidence and greater than 30 indicates "very strong" evidence (Dienes, 2016; Kass & Raftery, 1995; Kruschke & Liddell, 2018; Wetzel et al., 2011). BFs < 1, on the other hand, indicate varying degrees of evidence in favor of the null hypothesis (0.33-1=anecdotal, 0.1-0.33=moderate, 0.033-0.1=strong, 0.01-0.033=very strong, <0.01=extreme). To determine if there was evidence indicating non-zero slopes, which would be expected if the patterns of alpha contained any spatial information, one-sample BF t-tests were computed using the real location labels from each trial at each time point ("real" BFs). To test for evidence indicating differences between rest and exercise conditions, paired BF t-tests were used instead. The one-sample and paired-samples BF t-tests were conducted for each iteration and time point using the permuted location labels, to generate a permuted distribution of BFs (“permuted” BFs) for subsequent non-parametric comparisons.

Bayesian inference is more conservative than frequentist inference, and much less likely to result in false confidence (Gelman & Tuerlinckx, 2000). Despite this, the number of statistical tests conducted overall may still be of concern, such that it may be possible to observe large BFs by chance alone. Thus, a cluster-based correction procedure (Cohen, 2014) was performed to protect against spuriously large BFs. For each iteration of permuted slopes, we calculated the maximum cluster size of contiguous time points where BF ≥ 3; resulting in a null distribution of maximum cluster sizes. For both real and permuted BFs, only time points displaying at least moderate evidence (BF ≥ 3) in favor of the alternative hypothesis were considered for cluster-based correction. Then, the size of the real BF clusters was calculated and compared to the null distribution of cluster sizes. If a cluster was larger than 95% of the null distribution of maximum cluster sizes, it was considered to be unlikely due to chance alone.

The above statistical routine was also applied to the generalization matrix. To reduce computation time, the permutation procedure for the generalization analysis was conducted for 100 iterations rather than 250 iterations.

RESULTS

Exercise physiology

Table 7. Mean and standard error of physiological data for both conditions.

Exercise Physiology			
Condition	Heart Rate (BPM)	RPE	Cadence (RPM)
Rest	78.44 ± 2.66	6.59 ± 0.11	-
Exercise	105.78 ± 306	8.65 ± 0.25	54.77 ± 0.65

Average heart rate (**Table 7**) was greater during exercise

(105.78 ± 3.06) as compared to rest (78.44 ± 2.66) (BF > 1,000). A similar relationship was observed for mean RPE scores (BF > 1,000): rest (6.59 ± 0.11), exercise (8.65 ± 0.25). Notably, the average RPE score for the exercise condition was within the range of 9-10 on the RPE scale, which corresponds to "very light" intensity exercise. In addition, normalized pupil area was larger in the exercise condition ~1560-2000 ms post-stimulus onset (BF $\in$ $[3 - 14]$, i.e. Bayes factor ranged between 3-14).

Behavior

Task performance was measured using the sensitivity index *d'* (d-prime) and response criterion (*c*) (**Figure 8**) from signal detection theory (see Swets, 1961 for review). Hits were defined as accurately detecting a difference between the location of sample and test stimuli.

There was anecdotal-moderate evidence in favor of the null hypothesis for no difference between rest and exercise conditions in the measures *d'* (Rest: 2.23 ± 0.13, Exercise: 2.27 ± 0.12; BF = 0.2) and *c* (Rest: 0.15 ± 0.08, Exercise: 0.23 ± 0.07; BF = 0.56).

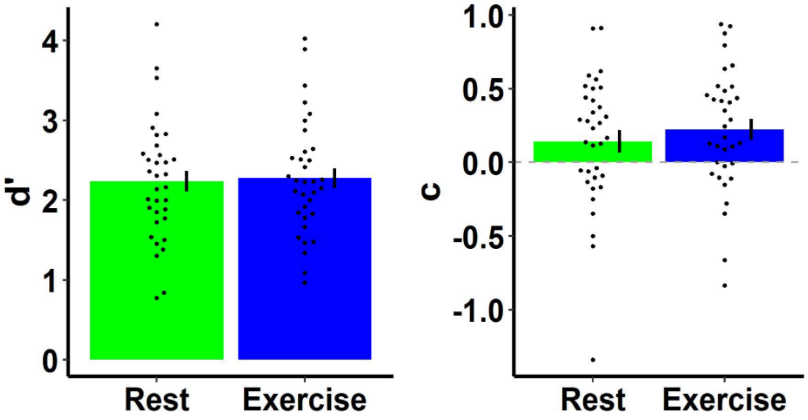

Figure 8. Working Memory task performance as measured by sensitivity (d') and response criterion (c) in both conditions. Points represent each individual's data, and error bars represent ± 1 SEM.

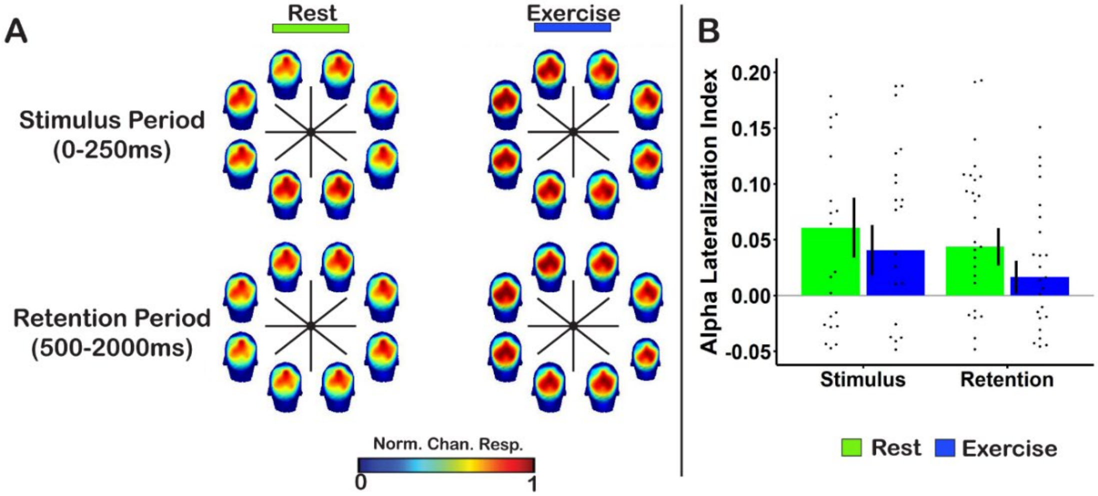

Figure 9. (A) Topographical distribution of alpha (8–12 Hz) power across the scalp during encoding and retention periods, normalized across parietal/parieto-occipital electrodes within each location bin. The location of each head plot reflects the corresponding sample stimulus location bin. Note, a time frame of 500–2000 msec was used for the retention period to avoid including stimulus evoked activity. (B) Alpha lateralization during the stimulus and retention periods as a function of exercise condition. Points represent each individual's data, and error bars represent ±1 SEM.

Topographical distribution of alpha power across the scalp

Prior to modeling the contribution of alpha activity to WM representations, the topographical distribution of power across the scalp was examined. Qualitatively, alpha power increased over posterior electrodes ipsilateral to the presented stimulus location in the resting condition, a finding consistent with prior work (**Figure 9A**) (Kelly et al., 2006; MacLean et al., 2019; Sauseng et al., 2005; Thut et al., 2006; Worden et al., 2000). More importantly, a similar

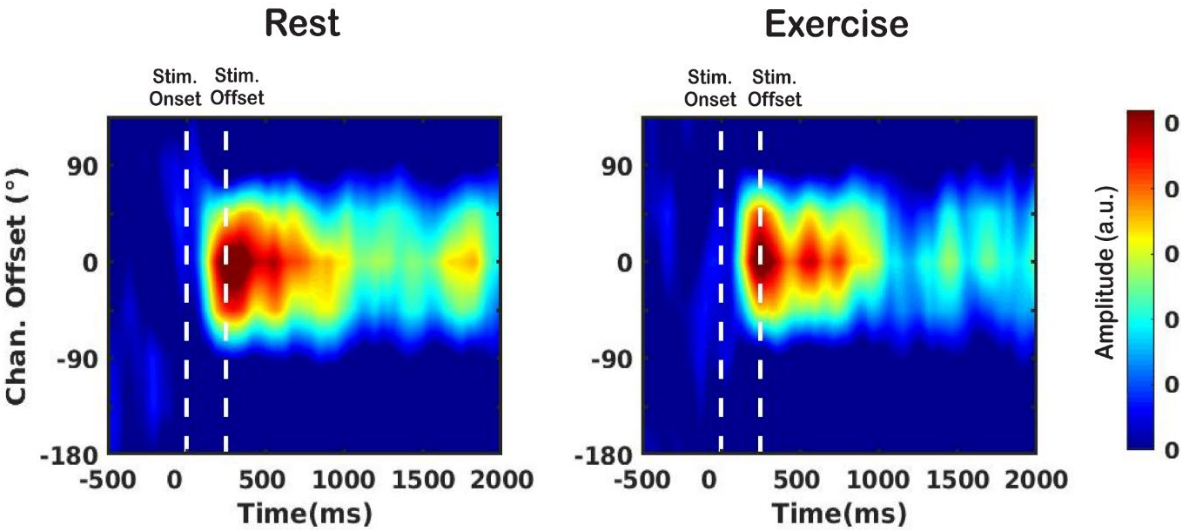

Figure 10. Estimated channel responses as a function of stimulus-centered location offset (−180°, −135°, −90°, −45°, 0°, 45°, 90°, 135°), reconstructed over time from patterns of alpha-band activity. Plotted CRFs are baseline corrected relative to the average amplitude across channels in a prestimulus window of −500 to 0 msec.

pattern was present in the exercise condition. When analyzing the degree of alpha lateralization, there was moderate evidence in favor of the null hypothesis for no difference between conditions during both the stimulus (0-250 ms; rest: 0.06 ± 0.03, exercise: 0.04 ± 0.02; $\mathrm{BF} = 0.22$) and retention (500-2000 ms; rest: 0.04 ± 0.02, exercise: 0.02 ± 0.01; $\mathrm{BF} = 0.37$) periods (**Figure 9B)**.

Reconstructing representations of stimulus location

The IEM analysis using alpha band activity yielded evidence for spatially selective responses in both conditions (**Figure 10**). Reconstructed response profiles reached peak amplitude ~200 ms after stimulus onset, which is consistent with previous studies using the IEM approach to track locations maintained in WM (Foster et al., 2016, MacLean et al., 2019). Comparing real slopes to the permuted null distribution revealed there was at least moderate evidence for differences throughout the encoding and retention periods in both

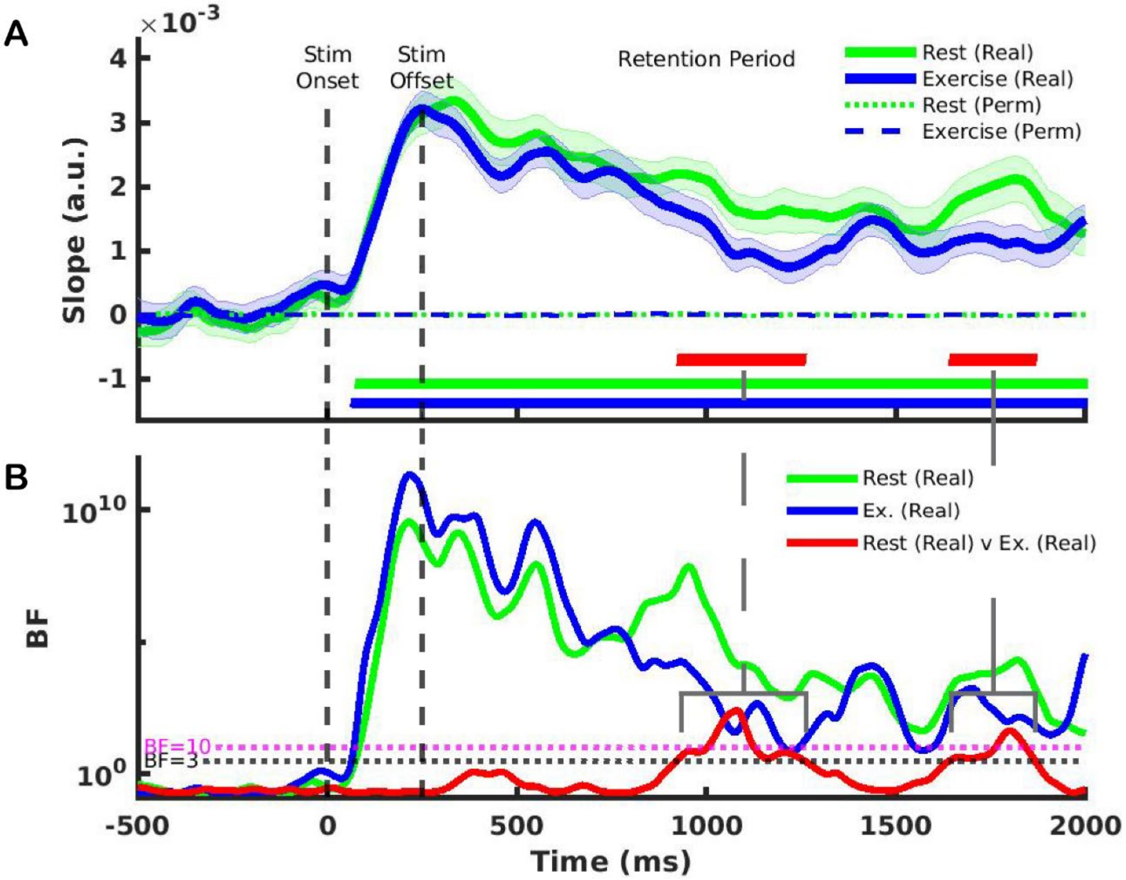

Figure 11. (A) Spatially selective CRF slopes. Horizontal green and blue bars indicate time points with at least moderate evidence for real rest and exercise slope estimates being different from zero, respectively. Horizontal red bars indicate time points with at least moderate evidence for a difference between real rest and exercise slopes. Cluster correction was applied to all comparisons, and clusters shown are those whose size exceeded 95% of a permuted null distribution. (B) BFs for comparisons made at each time point. Shaded error bars represent ± 1 SEM.

conditions (**Figure 11A**; Rest: $\mathrm{BF} \in [4, 3.55 \times 10^{9}]$, Exercise: $\mathrm{BF} \in [3, 2.23 \times 10^{11}]$), confirming that mental representations of remembered locations can be successfully reconstructed both at rest and during exercise. Nevertheless, there was evidence for decreases in slope between ~926-1255 ms ($\mathrm{BF} \in [3, 238]$) and ~1643-1864 ms ($\mathrm{BF} \in [3, 41]$) post-stimulus onset during exercise compared to rest. These results suggest that while there was evidence for a location selective representation in alpha activity during exercise, this representation was degraded during late stages of retention (**Figure 11B**).

