THE EFFECTS OF SINGLE BOUTS OF MODERATE-INTENSITY CONTINUOUS EXERCISE AND HIGH-INTENSITY INTERVAL EXERCISE ON THE MODULATIONS OF INHIBITORY CONTROL, WORKING MEMORY, AND LONG-TERM MEMORY

BY

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DISSERTATION

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ABSTRACT

Although existing literature has suggested facilitation on various aspects of cognitive function during the recovery period following a single bout of moderate-intensity continuous exercise (MICE), little is known regarding how to optimize the prescription of acute exercise for maximizing its transient benefits on cognition. High-intensity interval exercise (HIIE) is growing in popularity as a mode of exercise known for its effectiveness and efficiency toward improving multiple health outcomes. However, a limited understanding exists regarding the transient effects of HIIE on post-exercise cognition compared to MICE. Accordingly, the aim of this investigation was to compare the effect of acute HIIE and MICE on inhibitory control, working memory, and long-term memory. Using a within-participants design, event-related potentials (ERPs) and task performance were assessed while participants performed a free recall task, a modified flanker task, and a modified Sternberg task following 20 minutes of seated rest, MICE, and HIIE on three separate days in counterbalanced order. Following both MICE and HIIE, participants recalled more words in the free recall list and exhibited shorter reaction time during the flanker task relative to the rest condition. HIIE resulted in additional facilitation, as indexed by reduced reaction time interference scores during the flanker task and reduced overall reaction time during the Sternberg task relative to rest. Neuroelectric analysis indicated that MICE increased P3 amplitude compared to rest and HIIE, while HIIE decreased P3 latency relative to rest. CNV was unchanged following MICE compared to rest,

while HIIE increased initial CNV amplitude relative to rest. These results suggest that both types of exercise may improve cognitive performance, with HIIE having additional benefits relative to MICE. To support inhibitory control and working memory operations, MICE and HIIE may exert differential influences on brain function, with MICE increasing attentional resource allocation and HIIE improving stimulus identification and cognitive processing speed. Taken together, the findings of the present investigation demonstrate transient facilitating effects on cognition following acute bouts of MICE and HIIT, and provide preliminary evidence to support HIIE as a promising alternative approach for enhancing cognitive performance.

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CHAPTER 1: INTRODUCTION

According to recent statistics (World Health Organization, 2010c, 2010d), more than 80% of adolescents and 23% of adults around the world are considered physically inactive, despite the fact that an insufficient amount of physical activity is known to increase the risk of non-communicable diseases (i.e. cardiovascular diseases, diabetes, and cancers) and shorten life expectancy (Lee et al., 2012). This unhealthy trend is especially concerning because participation in physical activity has important implications for the optimization of cognitive development and the alleviation of age-related cognitive decline (Hillman, Erickson, & Kramer, 2008). Of the various means for increasing physical activity, engagement in short bouts of acute exercise has been proposed as a promising approach for accumulating physical activity to meet daily recommendation (World Health Organization, 2010a). More importantly, acute exercise has been demonstrated to have facilitating effects on cognition (Chang, Labban, Gapin, & Etnier, 2012).

Among the various domains of cognition, cognitive control (also known as executive control or executive function) has received considerable attention in the study of acute exercise and cognition. Of the core cognitive control processes, inhibitory control enables interference regulation at perceptual and cognitive levels, aiding selective and focused attention, impulse control, and behavioral outcomes throughout life (Diamond, 2013). The acute exercise literature has consistently reported that a single 20-30 minutes bout of