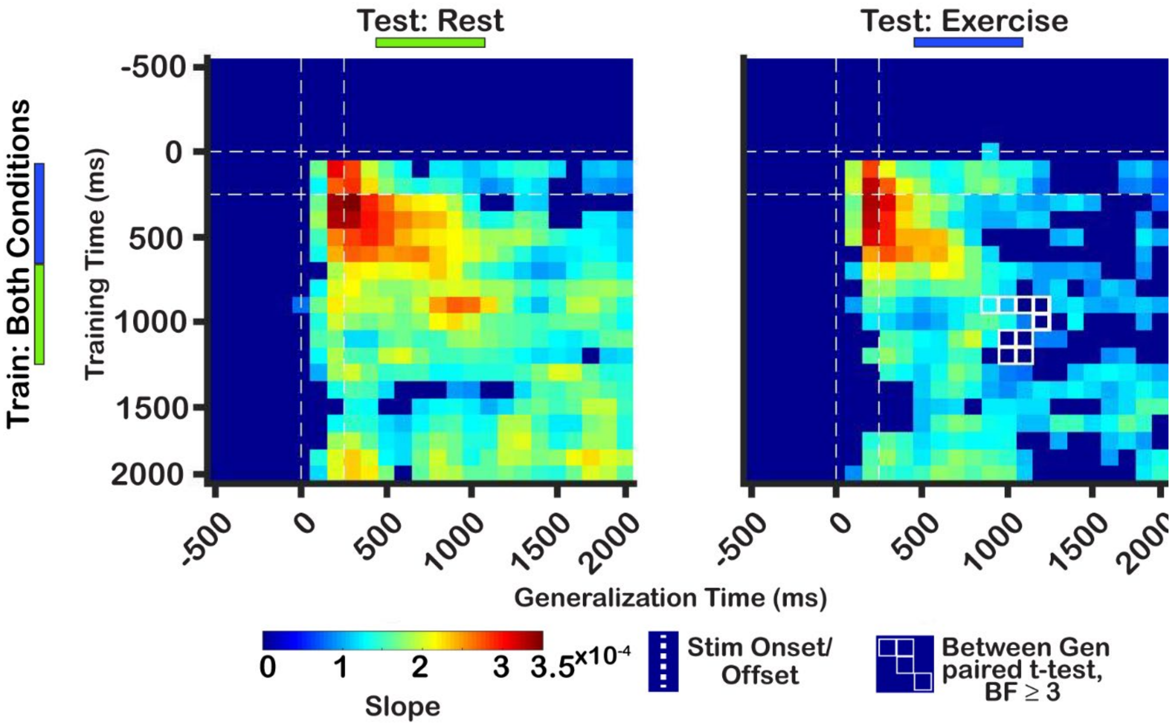

Figure 12. IEM generalizations. Only contiguous time points with at least moderate evidence for slope estimates being different from zero (cluster corrected) are shown. All other time points are in dark blue. The y-axis represents time points trained on, whereas the x-axis is time points tested on. Successful generalization to the right of the main diagonal indicates forward temporal generalization, whereas the opposite direction indicates backward temporal generalization.

Models trained on patterns of activity within a specific time period that can recover spatially selective responses when tested on activity from a differing time period exhibit generalization (King & Dehaene, 2014; van Moorselaar et al., 2018, MacLean et al., 2019). Successful generalization suggests that a stable unitary code underlies a cognitive process or processes throughout time. In contrast, the failure of models to generalize in this fashion implies that the trained/tested patterns of activity represent different codes. Note, a lack of generalization is not an indication that neural activity during that time period does not support representations of location in WM, given that reconstruction was successful at all time points after ~100 ms.

When testing the fixed encoding model on activity in the resting condition, there was evidence for temporal generalization throughout the entire trial period post-stimulus onset (**Figure 12 “Test: Rest”**). Strong generalization throughout time indicates that spatial selectivity at rest is supported by a stable unitary code. There was also evidence for temporal generalization during exercise, but it was degraded relative to a permuted null distribution (**Figure 12 “Test: Exercise”**). Comparing the degree of generalization between conditions, there was evidence for greater generalization when training on activity between ~900-1200 ms and testing on activity within the same time period in the resting condition (BF ∈ [4.89,148.12]). Taken together, these results imply that similar unitary codes underlie the representation of locations in WM during both rest and exercise, but that the stability of this code over time is degraded during exercise.

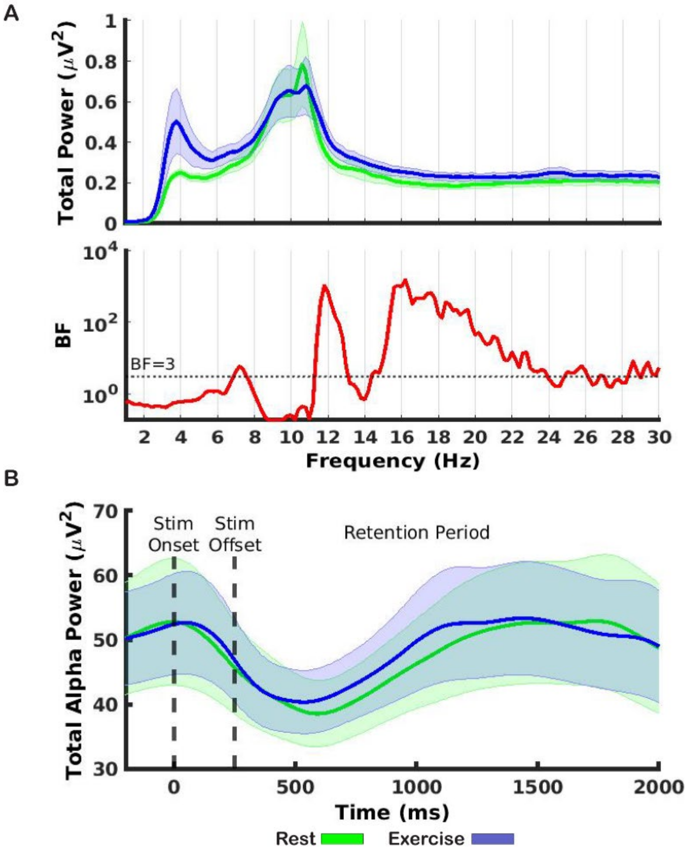

Figure 13. Control analyses on spectral activity conducted to assess the validity of IEM findings. (A) Top: Total power averaged across time for all frequency bands between 4 and 30 Hz. Peak response occurred over the alpha band range. Bottom: BF values comparing power at each frequency between rest and exercise. (B) Alpha power over time. Dashed lines indicate stimulus onset (0 msec) and stimulus offset (250 msec). Shaded error bars represent ±1 SEM.

Control analyses

Differences in reconstruction are not due to differences in spectral activity

A series of control analyses were performed on spectral activity to determine any confounding factors in our observed differences of selectivity between conditions. One such analysis was the comparison of total spectral power between the rest and exercise conditions. Spectral power across a range of frequency bands has been shown to be modulated during exercise (e.g. Bullock et al., 2017; Kubitz & Mott, 1996). Thus, it is possible that the observed differences in spatial selectivity and generalization may reflect exercised-induced fluctuations in power that are independent of working memory processes. EEG data were high pass filtered at 4Hz and spectral power was computed for post-stimulus neural activity (0-2000 ms) using a fast Fourier transform (MATLAB function *fft*). There was at least moderate evidence for a difference in power between the following frequency ranges: 7-7.4 Hz ($\mathrm{BF} \in [4.11, 5.81]$), 11.4-13 Hz ($\mathrm{BF} \in [5.85, 1.04 \times 10^3]$), and ~14-30 Hz ($\mathrm{BF} \in [3.12, 1.51 \times 10^3]$) (**Figure 13A**).

Considering there was evidence for a difference between conditions in the upper range of alpha total power averaged over the trial period (~11-12 Hz), it is possible that fluctuations in alpha power overtime may be driving decreased selectivity in the exercise condition. To assess this possibility the time-course of mean total alpha power was compared between both conditions. There was no evidence for differences, if anything there was evidence in favor of the null hypothesis ($\mathrm{BF} \in [0.18, 0.71]$) (**Figure 13B**). Importantly, this suggests that decreased spatial selectivity during exercise is a product of alterations in the topographical distribution of alpha power over time rather than dramatic changes in global alpha power.

Degraded reconstructions are not due to location information being carried by other frequencies during exercise

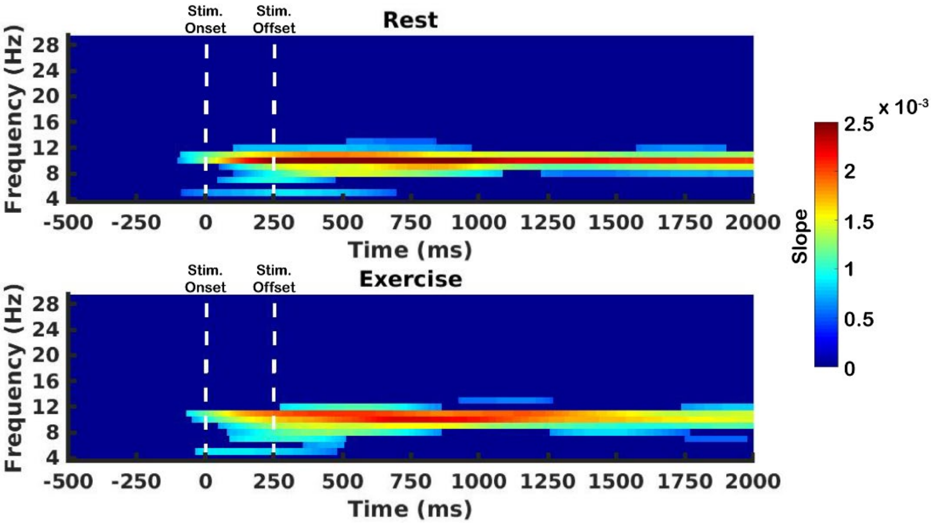

Figure 14. The IEM routine was applied to frequencies within the range of 4–30 Hz at 1-Hz increments. Shown here are the slopes of reconstructed CRFs with at least moderate evidence for being different from zero (cluster corrected). Those that were not different are colored in dark blue.

Previous research has shown that topographical patterns of oscillatory activity outside the alpha frequency range do not track the contents of spatial WM (Foster et al., 2016). Yet, it is possible that these frequency bands may be recruited during a bout of exercise. This would imply that decreases in slope amplitude in the exercise condition reflects a possible change between

frequency bands that support representations. Considering this, the IEM routine was applied to total power in a broad range of frequencies (4-30 Hz in 1 Hz increments) (**Figure 14**). When testing for non-zero slopes in the computed single frequency CRFs, at least moderate

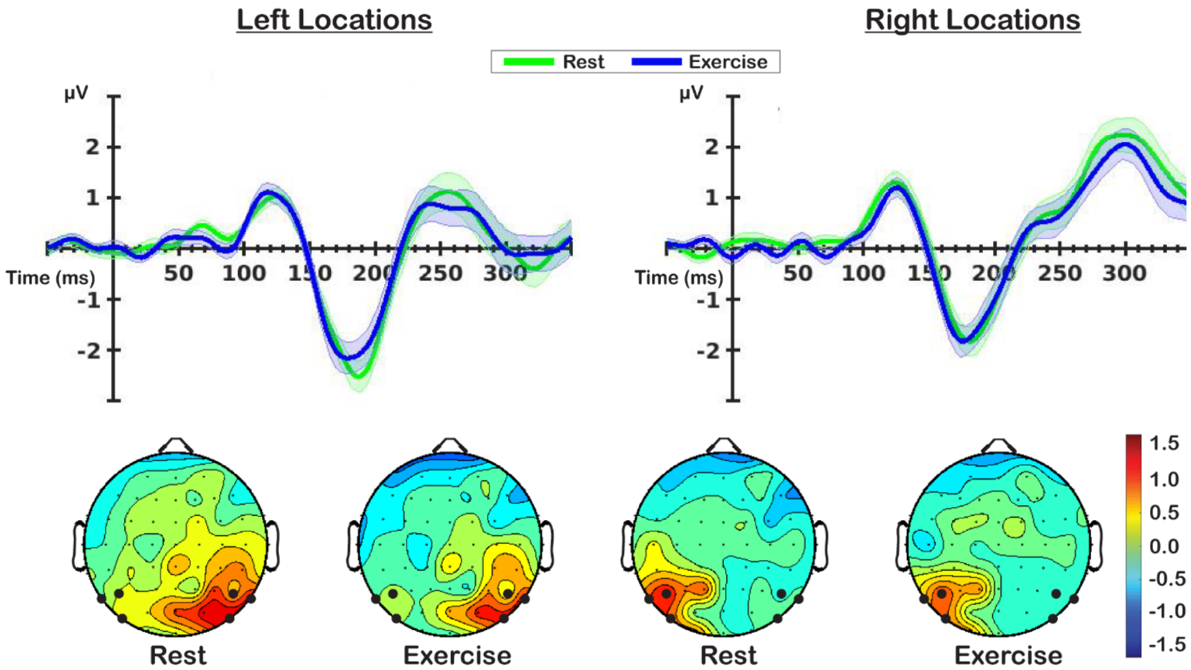

Figure 15. P1 analyses. Top plots depict P1 components for memoranda presented at left and right locations in the display. Bottom plots show topographical distribution of mean P1 amplitude between 116 and 136 msec. Electrodes colored in black represent the ones used for computation of lateralized difference ERPs.

evidence in favor of the alternative hypothesis was only observed for activity within the alpha frequency band range for both rest (BF $\in [3, 1.86 \times 10^6]$) and exercise (BF $\in [3, 2.15 \times 10^7]$). Evidence in favor of differences in single frequency slopes between conditions did not survive cluster-based corrections. Thus, decreases in alpha slope amplitude in the retention period during exercise (**Figure 11A**) do not reflect the recruitment of non-alpha frequency bands to support representations of location specific information.

Visual evoked response

For each location we calculated the difference of activity in parieto-occipital electrodes (PO7/O8, P5/6, P7/8) ipsilateral to the presented stimulus locations from those that were contralateral. Then, difference waves were averaged for locations on either side of the vertical meridian, yielding two P1 components: one for left locations and the other for right locations (**Figure 15**). P1 mean amplitude was calculated by finding the peak latency of the positive going component between 100-150 ms post-stimulus onset, and subsequently amplitude ±10 ms around this peak. There was moderate evidence in favor of the null hypothesis of no difference between rest and exercise P1 mean amplitudes for left (Rest: 1.19 ± 0.13, Exercise: 1.3 ± 0.15; BF = 0.26) and right locations (Rest: 1.49 ± 0.17, Exercise: 1.44 ± 0.15; BF = 0.19). These results suggest that our observed differences in spatial selectivity are not due to modulations of the visual evoked response.

Eye position

To assess whether the difference in the spatially selective responses derived from alpha band activity are contaminated by differential eye movements toward remembered locations in the rest and exercise conditions, we compared eye position throughout the stimulus and retention periods. There was a small increase in eye position bias throughout the trial period in both conditions, but this bias toward the stimulus location did not exceed 0.15° in either condition. Moreover, point-wise comparisons

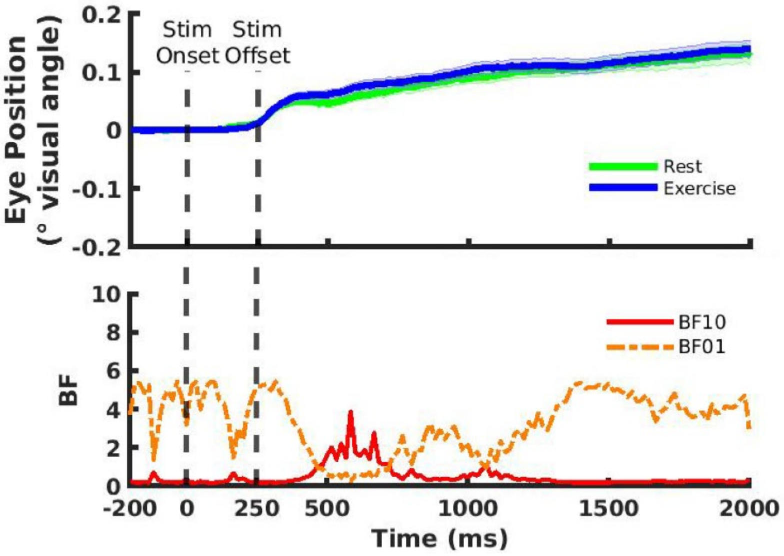

Figure 16. Top: Eye position bias (i.e., baseline corrected distance of gaze from stimulus location in units of degrees of visual angle) for both the rest and exercise conditions. Bottom: BF values for comparisons between rest and exercise. One time point at 538 msec showing at least moderate evidence in favor of the alternative hypothesis did not survive cluster correction. Shaded error bars represent ± 1 SEM.

did not reveal evidence for differences that survived cluster correction (**Figure 16**). If the cluster correction was not applied, there was a single time point that indicated moderate evidence (BF = 3.86) for a difference between rest and exercise conditions at ~538 ms post stimulus onset, but this difference was small (0.02°), occurred during a period when the slopes of the spatial reconstructions were declining, and did not occur at the same time point when evidence for differences between the slope of the spatial reconstructions in exercise and rest were observed. In contrast, there was moderate evidence in favor of the null hypothesis of no difference in eye position bias between rest and exercise at multiple timepoints throughout the trial period ($BF \in [3,5.44]$). Therefore, eye position biases were likely not the cause of decreased spatial selectivity during exercise.

DISCUSSION

Evidence from human, non-human animal, and invertebrate studies has demonstrated that early sensory visual processes are modulated during bouts of acute physical activity (Ayaz et al., 2013; Bullock et al., 2015; Fu et al., 2014; Kaneko et al., 2017; Pontifex & Hillman, 2007). The goal of the present study was to determine whether higher-order cognitive operations that depend on these sensory responses are also impacted during physical activity. EEG was recorded from human participants while they engaged in a spatial change detection task at rest and during a bout of cycling exercise. The IEM technique was then applied to activity in the alpha band in order to reconstruct spatially selective response profiles for item locations stored in WM. There were two key results. First, in addition to replicating previous work demonstrating that topographically specific patterns of alpha band activity track the contents of WM at rest, (Foster et al., 2016; MacLean et al., 2019), the present results also demonstrate that it is possible to reconstruct spatially selective response profiles during item encoding and retention while participants are engaged in a bout of physical activity. Second, while there was evidence for a spatially selective response during exercise, our results also indicate that the quality of this reconstructed location information is degraded relative to the rest condition, but only during the late stages of the retention period.

The finding that topographic patterns of total alpha activity track the specific position of a behaviorally relevant stimulus both during encoding and retention replicates a number of studies in the literature indicating that the neural populations that give rise to alpha oscillations in human EEG code information in WM in a location-selective manner (Foster et al., 2016; MacLean et al., 2019; Sutter et al., 2019; Sutterer, Polyn, & Woodman, 2021). The results reported here also show that these location-selective codes can be reconstructed from patterns of neural activity acquired during exercise. Critically, the slopes of the location selective profiles were greater than zero throughout the trial, indicating that the location selective WM representations coded in alpha band activity are robust to changes in global behavioral state.

Despite the robust location-selective reconstructions during encoding and retention observed here, there was also clear evidence during the late stages of retention (> 900 ms) that the selectivity of these reconstructions was degraded during exercise relative to rest. One possible explanation for the degraded reconstructions of spatially selective response profiles is that WM representations coded in the alpha band are more fragile later in the retention period and vulnerable to decay during exercise. Another possible explanation, that is not mutually exclusive with the first, is that the rest and exercise conditions may differ in their attentional demands. The similar level of behavioral performance in the two tasks is inconsistent with this interpretation, however, the behavioral task was very easy and may thus not have been sensitive to more subtle differences in attentional demands between the two conditions. While we took measures to equate the conditions by requiring participants to cycle to the beat of a metronome in the exercise condition and to tap their feet to the metronome in the rest condition, it is still possible that cycling to the beat of a metronome requires greater attentional control than foot tapping and interferes with attention-based rehearsal of locations in WM (Awh et al., 1998, 1999; Postle et al., 2004). Importantly, previous work has shown that shifts in attention from memoranda in WM towards an opposing task disrupts spatial selectivity (van Moorselaar et al., 2018). The notion that cycling can impact resource allocation in a concurrent cognitive task is supported by previous work demonstrating modulation of various sensory and cognitive ERP components (Bullock et al. 2015; Pontifex & Hillman, 2007; Yagi, Coburn, Estes, & Arruda, 1999; Grego et al., 2004). Future work that manipulates levels of dual-task interference between conditions (e.g., higher levels during rest) and employs a more complex WM task is necessary to elucidate the cause of decreased spatial selectivity during exercise.

Given that topographic patterns of alpha activity also track with attended locations in spatial attention tasks (Samaha et al., 2016; Sauseng, Klimesch, Stadler, et al., 2005), it is reasonable to question whether the location selective response profiles observed here at rest and during exercise represent WM activity or covert spatial attention to the location of the memoranda. There is some evidence against a solely attention-based interpretation of the present results. For example, in covert attention tasks that have revealed spatially specific responses to attended locations, alpha power tends to ramp-up in amplitude prior to the attended stimulus over ipsilateral sites (Banerjee et al., 2011; Rihs et al., 2007). Here, however, after the initial reduction in alpha power driven by the evoked response, total alpha was relatively constant up to the presentation of the test stimulus. Secondly, the presence of sustained delay period activity in the absence of a stimulus is a classic indicator of WM (Sreenivasan & DEsposito, 2019; Vogel et al., 2005; Vogel & Machizawa, 2004). Though the quality of reconstructions degraded over time, the slopes of profiles were greater than zero throughout the entire trial period. In contrast, the profiles of reconstructions observed in spatial attention tasks increase during periods prior to target onset (Samaha et al., 2016). It is important to note that we are not arguing that spatial attention is not involved, rather we are arguing that the pattern of results is unlikely to be driven by covert attention alone. Moreover, when considering the present findings together with those in the literature providing evidence for the strong connection between spatial WM and spatial attention, our results are consistent with the notion that spatial attention facilitates the coding and maintenance of spatial representations held in WM (Awh et al., 1998, 1999; Postle et al., 2004, (Oberauer, 2019).

Previous studies have reported evidence for exercise-induced enhancements of visual processing (Bullock et al., 2015;2017). Here, however, there was no difference in P1 mean amplitude or location selectivity between the two conditions during this period, indicating that the initial sensory coding was similar in the two conditions. These contrasting findings between our studies may be due to the considerable differences in visual stimulation, task demands, or the nature of the data submitted to an IEM. For instance, in Bullock et al., (2015), participants performed an oddball task with large stimuli presented at fixation. Bullock et al. (2017) required participants to judge orientation changes occurring in large, high contrast, centrally presented flickering grating stimuli. Further, they estimated orientation-selective stimulus reconstructions using 15 Hz steady state stimulus evoked activity. Here, participants were required to remember the location of a small, gray item presented in the periphery and location-selective reconstructions are based on induced alpha band activity. The discrepancy between the results reported here and the exercise-induced enhancements observed in previous work from our lab (Bullock et al., 2015;2017) and by others (Pesce, Capranica, Tessitore, & Figura, 2003), may also reflect a difference in the effect of global physiological states on sensory evoked responses to attended stimuli (i.e., as in the previous work) and in activity that persists well-beyond the sensory evoked response, such as working memory retention-related activity.

Patterns of activity coding for spatial locations displayed robust generalization throughout time when testing on activity in the resting condition, indicating the presence of a stable unitary code. This pattern of generalization is consistent with previous research showing the presence of a rapid selection process that supports locations held in WM when external visual input is continuous (MacLean et al., 2019). Although generalization when testing on activity in the exercise condition was not as robust relative to the resting condition, a stable unitary code was also found to support spatial selectivity when participants are in a physically active state. Importantly, the successful reconstruction of spatially selective responses when applying the fixed IEM to activity throughout time from each condition separately suggests a common unitary code underlies the maintenance of locations in WM in both physiological states. In later stages of the retention period, this unitary code is degraded when one is concurrently engaged in exercise.

As with all simultaneous neuroimaging and exercise studies, electromyographic (EMG) and sweat artifacts are potentially confounding factors in our results. The contribution of EMG artifacts was minimized by stabilizing each participant's position on the bike using aero bars and coaching them to ensure they limited upper body movement during cycling or foot tapping. EMG typically occurs at higher frequencies (> 30 Hz), while sweat artifacts are low frequency (< 1 Hz) oscillations (Thompson, Steffert, Ros, Leach, & Gruzelier, 2008). Since the IEM analyses presented here were based on alpha power (8-12 Hz), it is unlikely that our results were seriously contaminated by these artifacts.

In summary, we used the IEM technique to investigate how spatial selectivity for locations held in WM is modulated during an acute bout of aerobic exercise when compared to rest. Reconstruction of location-selective representations was successful during both rest and exercise, but stimulus representations were degraded at specific timepoints during the retention period as a function of exercise. Evidence was also found for processes underlying WM representations that were supported by a single unitary code during both rest and exercise. The current study is the first to demonstrate that representations of items stored in WM can be reconstructed during a bout of physical exercise and provides novel insight into both the modulation and composition of these representations during exercise when compared to rest. Future research will focus on uncovering how exercise-induced degradation of stimulus representations in WM impacts behavior in the human.