moderate-intensity continuous exercise (MICE) facilitates performance across a variety of inhibitory control tasks (Chang et al., 2012; Chang, Chu, Wang, Song, & Wei, 2015; Drollette et al., 2014; Drollette, Shishido, Pontifex, & Hillman, 2012; Joyce, Graydon, McMorris, & Davranche, 2009; Kamijo et al., 2009; Kamijo, Nishihira, Higashiura, & Kuroiwa, 2007; Pontifex, Saliba, Raine, Picchietti, & Hillman, 2013), particularly during tasks requiring the upregulation of inhibitory control (Chu, Alderman, Wei, & Chang, 2015; Hillman et al., 2009; O'Leary, Pontifex, Scudder, Brown, & Hillman, 2011; Sibley, Etnier, & Masurier, 2006; Yanagisawa et al., 2010). In addition to inhibitory control, acute MICE may positively affect working memory (McMorris, Sproule, Turner, & Hale, 2011; Roig, Nordbrandt, Geertsen, &Nielsen, 2013), another sub-discipline of cognitive control that describes the temporal storage and manipulation of information as part of the performance of complex cognitive tasks (Baddeley, 1992). Examination within the body of research targeting post-exercise working memory revealed beneficial effects of acute MICE on performance during tasks requiring information manipulation (Chen, Yan, Yin, Pan, & Chang, 2014; Hogan, Mata, & Carstensen, 2013), with disproportionally larger benefits for individuals with lower working memory capacity (Sibley & Beilock, 2007) and under task conditions that imposed increased amounts of working memory operation (Weng, Pierce, Darling, &Voss, 2015). Collectively, these findings suggest a transient beneficial effect of MICE on cognitive control.

Memory is another core component of human cognition that benefits from acute MICE. Roig et al. (2013) indicated that acute cardiovascular exercise has a moderate-to-large positive effect on performance during a wide variety of tasks involving different types of learning and memory. This exercise-induced facilitation on memory may be in a time-dependent fashion, such that memory performance may be facilitated following exercise performed in close temporal proximity to memory encoding (Roig et al., 2016). Such a positive effect was particularly significant in studies using free recall paradigms (Chang et al., 2012). Specifically, Coles and Tomporowski (2008) indicated maintained performance during a free recall vocabulary test following 40 minutes of MICE compared to baseline, while decreases in performance from pre- to post-test were observed following inactive control conditions. Similar exercise-induced facilitation on memory retention was observed in school-aged children (Etnier, Labban, Piepmeier, David, & Henning, 2014; Pesce, Crova, Cereatti, Casella, & Bellucci, 2009). Further, Labban and Etnier (2011) investigated the effects of exercise timing on exercise-induced memory facilitation, and found that memory retention only improved when exercise was performed prior to memory encoding. Taken together, these findings suggest that a single bout of MICE may have facilitating effects on memory processing, particularly during the stage of memory encoding.

Although the majority of previous studies have focused on the relationship between MICE and cognition, emerging evidence has indicated that exercise at a higher intensity may

be a promising means for gaining benefits on cognitive control and memory. A meta-analysis indicated that high-intensity exercise resulted in the largest enhancement in cognitive performance during the post-exercise period compared to exercise at other intensities (Chang et al., 2012). Further, empirical evidence has demonstrated that acute bouts of exercise at high-intensity may result in similar facilitation on cognitive performance associated with MICE (Hwang, Castelli, & Gonzales-Lima, 2016; Kamijo et al., 2007; Pontifex, Hillman, Fernhall, Thompson, & Valentini, 2009; Roig, Skriver, Lundbye-Jensen, Kien, & Nielsen, 2012; Skriver et al., 2014; Thomas et al., 2016). Moreover, such exercise-induced benefits may be disproportionally larger following high-intensity exercise compared to MICE or low-intensity exercise (Ferris et al., 2007; Hötting, Schickert, Kaiser, Röder, & Schmidt-Kassow, 2016; Thomas et al., 2016; Winter et al., 2007). Collectively, these findings provide evidence to support that manipulating exercise intensity is a viable approach to optimize exercise prescription for maximizing its transient benefits on cognition.