Chapter IV: Working Memory Encoding and Storage Dynamics During Cycling

INTRODUCTION

Naturalistic environments are rich with a vast amount of complex visual stimuli that far exceed the brain's processing capacity. Selectively attending to task-relevant information and retaining it over short periods of time in working memory (WM) are two critical cognitive abilities that can be used to circumvent these processing constraints and enable the successful execution of goal-directed behavior. Though these cognitive functions have been studied extensively in sedentary organisms, little is known about how selective attention and WM are affected by changes in global physiological state, which fluctuates continuously when behaving in real-world settings. Such changes in physiological state can have a profound effect on neural responses to sensory inputs and the ability to process information (McCormick et al., 2020; McGinley et al., 2015). A powerful method to manipulate physiological state is to have an organism engage in physical exercise, which causes widespread changes in neurochemical levels and neural activity across various brain regions (Basso & Suzuki, 2017). Rodent and invertebrates show a robust response gain to visual inputs during periods of locomotion (Ayaz et al., 2013; Kaneko et al., 2017; Maimon et al., 2010; Niell & Stryker, 2010; Vinck et al., 2015), while human electroencephalography (EEG) studies have shown modulations in early visual processing during an acute bout of aerobic exercise (Bullock et al., 2015, 2017; Cao & Händel, 2019). Considering the evidence for modulations in visual processing during physical activity across multiple model organisms, it is reasonable to expect that cognitive functions reliant on this sensory information are also affected. Here, we test whether engaging in an acute bout of aerobic cycling influences the neural substrates of selective attention and WM.

Lateralized change detection tasks are a ubiquitous approach for testing encoding and maintenance mechanisms of WM, and an event-related potential component known as contralateral delay activity (CDA) recorded during these tasks can be used to track the amount of information that has been stored in this transient memory system. This component emerges when participants are required to memorize a stimulus array in one visual hemifield while ignoring items in the other visual hemifield and can be observed by taking the difference in voltage potentials recorded over posterior electrodes ipsilateral the attended hemifield from those that are contralateral. During maintenance periods, the CDA is characterized by a sustained negative potential whose amplitude scales with memory set size up to typical estimates of WM capacity (Adam et al., 2018; Hakim et al., 2019; Vogel & Machizawa, 2004). Using this connection between the CDA and WM storage, one can also discern how efficiently selective attention encodes target stimuli from the environment into memory while simultaneously ignoring distractors. For example, Vogel, McCollough, & Machizawa (2005) recorded CDA amplitude for both low and high WM capacity individuals in response to memory arrays that consisted of either two targets, four targets, or two targets and two distractors. Low-capacity individuals displayed a CDA amplitude on trials with distractors similar to those with four targets, implying that WM load was higher and task-irrelevant stimuli were erroneously encoded into memory. In contrast, the CDA amplitude for high-capacity individuals on distractor trials was similar to trials with only two targets, suggesting that WM load was lower, and distractors were sufficiently filtered during encoding. A drawback of using CDA amplitude as an index of WM load, though, is that it requires the aggregation of neural activity across trials thereby obscuring storage dynamics that occur on a trial-by-trial basis. Multivariate classification analyses of voltage potential distributions across the scalp, on the other hand, enable the tracking of retained stimuli in a more sensitive and temporally resolved fashion (Adam et al., 2020). Furthermore, they can provide insights into how patterns of neural activity underlying WM encoding and maintenance mechanisms are influenced by changes in physiological state.

Neural oscillations within the theta (4-7 Hz) and alpha (8-12 Hz) frequency bands play a critical role in WM encoding and maintenance processes. Indeed, there is evidence for alterations in frontal midline theta power as a function of WM load (Canolty et al., 2006; Jensen & Colgin, 2007; Jensen & Lisman, 2001; Jensen & Tesche, 2002; Moran et al., 2010; Sauseng et al., 2009, 2010), and that theta oscillations reflect the ability to selectively attend to and store task-relevant stimuli (Raghavachari et al., 2001; Sauseng et al., 2010). Similar to the CDA, lateralized alpha power decreases as set size increases (Adam et al., 2018) and this effect is more pronounced when stimuli are stored in WM relative to when sensory input remains constant and they are covertly attended (Hakim et al., 2019). Additionally, there exist a wealth of evidence that patterns of alpha power covary with spatial locations stored in WM and can be used to reconstruct feature-selective representations of remembered stimuli (Bullock et al., 2023; Foster et al., 2016; Garrett et al., 2021; MacLean et al., 2019; Sutterer et al., 2019). Altogether, both voltage potentials and neural oscillations can be used to capture the efficiency of selective attention during memory encoding and track the number of items that are actively retained.

A growing number of studies have reported a beneficial influence of acute exercise on selective attention. Bullock et al., (2015) observed a decrease in target detection speed on a visual-oddball task during high-intensity cycling relative to low-intensity and resting conditions. The amplitude of the visual P1 component evoked by non-target stimuli was also larger during low-intensity exercise compared to rest, and P3a latency decreased during exercise, indicating that attentional selection during sensory encoding stages and post-perceptual discrimination processes may be enhanced while in a physically active state (Bullock & Giesbrecht, 2014; Davranche & Pichon, 2005). Indeed, Ligeza et al., (2023) detected increased activation in occipito-temporo-parietal cortex for to attended stimuli on a perceptual discrimination task subsequent a bout of high-intensity cycling compared to a resting condition. Performance on Stroop and flanker tasks have also consistently been reported to be impacted by manipulations of physical state, with exercise reducing the magnitude of target processing interference on incongruent trials (Hogervorst et al., 1996; Kamijo et al., 2004, 2007; Tian et al., 2021; Yanagisawa et al., 2010). Thus, engaging in acute exercise may also improve inhibitory control and prevent attentional resources from being allocated to distracting stimuli. In regard to WM, systematic reviews and meta-analyses propose that aspects of this cognitive function are improved by exercise (Loprinzi et al., 2021; Moreau & Chou, 2019), and that this relationship is dependent on multiple exercise intervention and participant characteristics (Cantelon & Giles, 2021). Recently, Kao et al., (2021) measured EEG on a modified Sternberg task with varying set sizes following high intensity interval training (HIIT) and moderate intensity cycling. Relative to a sedentary condition, response times were faster subsequent HIIT while accuracy remained unchanged. Critically, set size was inversely related to frontal alpha power subsequent HIIT, but not rest, suggesting that exercise may facilitate the storage of information in WM. Similarly, Drollette & Meadows (2022) detected an increase in the temporal stability of the CDA (i.e., amplitude correlation across sessions) after the cessation of a HIIT relative to rest. Thus, there is evidence for modulations in the WM storage dynamics post-exercise. However, what remains unclear is whether the neural substrates of WM storage mechanisms are influenced *during* exercise, and if modulations in sensory responses affect the ability to selectively encode targets and ignore distractors.

Here, we investigated WM encoding and storage processes during exercise. To test this, participants completed a lateralized change detection task at rest and during a bout of low-intensity cycling while EEG was recorded at the scalp. WM load was measured using a set of neural signals, including CDA amplitude, lateralized alpha power, and multivariate classifiers to ascertain how exercise influences the temporal dynamics of WM encoding and maintenance. Replicating previous work, CDA amplitude scaled with the number of items stored in WM, regardless of physiological state. Furthermore, it was possible to decode WM load from the distribution of voltage potentials across the scalp during rest and exercise. Direct comparisons of CDA amplitude and classifier accuracy revealed no major differences between conditions, suggesting that WM encoding and maintenance mechanisms are preserved during low-intensity exercise.

MATERIALS AND METHODS

Participants

Thirty-two (N=32; 21 females) adult student volunteers from the University of California, Santa Barbara community took part in the study in exchange for financial compensation ($20/hr). All participants completed the Physical Activity Readiness Questionnaire (PAR-Q; National Academy of Sports Medicine) to determine their eligibility to participate in aerobic activity. Informed consent was provided before the study began. All participants reported normal vision. The procedures detailed below were approved by the UCSB Human Subjects Committee and the US Army Human Research Protection Office.

WM Capacity Task

A visual change detection task was used to estimate each participants' WM capacity (Luck & Vogel, 1997). Stimulus arrays were presented within a rectangular region, subtending 7° x 5.2° visual angle, on a 28-in. monitor (ASUS VG278Q, 1920 × 1080) with a dark grey background. Colored squares (subtending 1.5° x 1.5° visual angle) served as the sample stimuli, each of which were randomly selected from a set of 7 discriminable colors (blue, green, red, yellow, magenta, cyan, orange, white, black) and were separated by at least 1.5°. Sample arrays consisted of either 3, 6, or 8 targets. A single sample stimulus was randomly selected to act as a subsequent target, and on 50% of trials its color was changed. Capacity was estimated using the following formula, $K = N(H - FA)$, where N represents the set size. H and FA indicate the hit rate (proportion of correct change trials) and false alarm rate (proportion of incorrect no-change trials), respectively (Cowan, 2001). Maximum K across set sizes served as the estimate of WM capacity, and participants were partitioned into low- and high-capacity groups based on a median split.

Filtering Task Visual Stimuli

Participants performed a visual memory task (**Figure 17A**) to measure the efficiency of selective attention and WM maintenance (Vogel, McCollough, Machizawa, 2005). A black arrow (subtending 3° visual angle) presented above a center white fixation dot (subtending 0.1° visual angle) served as a cue that indicated which side of the screen participants needed to allocation their attention towards. All stimulus arrays were presented within two 4°×7.3° rectangular regions that were centered 3° to the left and right of the fixation dot on a grey background. Colored rectangles (subtending 0.65°×1.3° visual angle) served as sample and test stimuli. Memory target stimuli were colored red and distractors were colored blue. Sample stimuli orientations were drawn randomly from a set of orientations [0°, 45°, 90°, 135°]. Their positions were randomized on each trial, with the constraint that the distance between each individual stimulus within a hemifield was at least 2° (center to center). The task consisted of 600 trials (10 blocks of 60 trials per block) and was presented via custom scripts that used functions from Psychophysics Toolbox for MATLAB (Brainard, 1997). The viewing distance was ~100 cm.

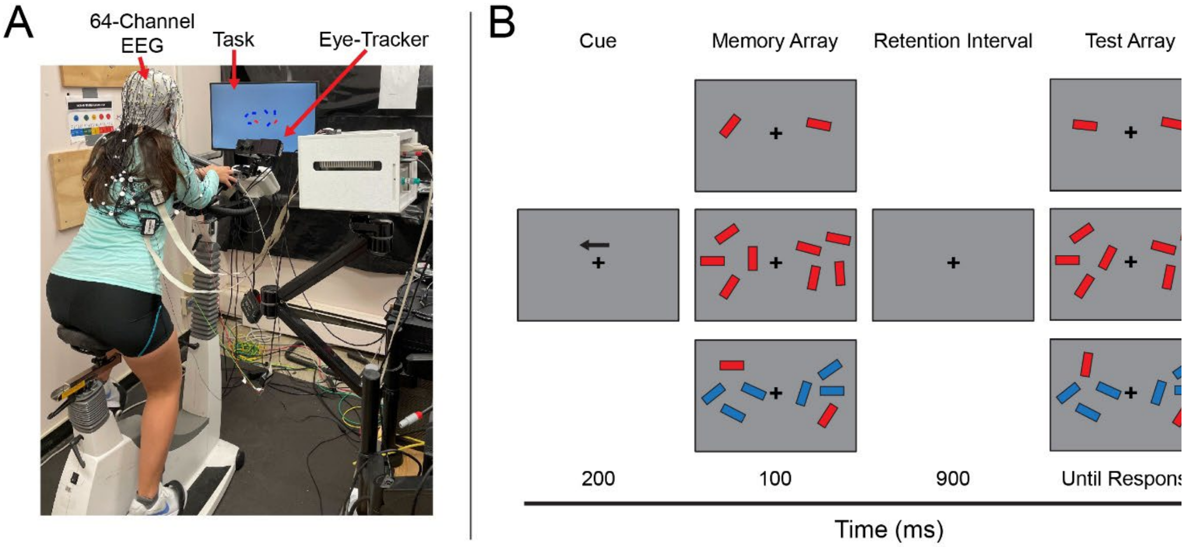

Figure 17. A) Working memory filtering efficiency task. B) Experimental setup.

Eye-Tracking

Gaze contingent eye-tracking was employed to ensure participants fixated throughout the trial period, and to minimize the presence of ocular artifacts in recorded EEG. This also ensured a stable projection of the visual display on the retina. The eye-tracker (Eyelink 1000, SR Research Ltd., Mississauga, Ontario, Canada) was positioned 50-70 cm from both eyes and binocular tracking sampling at 500 Hz was enabled. Pupil area and gaze position were collected throughout the trial period.

Stationary bike

The task was completed on the stationary ergometer ViaSprint 150p (ergoline GmbH, Bitz, Germany), which was controlled using a Vyntus CPX metabolic cart (Vyaire Medical Inc., Mettawa, Illinois, USA). Heart rate was tracked with an on-board pulse oximeter attached to the participant's finger. T2 + Profile Design Aero Bars (Profile Design, Long Beach, CA, USA) were attached to the handlebars of the ergometer, and a Logitech Trackball Mouse (Logitech, Newark, CA, USA) was fixed to the end of the bars (**Figure 17B**). The addition of aero bars served two important purposes. First, participants were able to lean their elbows onto the bars, leaving their hands free to respond to the task. Second, the bars helped stabilize the participants and minimize head and body movement, which is a critical factor for reducing noise during EEG recording. To attenuate discomfort, each participant was given a pair of bike shorts, and both the bike seat and handlebar were carefully adjusted to their preferred dimensions. Cadence in the exercise condition was tracked by placing reflective tape on the pedal crank arms and adhering a USB photodiode to the bike. In the resting condition, cadence was tracked using two foot-pedal switches (PCsensor, Shenzhen, Guangdong Province, China).

EEG

EEG data were recorded using a Brain Products ActiCHamp system (Brain Vision LLC, Morrisville, NC) consisting of 64 active electrodes arranged in an actiCAP elastic cap and placed in accordance with to the 10-20 system. The TP9/10 electrodes were adhered directly to the left and right mastoids. Connections were established between electrodes and the scalp using SuperVisc gel (Brain Products), which is especially viscous, thus mitigating the potential for both a loss of signal due to gel dispersion and the potential for electrodes to bridge due to increased sweating during exercise. At the beginning of each condition, all impedances were reduced to below 15 kΩ. Data were sampled at 1000 Hz and referenced offline to the average of the mastoid signals.

Procedure

In the first session, participants were informed of the study’s design and of both the intensity and duration they would be required to exercise. Then, they completed a change detection task to determine their WM capacity and a maximal aerobic test to determine their fitness level (VO_2 max). The second session began with participants completing a brief set of practice trials to become familiar with the filtering efficiency task and assess the stability of the eye-tracker. Participants were also acquainted with the Rating of Perceived Exertion (RPE) scale (Borg, 1970, 1982), which is a subjective rating for the intensity of a physical activity that ranges from 6 (no exertion) to 20 (maximal exertion).

Prior to mounting the stationary bike, participants were fitted with an EEG cap. Once on the bike, the seat and handlebar positions were carefully adjusted to maximize participant comfort. The pulse-oximeter was placed on their finger to record heart rate throughout the experimental session. Next, three minutes of resting EEG activity was recorded during which participants opened/closed their eyes every 30 seconds. When ready, participants initiated the filtering efficiency task. Each trial began with the fixation dot in the center of the screen, along with a green dot (subtending 0.4° visual angle) representing the location of the participant's gaze. The participant aligned their gaze dot with fixation dot and pressed a mouse button with their right thumb to start the trial. The attentional cue was then presented for 200 ms (with onset jittered randomly between 600-1500 ms post-trial initiation). On half of the trials either the left or right hemifield was cued, respectively. Cue offset was then followed by the presentation of a set of sample stimuli in each hemifield for 100 ms. The set of sample stimuli consisted of either a single target (set size 1), four targets (set size 4), or a single target and three distractors (set size 1+3) on a third of the total number of trials, respectively. Memory array offset was followed by a 900 ms retention interval, where only the fixation dot remained on the screen. During fixation, memory array presentation, and retention periods, participants were instructed to maintain their gaze at center of the screen and covertly memorize the orientation of only target (red) rectangles in the cued hemifield. If gaze position deviated from fixation > 2.1° or eye-blinks occurred during these periods, the trial was aborted and the message "Broken Fixation!" appeared on the screen. Aborted trials were appended to the end of the trial sequence, to ensure that a complete set of trials free from blinks and other eye movements was obtained. At the end of the retention period, a test array that was identical in size and color to the memory array appeared. On half of the trials, the orientation of a single target stimulus in the cued hemifield was rotated clockwise or anticlockwise by 20°. On the other half of trials, the orientations of all stimuli in the test array were identical to the memory array. Participants were required to indicate if any of the memorized target orientations were the same or different by pressing either the left or right mouse button, respectively.

Participants completed this task in both rest and exercise conditions (counter-balanced) while seated on the stationary bike. In the exercise condition, they engaged in low-intensity cycling with a resistance of 50 watts of power and at a pedaling cadence ~50 revolutions per minute (RPM). These resistance and cadence levels were based on intensity and cadence used in previous studies (Bullock et al., 2017; Garrett, Bullock, & Giesbrecht, 2021). To ensure that participants maintained this cadence, they were instructed to pedal in synchrony with a metronome set at 100 beats per minute (equaling 50 RPM). Cadence was continuously monitored throughout exercise. In the resting condition, the pedals were removed and replaced with a box positioned under each foot. Adhered to each box were the USB foot-pedals, and participants used their feet to depress the pedals to the beat of a metronome set at the same frequency as the exercise condition, totaling to 50 taps per foot per minute (equivalent to a cycling cadence of 50 RPM). This manipulation was intended to attenuate possible dual-task differences between conditions that may confound modulations in WM filtering efficiency. To mitigate any possible exercise-induced arousal carry-over effects, participants who completed the exercise condition first were required to sit quietly for five minutes.

Excluding the five-minute warm-up and cool-down periods, each condition took ~50 minutes to complete. The warm-up consisted of either cycling at the intensity/cadence previously detailed, or foot tapping for the same duration. Prior to, and following warm-up, the RPE scale was displayed to the participant, who then verbally reported their current level of exercise to the experimenter. Each experimental session took ~3.5 hours, including instrumentation time.

EEG Preprocessing

Custom scripts in MATLAB (version 2019a, Massachusetts, The MathWorks Inc.) and functions from the EEGLAB toolbox (Delorme & Makeig, 2004) were used for offline processing of the EEG data. The continuous data were first high- and low-pass filtered between 1 Hz and 30 Hz, respectively (EEGLAB function *pop_eegfiltnew*). The data were then resampled at 250 Hz (EEGLAB function *pop_resample*), to reduce computation time and memory demands. Noisy electrodes were automatically detected using the EEGLAB functions *clean_artifacts*. Note, despite its utility for removing noisy segments of EEG recordings, artifact subspace reconstruction (ASR) was not used to maintain the continuity of the data. After interpolating noisy electrodes, the data was re-referenced to the average of the mastoid signals. Next, the EEG data was decomposed using adaptive mixture independent component analysis (AMICA) (Palmer, Kreutz-Delgado, & Makeig, 2012). Only components that were classified as consisting of true brain activity based on ICLabel (Pion-Tonachini et al., 2019) and a confidence threshold of at least 80% were retained. Next, the data was epoched between -500 and 1100 ms around the onset of the memory array. Trials that were aborted due to eye-movements and trials where incorrect responses were made were excluded from any analysis.

Contralateral Delay Activity

Preprocessed EEG trials were baseline corrected between -200-0 ms prior to memory array onset. Lateralized event related potentials were computed by subtracting the average activity of ipsilateral electrodes from the average of contralateral electrodes, with respect to cue direction. CDA amplitude at the following electrode pairs were used to index WM load and filtering efficiency: O1/O2, PO7/PO8, PO3/PO4, P7/P8, P5/P6, P3/P4.

Time-Frequency Analyses

Epoched data were filtered using a 3rd order Butterworth bandpass filter (MATLAB function *butter*) between 4-7 and 8-12 Hz to extract theta and alpha band activity, respectively. Instantaneous amplitude and phase of filtered signal were computed using the Hilbert transformation (MATLAB function *hilbert*). Total power, which reflects continuous oscillatory activity independent of its phase relationship with stimulus onsets, was calculated as the square of the absolute value of the complex analytic signal.

There is ample evidence that the topography of alpha power over posterior electrodes tracks the locus of covert spatial attention (Foster et al., 2016; MacLean, Giesbrecht, & Bullock, 2019; Sutterer et al., 2019; Garrett, Bullock, & Giesbrecht, 2021; Bullock et al., 2023). Considering that the suppression of alpha power over electrodes contralateral to an attended hemifield has been shown to track with WM load (Adam et al., 2018; Fukuda et al., 2015, 2016; Hakim et al., 2019), lateralized alpha power was also used to index WM filtering efficiency. Lateralized alpha power was computed by subtracting the percent change in power, relative to a baseline period (-500 to -200 ms), in ipsilateral from contralateral electrodes. Identical electrode pairs used to compute the CDA were also used to calculate lateralized alpha power. Midline frontal theta power was calculated by averaging activity over the electrodes AFz, Fz, F1, F2, F3, and F4.

Decoding

A linear discriminant pattern classifier was used to determine the extent to which the neural signatures of WM load and filtering efficiency were modulated by exercise. Employing a 10-fold cross validation scheme, three separate binary classification models were trained on topographical patterns of voltage activity to discriminate between pairs of the different WM set sizes (i.e., set size 1 vs 4, 1 vs 1+3, 1+3 vs 4). Within each fold, the number of trials for each set size label were balanced to ensure the classifier was not biased toward the more frequent label. Furthermore, each fold contained an equivalent number of trials between both the rest and exercise conditions, to mitigate the possibility that differences in decoding accuracy were merely a reflection of differences in signal-to-noise ratio between conditions. WM load was decoded independently at each time point using average voltage power within a 10 ms sliding window with 80% overlap. This decoding procedure was also applied to topographical patterns of delta (1-3 Hz), alpha, and theta power to determine if neural oscillations within these frequency bands carried information about WM load and filtering efficiency.

Statistical Inference

All statistical inference was performed within a Bayesian framework. Statistical inference within this framework can be viewed as a model selection problem, and one popular criterion is Bayes Factors (BFs) which indicate the degree of probabilistic evidence in favor of one model compared to another. Memory strength (i.e., d' or d-prime) and reaction time (RT) on the filtering efficiency task were compared across conditions, set sizes, and K through a repeated measures ANOVA using the *anovaBF* function from the R package *BayesFactor* (Morey & Rouder, 2023). Rather than selecting the best fit model in an all-or-none fashion, Bayesian Model Averaging (BMA) was implemented to estimate an inclusion BF (i.e., $\text{BF}_{\text{Inclusion}}$) for each factor (*bayesfactor_inclusion*; *bayestestR*) (Makowski et al., 2019). In short, $\text{BF}_{\text{Inclusion}}$ indicates how probable the observed data are, on average, under a model that included the factor of interest (Hinne et al., 2020). This statistical routine was also implemented at each time point independently to test for differences in CDA amplitude and power in both the theta and alpha frequency bands. Post-hoc comparisons were subsequently conducted using Bayesian paired samples *t*-tests, which were implemented using the function *bf.ttest* from the MATLAB package *bayesFactor* (Krekelberg, 2022). Note, this function utilizes a Cauchy and Jeffreys prior to estimate JZS BFs from a frequentist *t*-statistic and degrees of freedom (Morey et al., 2015; Rouder et al., 2012). A BF between 1 and 3 indicates "anecdotal" evidence for the alternative hypothesis, between 3 and 10 indicates "moderate" evidence, between 10 and 30 indicates "strong" evidence, and greater than 30 indicates "very strong" evidence (Dienes, 2016; Kass & Raftery, 1995; Kruschke & Liddell, 2018; Wetzels et al., 2011). BFs < 1, on the other hand, indicate varying degrees of evidence in favor of the null hypothesis (0.33–1 = anecdotal, 0.1–0.33 = moderate, 0.033–0.1 = strong, 0.01–0.033 = very strong, < 0.01 = extreme).

Classifier results were evaluated using the following procedure. First, classifier accuracy at each time point was compared to chance (i.e., 50%) using a one-sample BF *t*-test to determine if WM load and filtering efficiency could be decoded from patterns of neural activity. To assess if classifier accuracy differed between experimental conditions, paired-sample BF *t*-tests were used instead. Next, the decoding procedure was carried out with randomly permuted set size labels for 250 iterations. For each of these iterations, one-sample or paired-samples BF *t*-tests were conducted to generate a permuted distribution of BFs ("permuted" BFs) for subsequent nonparametric comparisons. Although Bayesian inference is more conservative than its frequentist counterpart and less likely to result in false confidence (Gelman & Tuerlinckx, 2000), the number of statistical tests conducted to evaluate classifier performance may still lead to concerns toward observing large BFs by chance alone. Thus, a cluster-based correction procedure (Cohen, 2014; Garrett et al., 2021) was performed to mitigate the misinterpretation of spuriously large BFs. For each iteration of permuted classifier accuracies, the maximum cluster size of contiguous time points where BF ≥ 3 was recorded, yielding a null distribution of maximum cluster sizes. Then, clusters of contiguous time points where true classifier accuracies achieved a BF ≥ 3 were compared to the null distribution of maximum cluster sizes. If a cluster was larger than 95% of the null distribution, it was considered unlikely to be spurious.

RESULTS

Exercise Physiology

Average heart rate was greater during exercise (107.76 ± 14.58) as compared to rest (83.13 ± 11.96; BF $= 8.66$e22). RPE scores post cycling indicated that on average the exercise intensity was perceived as "very light" (9.59 ± 2.06), and these ratings were higher relative to the resting condition (6.97 ± 0.97; BF $= 3.45$e6).

Behavior

There was at least strong evidence for an effect of set size on d' ($\mathrm{BF}_{\mathrm{Inclusion}} = 7.02$e20) and RT ($\mathrm{BF}_{\mathrm{Inclusion}} = 5.82$). Memory strength also differed as a function of *K* ($\mathrm{BF}_{\mathrm{Inclusion}} = 6.26$e6). In contrast, there was evidence against an effect of experimental condition on d' ($\mathrm{BF}_{\mathrm{Inclusion}} = 0.12$) and RT ($\mathrm{BF}_{\mathrm{Inclusion}} = 0.2$). Further, there was evidence in favor of the null hypothesis for the absence of any interaction between these factors on behavioral performance ($\mathrm{BF}_{\mathrm{Inclusion}} \leq 0.11$). Post-hoc comparisons indicated that d' was

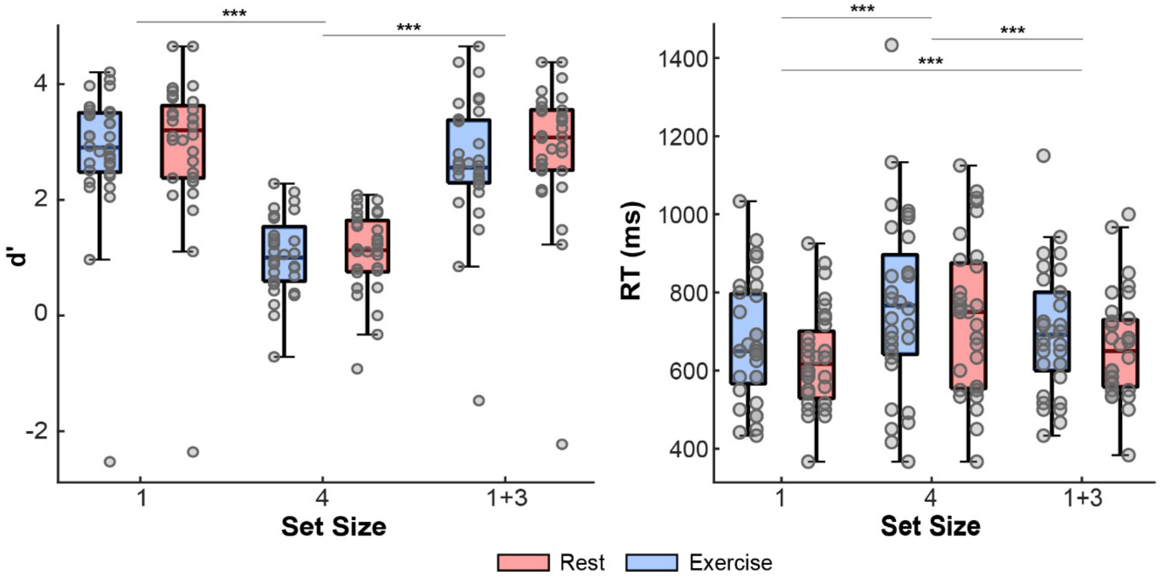

Figure 18. Behavioral performance on working memory filtering efficiency task as measured by sensitivity (d') and response time (RT). Points represent individual's data, and error bars represent $\pm$ 1 SEM. Asterisks indicate at least moderate evidence in favor of the alternative hypothesis for a non-zero difference.