In addition to traditional high-intensity exercise, emerging evidence has indicated that acute bouts of high-intensity interval exercise (HIIE) may be a promising alternative for facilitating cognitive functioning. HIIE has generally been referred to as repeated bouts of short to moderate duration exercise at an intensity that is greater than the anaerobic threshold, interspersed with recovery periods or light exercise (Laursen & Jenkins, 2002; Weston, Wisløff, & Coombes, 2014). Compared to MICE, participation in HIIE has been shown to be

more effective and efficient for improving physical health, given that HIIE requires lower total exercise volume and less time commitment to achieve greater metabolic adaptations (Gibala & McGee, 2008; Ramos, Dalleck, Tjonna, Beetham, & Coombes, 2015). Research has shown that HIIE has short-term and long-term benefits on cognitive function (Alves et al., 2014; Ma, Le Mare, & Gurd, 2015; Tsukamoto et al., 2016; van Dongen et al., 2016). Some of these studies further demonstrated that HIIE may be a feasible approach that fits in with real-life settings (Costigan, Eather, Plotnikoff, Hillman, & Lubans, 2016; Ma et al., 2015). To further determine the effect of HIIE versus MICE on cognition, Tsukamoto et al. (2016) adopted a HIIE protocol with four 4-min high-intensity cycling bouts separated by 3-min active breaks, and indicated that RT interference score (color-word condition – neutral condition) during Stroop task was reduced immediately following both MICE and HIIE compared to a pretest baseline assessment. Notably, such a positive effect was sustained for only 30 minutes following HIIE, suggesting that acute MICE and HIIE may have both similar and differential benefits on inhibitory control. However, the interpretation of these findings is limited by the absence of a non-exercise comparison condition. A more recent study included an inactive control condition and compared the effect of 9 minutes of HIIE and 20 minutes of MICE on inhibitory control (Kao et al., 2017). With smaller amounts of energy expenditure and time commitment, the results replicated Tsukamoto's findings in that HIIE resulted in additional improvements in inhibitory control compared to MICE. Taken together, these

findings shed light on the possible differential effects of MICE and HIIE on cognitive performance, suggesting that HIIE may be a better option for gaining the transient beneficial effects on cognition. However, further investigation into these differential effects on other aspects of cognition, such as working memory and long-term memory, is currently lacking.

The examination into the differential acute effects of MICE and HIIE on cognition may be achieved more precisely using event-related potentials (ERPs). The high temporal resolution of ERP offers a comprehensive means for assessing the dynamics of information processing related to cognitive function. This technique has been widely used to investigate alterations in neuroelectric activity underlying exercise-induced acute changes in cognitive performance during modified flanker tasks (Drollette et al., 2014; Hillman et al., 2009; Hillman, Snook, & Jerome, 2003; O'Leary et al., 2011; Pontifex et al., 2013). The flanker paradigm is a common tool to assess inhibition, which imposes variable amounts of inhibitory control through manipulating the congruency of target-noise arrays (Eriksen & Eriksen, 1974). The P3 potential, can be easily collected during flanker tasks and is one of the most investigated components of an ERP that reflects information processing during cognitive operations. The amplitude and latency of the P3 are thought to reflect attentional resource allocation during stimulus engagement and information processing speed, respectively (Polich, 2007). Previous studies utilizing ERPs have observed improved flanker task performance, accompanied by larger or maintained P3 amplitude and shorter P3 latency

following acute MICE compared to control conditions, suggesting that acute MICE not only improved behavioral indices of inhibitory control but also modulate the underlying brain implementation characterized by increased attentional resource allocation and faster cognitive processing speed during stimulus engagement (Drollette et al., 2014; Hillman et al., 2009; O'Leary et al., 2011; Pontifex, Parks, Henning, & Kamijo, 2015; Pontifex et al., 2013). Prior investigations into the modulatory effect of exercise intensity on the relationship between continuous exercise and cognition have indicated an inverted U-shaped relationship of exercise intensity on the P3 amplitude (Kamijo et al., 2007). Specifically, Kamijo et al. (2007) indicated that continuous exercise at light- and moderate-intensities resulted in increased P3 amplitude during a flanker task compared to high-intensity continuous exercise and baseline condition, which did not differ from each other. A similar curvilinear relationship was observed in a recent study indicating increased P3 amplitude following MICE, but decreased P3 amplitude following HIIE, compared to inactive control condition. Interestingly, the HIIE-induced decreases in P3 amplitude might not necessarily indicate poorer cognition because it was paired with improved behavioral performance and enhanced speed of stimulus identification, as indexed by reduced P3 latency (Kao et al., 2017). Such uncoupled behavioral and neuroelectrical findings are not uncommon in the literature, and were interpreted to suggest enhanced neural efficiency in response to exercise (Kao et al., 2017; Malinowski, 2013; Moore, Gruber, Derose, & Malinowski, 2012; Pontifex et al., 2011; Voss