greater for set size 1 (2.87 ± 0.15; BF = 3.05e11) and 1+3 (2.77 ± 0.14; BF = 27.25) relative to set size 4 (1.06 ± 0.08; BF = 2.70e11), and equivalent between set size 1 versus 1+3 (BF = 0.76) (**Figure 18**). Memory strength was also greater for high-capacity (2.68 ± 0.13) relative to low-capacity subjects (1.78 ± 0.27; BF = 7.58). Lastly, RT was fastest on set size 1 (648.18ms ± 24.92) compared to set size 1+3 (678.00ms ±

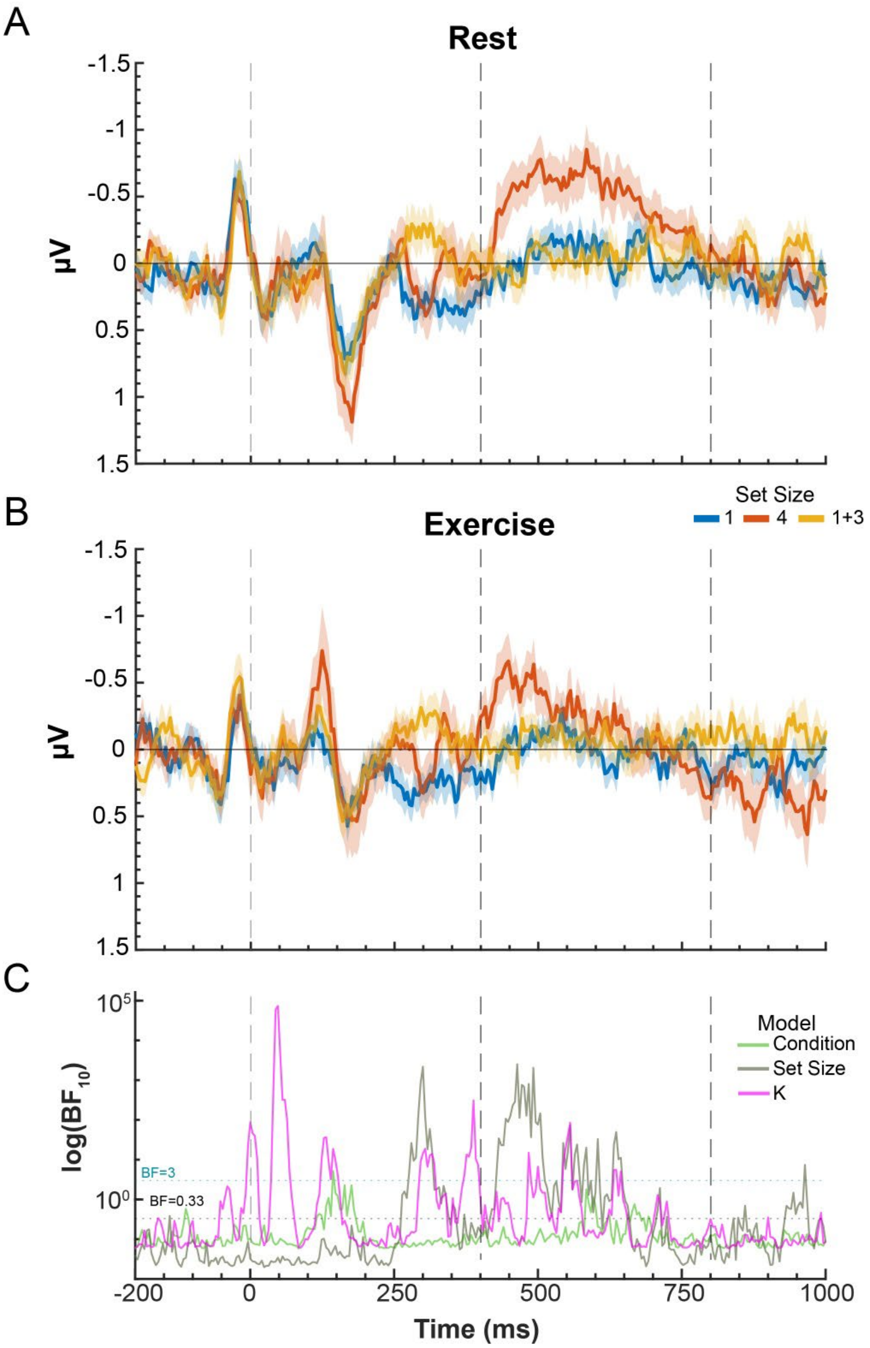

Figure 19. Contralateral delay activity (CDA) during both (A) rest and (B) exercise conditions. (C) Bayes factors for analysis of variance models testing the effect of condition, set size and WM capacity on CDA amplitude at each time point. Shaded error bars represent ± 1 SEM. Vertical dashed lines indicate stimulus onset, and the start and end of the CDA period, respectively.

26.04) and 4 (752.87ms ± 37.25) trials (1v4: BF = 1.94e3; 1v1+3: BF = 1.58e6; 1+3v4: BF = 91.70).

CDA amplitude tracks WM load when in a physiologically active state

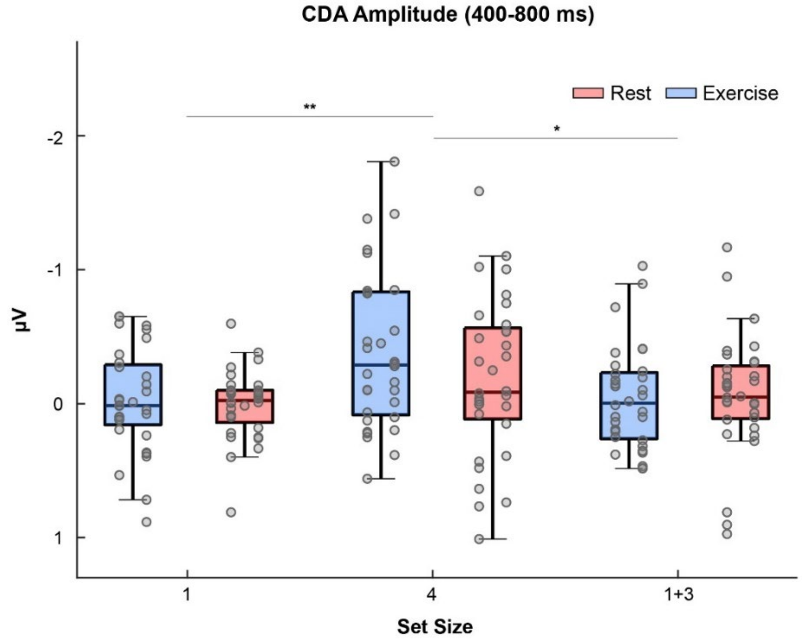

Figure 20. Average CDA amplitude between ~400-800 ms post-stimulus onset for both rest and exercise. Asterisks indicate at least moderate evidence in favor of the alternative hypothesis for a non-zero difference.

Bayesian repeated measures ANOVAs conducted at each time point revealed at least moderate evidence for an effect of set size on CDA amplitude between ~276-316 ms and ~432-508 ms post stimulus onset (**Figure 19**). However, there was little support for a modulation of amplitude by exercise, with only anecdotal evidence observed between ~144-180ms. Further, there was no support for an interaction between exercise and condition (BF < 1). Average CDA amplitude between 400-800 ms differed as a function of set size (BF = 19.44), and was more negative in set size 4 (-0.32μV ± 0.08) compared to set size 1 (-0.01μV ± 0.04) trials (BF = 17.11) (**Figure 20**). There was also strong evidence for a difference in average CDA amplitude within this time window between set size 1+3 (-0.05μV ± 0.05) and set size 4 trials (BF = 7.13), but not compared to set size 1 trials (BF = 0.28). Interestingly, there was only anecdotal

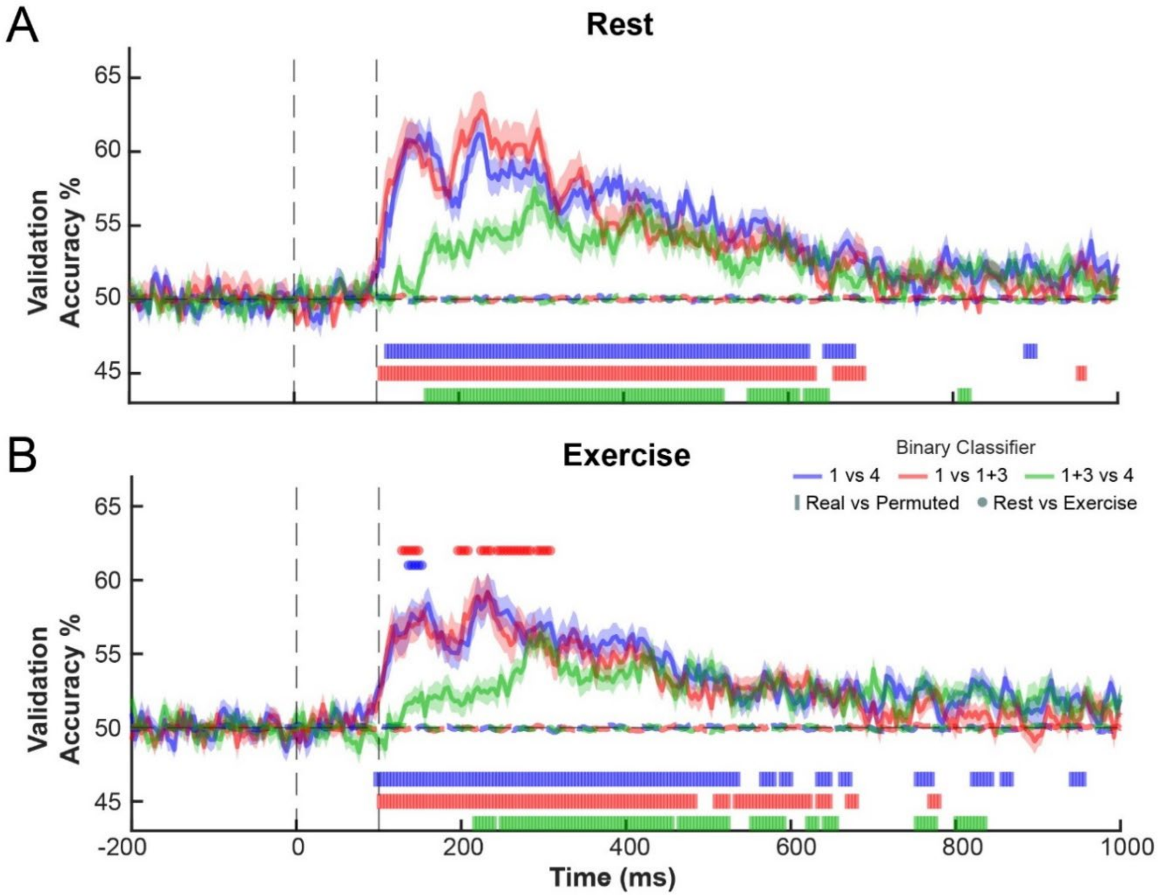

Figure 21. Cross-validation accuracy for binary classifiers trained to discriminate WM load using voltage distributions across the scalp from both conditions, and then testing on activity recorded during (A) rest and (B) exercise. Dashed blue (1 vs 4), red (1 vs 1+3), and green (1+3 vs 4) lines represent decoding accuracy for permuted controls. Vertical bars represent time points in which there was at least moderate evidence for greater decoding accuracy for classifiers trained with true versus permuted set size labels (after cluster correction). Colored dots in (B) represent reliable differences in decoding accuracy between rest and exercise. Dashed vertical lines indicate stimulus onset and offset. Shaded error bars represent ± 1 SEM.

evidence for a difference in average CDA amplitude between low- and high-capacity participants ($\text{BF} = 1.42$), and strong evidence against the presence of an interaction between WM capacity and set size ($\text{BF} = 0.30$). Altogether, the CDA is a marker of WM storage and filtering efficiency that is robust to exercise-induced changes in physiological state.

Topographical distribution of voltage potentials during exercise reflects WM load

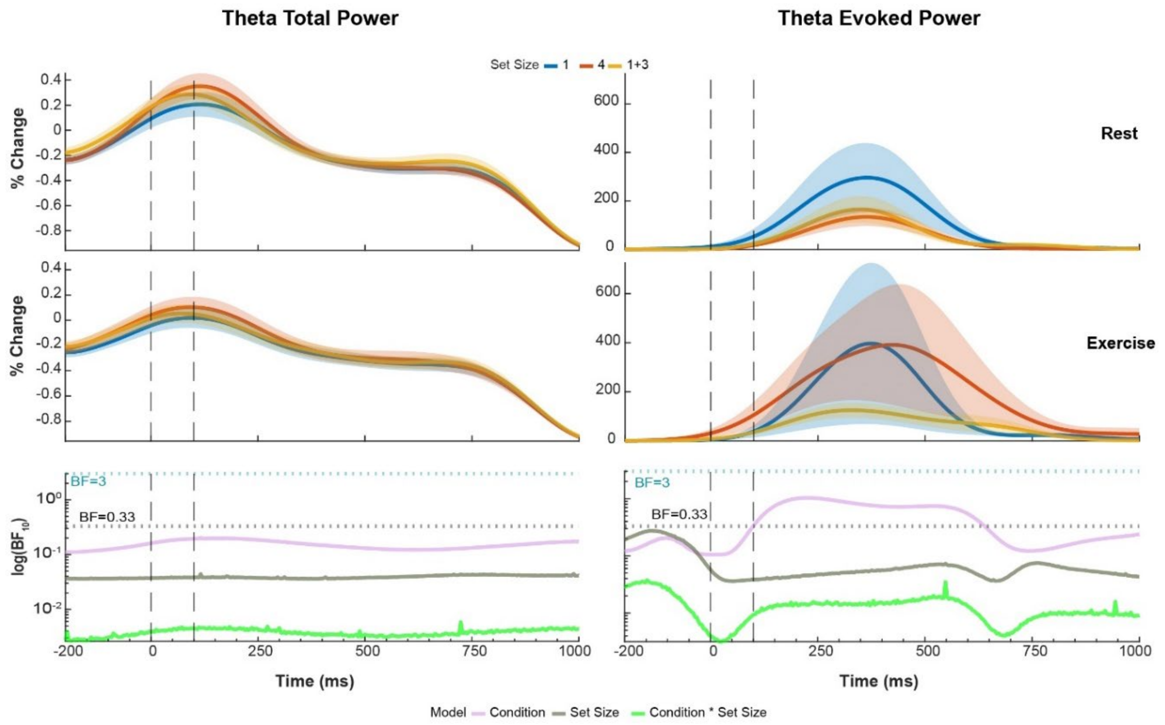

Figure 22. Percent change in total and evoked theta power as a function of set size across experimental conditions. Bayes factors for ANOVA models testing for effects of condition, set size, and their interaction shown in bottom two plots. Vertical dashed lines indicate stimulus onset and offset. Shaded error bars represent ± 1 SEM.

To determine if patterns of neural activity across the scalp reflected the number of items actively stored in WM, binary linear classifiers were trained on single trial voltage distributions from both experimental conditions and tested on a single condition using a cross-validation training scheme. For both the rest and exercise condition, at least moderate evidence for above chance classification accuracy was observed when discriminating between set sizes 1 vs 4 and 1+3 between ~100-700 ms post-stimulus onset (**Figure 21**). Evidence for a dissociation between set size 1 vs 1+3 trials emerged later (~150-250 ms) and was sustained until ~550 ms. Classifiers performed equivalently between rest and exercise, with only a few timepoints exhibiting higher accuracy during rest when decoding set size 1 vs 1+3 and 1 vs 4. Hence, there is little support for the neural representations of WM load being modulated by concurrent exercise.

WM load is decodable from patterns of theta and alpha power

Time frequency analyses were performed to ascertain the roles of theta- and alpha-band activity in WM filtering efficiency and maintenance, and their potential modulation by changes in global state. Across all timepoints, there was strong evidence in favor of the null for no effect of set size or experimental condition on total and evoked frontal midline theta power (**Figure 22**). Similarly, set size and experimental condition had no effect on lateralized posterior alpha power (**Figure 23**).

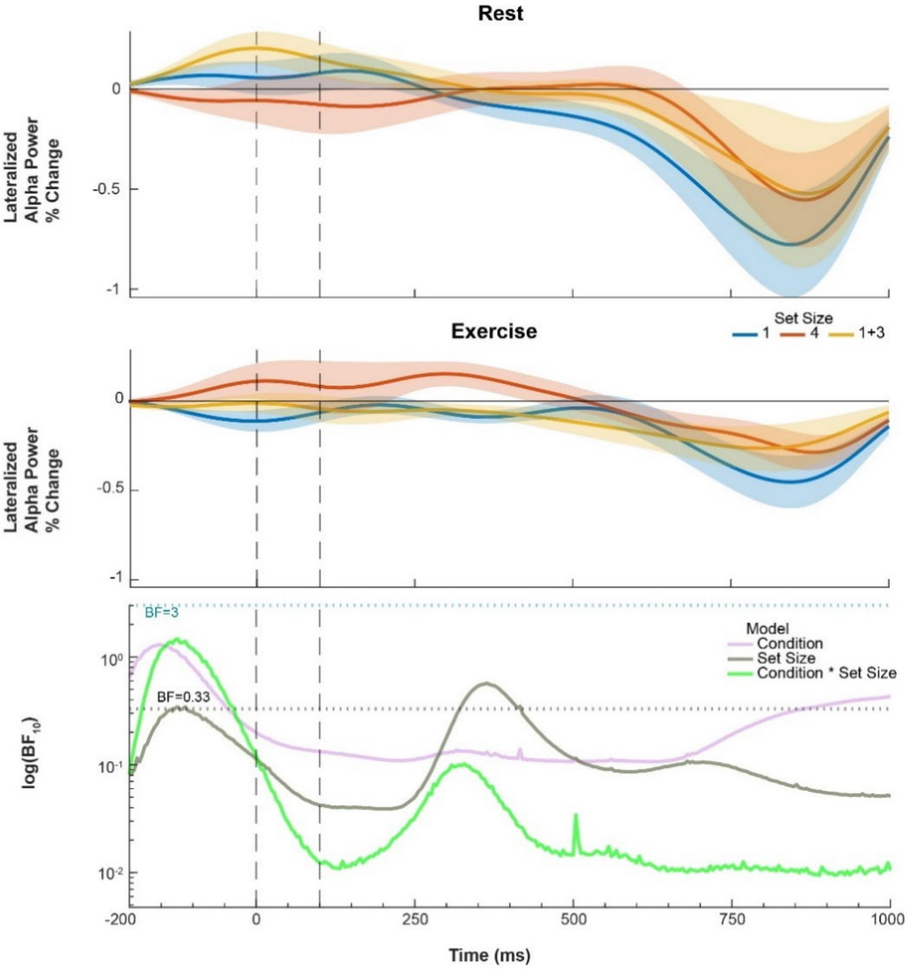

Figure 23. Lateralized alpha power as a function of set size during both rest and exercise. Bottom plot depicts Bayes factors for ANOVA models testing effects of condition, set size, and their interaction. Shaded error bars represent ± 1 SEM.

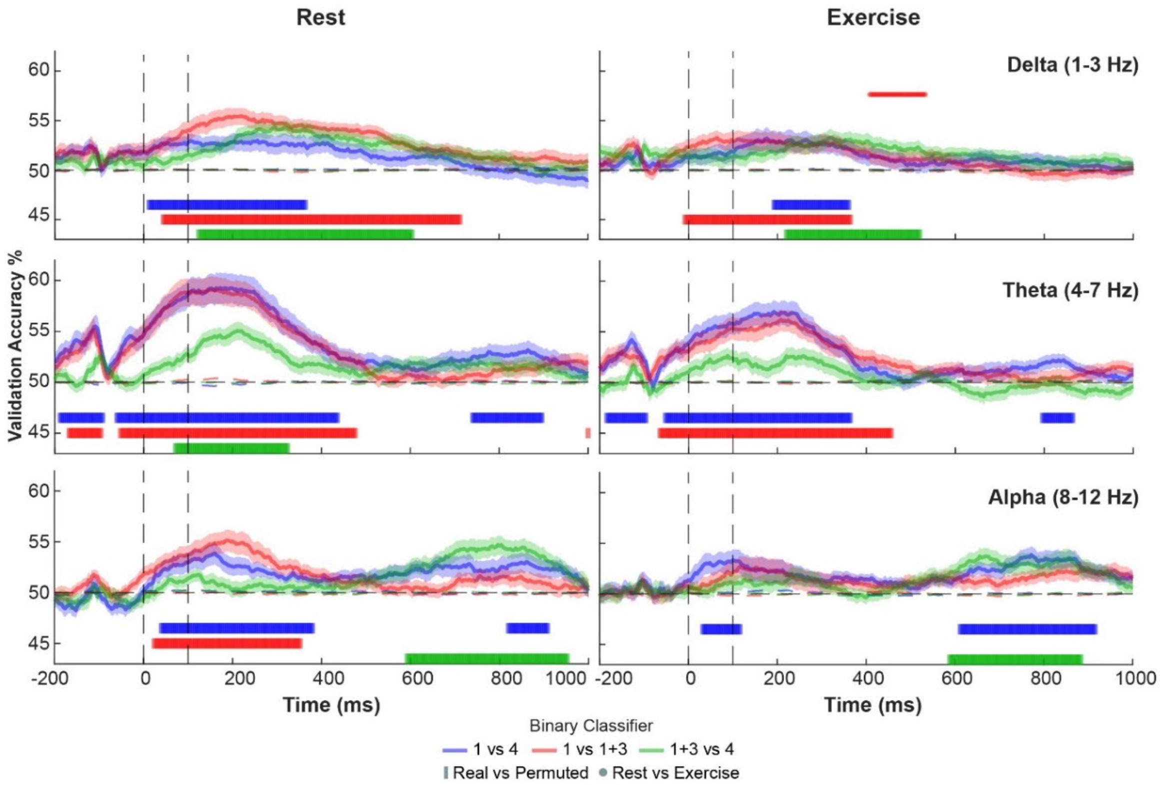

Figure 24. Cross-validation accuracy for binary classifiers trained on patterns of delta, theta, and alpha power during both rest and exercise. Vertical bars represent time points in which classifier accuracy was reliably higher than a permuted control for decoding set size 1 vs 4 (blue), 1 vs 1+3 (red), and 1+3 vs 4 (green). Shaded error bars represent ± 1 SEM.

Contrary to univariate analyses, multivariate pattern classification analyses indicated that total theta and alpha power carried information on the number of items stored in memory. In the resting condition, set size 1 was robustly discriminated from set size 4 using patterns of both theta and alpha power throughout stimulus presentation (~44-100 ms), the first half of the delay period (~100-436 ms), and later in the retention period (~744-908 ms) (**Figure 24**). Set size 1 vs 1+3 trials were also discriminable using patterns of theta and alpha power, but only during stimulus encoding and the first half of the delay period (~24-476 ms). Trials including distractors were also dissociable from those with four target stimuli during these time periods (~76-324 ms) using patterns of theta power, and later in the retention period using (~590-950 ms) patterns of alpha power. Classification results in the resting condition suggest that theta supports the filtering of distracting stimuli early on during stimulus encoding and maintenance, while alpha assists in the removal of accidentally encoded distractions later in the retention period. In the exercise condition, set size 1 trials were successfully discriminated from set size 4 trials during the first half of the trial period (~0-364 ms) and later in the delay period (~796-864 ms) using theta power. Patterns of theta power were also distinguishable between set size 1 and 1+3 trials during stimulus presentation and early in the retention period (~0-456 ms). Alpha power, on the other hand, was successful in discriminating between set size 1 v 4 trials during stimulus encoding (~32-116 ms) and later in the delay period (~616-916 ms). Furthermore, classifiers trained on alpha power discriminated between set size 1+3 v 4 trials later in the retention period (~588-884 ms). Classification results based on theta power during exercise suggest that distracting stimuli may have been erroneously encoded into working memory, while those based on alpha power indicate that encoded distractors may have been removed later in the retention period. A caveat with these interpretations, though, is that there were no observed differences in decoding accuracy between both rest and exercise conditions.

DISCUSSION

Systematic reviews and meta-analyses have consistently reported that acute exercise has a beneficial effect on aspects of executive function, especially working memory and cognitive control (Moreau & Chou, 2019; Cantelon & Giles, 2021). Accompanying these findings is a wealth of empirical evidence for the modulation of early sensory processing and oscillatory dynamics across multiple frequency bands during physically active states (Bullock, Cecotti, & Giesbrecht, 2015; 2017; Cao & Händel, 2019; Garrett et al., 2021; Kao et al., 2021). The aim of the current study was to determine whether acute exercise impacts the ability to selectively encode goal-relevant information into WM and the number of items that can be actively retained. EEG was recorded from participants while they completed a WM filtering efficiency task during a bout of light intensity cycling and at rest. Multivariate classifiers trained on patterns of voltage potentials, and power in the delta, theta, and alpha frequency bands were able to accurately detect WM load and the filtering of distractors in both conditions during the encoding and early retention period. However, classification accuracy did not robustly differ between rest and exercise. Similarly, CDA amplitude varied as a function of set size but not experimental condition. Taken together, these findings suggest that light intensity exercise does not impact the ability to ignore distracting information or the number of items that can be maintained in memory. More importantly, the present study demonstrates that it is possible to track WM load and filtering efficiency while individuals are in a physically active state.

ERP analyses reinforced the notion that CDA amplitude tracks the number of items retained in WM. Contrary to previous studies, though, average CDA amplitude did not differ as a function of WM capacity, challenging the validity of splitting individuals into low- and high-capacity groups in the current study. Given that memory strength on the filtering task differed between low- relative to high-capacity individuals, it is more likely that those in the former capacity group had enough cognitive control to perform adequately on distractor trials. Indeed, in both capacity groups the computed difference wave was more negative for trials that contained distractors ~250 ms post-stimulus onset, reflecting the N2pc component (Eimer, 1996; Luck & Hillyard, 1994). This component has been repeatedly shown to occur in visual search tasks for lateralized targets that are surrounded by distractors (Kiss et al., 2008), suggesting that it represents attentional selection mechanisms and the suppression of non-relevant information. Interestingly, Vogel, McCollough, & Machizawa (2005) did not report the presence of the N2pc and a dependency on WM capacity, which may have been due to the chosen baseline period. Based on the notion that low-capacity individuals fail to properly ignore non-relevant stimuli during the encoding period, leading to a more negative CDA for trials that contain distractors, it is reasonable to hypothesize that they would not display an N2pc component. However, this component was present in both low and high-capacity individuals, begetting to two possible interpretations. This first is that low-capacity individuals are able to suppress distractors only partially, leading to the contamination of target representations. The second is that in the current experiment the N2pc only reflects initial target selection processes rather than active distractor suppression mechanisms (Sawaki et al., 2012), which are masked by the presence of the CDA. An interesting follow up experiment for future research would be to test individuals across a range of WM capacity estimates and assess how N2pc amplitude predicts both subsequent CDA amplitude and task performance on distractor trials. Regardless, the N2pc component did not differ across both rest and exercise conditions, suggesting that attentional selection and distractor suppression are robust to perturbations in global state caused by light intensity exercise. Further, behavioral measures and similarities in CDA amplitude imply that exercise does not affect the number of items that can be held in memory.

Classification analyses revealed that theta oscillations support the selective encoding and maintenance of targets early in the delay period. There is considerable evidence for activity within theta band tracking demands on WM. Klimesch et al., (1999) observed that theta power increases over frontal midline and parietal electrodes as a function of the number of characters encoded and stored in short-term memory. Using MEG, Jensen & Tesche (2002) also detected an increase in frontal midline theta power that corresponded to the number of digits encoded and retained in memory on a modified Sternberg task. Cross-frequency phase synchronization between theta and gamma oscillations is a proposed mechanism by which representations of multiple stimuli are organized and stored in WM (Jensen & Colgin, 2007; Canolty et al., 2006; Jensen & Lisman, 2001; Sauseng et al., 2010). Indeed, Sauseng et al., (2009) detected an increase in theta-gamma phase coupling over posterior electrodes that were contralateral to cued targets in a bilateral change detection task. Importantly, phase synchronization increased as a function of memory load and positively correlated with individual WM capacity. Given their observed dynamics during encoding and maintenance of multi-item stimulus sets, theta oscillations are thought to reflect a gating mechanism that controls the processing and suppression of goal relevant and irrelevant stimuli, respectively (Raghavachari et al., 2001; Sauseng et al., 2010). Classifiers trained on patterns of alpha band activity were also able to decode WM load, albeit only later in the retention period. It is well established that alpha oscillations track the allocation of spatial attention towards items encoded and actively retained in WM (Foster et al., 2016, 2019; Sutterer et al., 2019; MacLean, Bullock, & Giesbrecht, 2019; Garrett, Bullock, & Giesbrecht, 2021). There is evidence that lateralized alpha power tracks the number of items stored in memory, with a greater degree of suppression later in the retention period as set size increases (Adam, Robinson, & Vogel, 2018; Fukuda, Kang, & Woodman, 2016; Fukuda, Mance, & Vogel, 2015). Contrary to previous work, univariate measures of theta and alpha band activity were not sensitive to WM and filtering of distracting information. The current study, though, differs in the degree of cognitive demand placed on participants while they completed the filtering efficiency task. Having to concurrently maintain the execution of gross motor movements at a specific cadence throughout the experimental session could have required the exertion of more cognitive control, thus increasing frontal midline theta power irrespective of set size. Further, shifts in attention away from the locations of memoranda during the maintenance period towards cadence alignment may have diminished differences in contralateral and ipsilateral alpha power. Nevertheless, multivariate analyses provide further support for the role of theta and alpha oscillations in the efficient storage of goal-relevant stimuli in WM.

There are multiple reasons for the absence of exercise-induced effects. First, subjects engaged in a light intensity exercise protocol in an attempt to induce modulations in sensory responses, yet no differences in the visual evoked activity were detected. One major difference between the current study and those that observed enhanced sensory responses is that stimuli were presented bilaterally and in the periphery, rather than at fixation (Bullock et al., 2015). Therefore, light intensity cycling may facilitate foveal processing but have little impact on peripheral processing (but see Cao & Händel, 2019). Second, a more intense exercise may have been necessary to engender the cascade of neuromodulatory changes (e.g., rise in catecholamine and neutrophin levels) that promote WM function. Indeed, Drolette & Meadows (2022) observed that change detection accuracy improved on trials with four targets 40-minutes post a high intensity interval calisthenics exercise relative to a sedentary state. Note, similar to the current study no differences were detected in CDA or N2pc amplitude between exercise and control conditions, providing further evidence for the notion that exercise does not impact WM storage capacity. Instead of influencing the number of items that can be stored, exercise may rather affect the resolution of WM representations

(Garrett et al., 2021). Since a “supra-threshold” degree of change was used between sample and test arrays, low-resolution representations could have been sufficient to complete the task (Bays & Husain, 2008), thereby masking potential behavioral and neural differences between conditions. Future studies implementing whole-report response are required to gain insights into the impact of exercise on the allocation of attentional resources towards multiple items stored in memory and the fidelity of their representations.

In summary, we investigated how an acute bout of aerobic exercise modulates the selective encoding of targets into WM and the number of items that can be stored. Behavioral and ERP analyses indicated that attentional control and storage mechanisms are preserved during cycling relative to a sedentary condition. Classification analyses revealed that it is possible to decode WM load and filtering efficiency while subjects are engaged in physical activity. The current study is the first to demonstrate that it is possible to track the number of items actively retained in memory during exercise and provides novel insights into the stability of WM encoding and maintenance mechanisms across changes in physiological state.

Chapter V: General Discussion

Behavioral and neural responses to sensory inputs are highly dynamic and inextricably linked to variations in global physiological state. Yet, research on how the brain processes information from the external environment has predominantly focused on behavior and its underlying neural activity while an organism is in a sedentary state—which consequently may only represent a single snapshot of brain function within a high-dimensional feature space of global states (McCormick, Nestvogel, & He, 2020). The current body of work serves as a collection of studies aimed toward understanding how perturbations in global state in turn modulate cognitive processes and their neural substrates. In particular, these studies examined the effects that ensue from engaging in aerobic exercise.

Chapter II details a data-driven approach to quantify the impact of exercise on cognitive task performance. A Bayesian hierarchical model was employed to meta-analytically synthesize reported effect sizes from a large corpus of empirical studies, and test for exercise protocol and cognitive task characteristics that moderate the magnitude of exercise-induced effects. The model revealed that there was moderate probabilistic evidence in favor of exercise having a small positive influence on general cognition. Engaging in high-intensity interval training (HIIT) or cycling increased the magnitude of this effect. Moreover, response time and executive processes such as WM and inhibition were especially sensitive to perturbations in global state caused by exercise. Building off these meta-analytic results, Chapter III and IV empirically investigated which aspects of WM and inhibitory control are modulated when an individual is in a physically active state. Chapter III demonstrates that the representations of spatial locations stored in WM can be reconstructed during a bout of low-intensity cycling by applying an inverted encoding model (IEM) to topographical distributions of alpha power recorded with EEG. The results of this study suggest that the fidelity of spatial WM representations is degraded during exercise relative to a sedentary period, which may be due to the continuous coordination of gross motor movements taxing attentional resources. Interestingly, Ayaz et al., (2013) observed that neurons in mouse primary visual cortex displayed an increased tuning for larger stimuli during locomotion relative to a sedentary period, suggesting that the ability to integrate information over larger areas of space is increases. If low-intensity cycling induced a similar change in human visual cortex, then diminished IEM reconstructions (i.e., smaller slopes) may rather reflect that the area of space neural populations are sensitive to has expanded and that exercise facilitates spatial integration. Chapter IV evaluated whether the neural substrates of selective attention and WM storage are modulated during low-intensity cycling. The key results from this study were that WM load and filtering efficiency can be tracked during exercise using traditional event-related potential (ERP) analyses and multivariate classification techniques. Importantly, no major differences in WM load or filtering efficiency were detected between rest and exercise, suggesting that both the ability to selectively encode targets while simultaneously ignoring distractors and the number of items that can be retained in WM are preserved across small perturbations in physical state.

Results from the presented studies highlight the complex relationship between global state and cognition. Exercise selectively influenced the ability to maintain high-resolution stimulus representations in WM but had no impact on encoding mechanisms or storage capacity. One possible explanation for this selective effect is that during exercise parietal areas are also constantly maintaining motor representations to coordinate limb movements in extrapersonal space, and spatial information from motor signals may erroneously be integrated into visual WM representations (Andersen et al., 1997; Andersen & Buneo, 2002; Beloozerova & Sirota, 2003; Snyder et al., 1998). Given their association to the allocation of spatial attention (Rihs et al., 2007; Sauseng, Klimesch, Schabus, et al., 2005; Thut et al., 2006), execution of voluntary motor movements (Pfurtscheller & Aranibar, 1979; Pfurtscheller & Berghold, 1989; Pfurtscheller & Lopes da Silva, 1999), and integration of information across sensory modalities (Cecere et al., 2015; van Driel et al., 2014), alpha oscillations likely would reflect contaminations of spatial WM representations from motor signals. Provided that increased levels of representational noise during exercise is distributed uniformly across multiple stimuli retained in WM, then their discriminative relationship is preserved and the number of items that can be stored remains unchanged. An alternative account is that low-intensity exercise has no impact on the resolution of WM representation. Rather, diminished IEM reconstructions reflect an expansion in the areas that neural populations in visual cortex are tuned to respond to (Ayaz et al., 2013) and a facilitation of spatial integration. Future research in which multiple WM representations are reconstructed during exercise is required to adjudicate between these possible explanations. In any case, it is clear that specific mechanisms of a single cognitive process are sensitive to changes in global state.

A consistent finding across empirical assessments of exercise-induced effects on WM in Chapter III and IV is an absence of change in behavioral performance. This contrasts with the results of the meta-analysis discussed in Chapter I, however it is important to consider two key points. First, exercise was estimated to only have a small positive effect on WM performance ($g = 0.22$), thus larger sample sizes may be necessary to reliably detect differences in behavioral measures. Second, the behavioral tasks were relatively simple and consisted of large changes between memorized and probe stimuli (Bays & Husain, 2008). Participants could have been performing at ceiling on these tasks, masking differences between conditions. Change detection designs were used to increase the number of trials that could be completed within experimental sessions and improve EEG recordings. Tasks requiring whole-report may be sensitive to exercise-induced changes in behavior and provide greater insights into how the structure of WM representations are modified in a physically active state. A more interesting factor to consider is that task goals were orthogonal to the exercise. In other words, there was no need to physically engage one's body to accomplish the cognitive task, which contrasts with goal-directed behavior in real-world scenarios (e.g., rock climbing or playing sports). When viewed through the lens of the embodied cognition framework, perception and decision-making are inextricably intertwined with action dynamics (Foglia & Wilson, 2013; Gordon et al., 2021). This relationship can be observed when stimulus representations are associated with specific motor plans. For example, van Ede et al., (2019) recorded EEG on a visual WM task in which participants had to use the left or right index finger to rotate probe stimuli either counterclockwise or clockwise, respectively. Critically, classification analyses revealed a high degree of overlap in the temporal profiles of visual (i.e., stimulus location) and motor (i.e., response hand) selection. This suggests that representations of visual and motor attributes are concurrently available to which allows for the speedy execution of precise actions to accomplish task-goals. Furthermore, there is evidence that the execution of hand or eye movements can affect visual stimulus representations stored in WM, implying that there is a bi-directional link between visual WM and motor movements (see van Ede, 2020 for review). Therefore, aligning the exercise with cognitive task-goals is a promising experimental manipulation that may produce much larger behavioral effects that better generalize to real-world scenarios.

Why does engaging in physical activity modulate cognitive processes and their underlying neural substrates? The Adaptive Capacity Model (ACM) proposes a mechanistic explanation for exercise-induced effects that is grounded in evolutionary neuroscience (Raichlen & Alexander, 2017b). The ACM posits that widespread changes in neurochemical levels and neural activity that occur during physical activity are the product of selection pressures that promoted successful foraging when humans led a highly active hunter-gatherer lifestyle (Kempermann et al., 2010). Analysis of modern-day hunter-gatherer communities shows that a majority of their daily routine is spent engaged in light to moderate physical activity (Gurven et al., 2013; Raichlen & Alexander, 2017b)—suggesting that cognitive abilities such as executive function, memory, attention, navigation, and perception evolved to perform optimally in a physiologically aroused state. Movement through complex naturalistic environments would engage each of these cognitive abilities, and as locomotor speed increases so too does processing demands on the brain. The ACM also proposes that the high degree of variability in the impact of acute physical activity on cognition across individuals (i.e., small effect sizes) is likely a reflection of differences in their inherited adaptive physiological capacity (Bouchard et al., 1999). This physiological capacity can be trained, however, through long-term exercise interventions that strengthen the neural architecture of multiple cognitive systems as evidenced by changes in structural and functional connectivity (Baniqued et al., 2018; Erickson et al., 2011; Hsu et al., 2017; Raichlen et al., 2016). Hence, a case can be made for the notion that cognition evolved to operate in a physically active state rather than a sedentary one, underscoring the importance of developing a fundamental understanding of the bi-directional influence between the brain and body.

The set of studies presented here aimed to determine the impact of acute exercise on the neural mechanisms that support the encoding and maintenance of stimulus representations over short periods of time. Novel statistical methods were employed to synthesize results across empirical studies and to demonstrate that both the number of stimuli held in WM and the fidelity of their representations can be tracked during an acute bout of cycling. These studies serve as an important first step towards developing a comprehensive understanding of how the brain is capable of achieving goal-directed behavior throughout our daily routine across variations in global state.

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