et al., 2011). Nevertheless, these differential effects of acute MICE and HIIE on uncoupled behavioral performance with neuroelectric mechanisms warrant further replication.

The contingent negative variation (CNV) is another ERP component elicited during the preparatory interval between a warning signal (S1) and an imperative stimulus (S2) that requires a response, and is thought to reflect sensory, cognitive, and motor preparation processes (Walter, Cooper, Aldridge, McCallum, & Winter, 1964). CNV can be further dissociated into an initial component (iCNV) following S1 reflecting stimulus orientation and a terminal component (tCNV) preceding S2 indicating stimulus anticipation or response preparation (Loveless & Sanford, 1974; Weerts & Lang, 1973). Results have indicated that CNV modulation during working memory operations is a possible indicator reflecting the adaptation of cognitive functioning related to cardiovascular fitness and a long-term physical activity intervention (Kamijo, O'Leary, Pontifex, Themanson, & Hillman, 2010; Kamijo et al., 2011). Prior studies have also investigated the modulation of CNV activity in response to acute exercise, with inconsistent findings in different populations. For instance, Chaung, Tsai, Chang, Huang, and Hung (2015) indicated MICE-induced improvements of performance during an inhibitory control task in ADHD children, as indexed by shorter RT and smaller tCNV amplitude. These findings suggested that an acute bout of MICE may optimize the response preparation in individuals with ADHD, who typically have difficulties in deliberately inhibiting dominant, automatic, or prepotent responses. However, such effects of

CNV modulation in response to MICE were not observed in adolescents without ADHD (Stroth et al., 2009). To further investigate the effect of exercise parameters on the relationship between acute exercise and cognition, Kamijo et al. (2004) assessed CNV amplitude during a simple RT task following acute bouts of duration-matched low-, moderate-, and high-intensity continuous exercise. The results indicated that MICE resulted in the largest amplitude for both iCNV and tCNV relative to exercise at low- and high-intensities. These findings provided evidence to substantiate the inverted-U shaped relationship between exercise intensity and neuroelectric activity. Taken together, the current literature suggests that exercise-related effects on processing underlying working memory may be detectable by the modulation of CNV (Kamijo et al., 2010; Kamijo et al., 2011). Further, CNV amplitude may reflect the differential effects of acute exercise at different intensities on cognition. However, no study has assessed CNV to investigate the neuroelectric mechanisms of cognitive preparation underlying acute changes in working memory performance following MICE and HIIE.

Rationale and Study Purpose

Despite convergent evidence suggesting a positive association between exercise intensity and cognitive performance during the recovery period following exercise, more studies are warranted to corroborate this intensity-dependent effect on cognition using a HIIE protocol, whose effectiveness and feasibility appears promising. In addition, given that prior

research has focused on the differential effects of MICE and HIIE on inhibitory control, investigations are warranted to determine the MICE- versus HIIE-induced modulations of behavioral and neuroelectric indices during other aspects of cognitive processes, such as working memory and long-term memory. Accordingly, the purpose of this study was to understand the effects of acute bouts of MICE and HIIE on multiple aspects of cognition in a young adult population. Inhibitory control, working memory, and long-term memory were assessed by a modified flanker task, a Sternberg task, and a free recall task, respectively. ERP was measured to understand the neuroelectric mechanisms underlying acute exercise-induced changes in cognitive processes related to inhibitory control and working memory operations.

To date, although accumulating evidence has suggested a role of acute exercise for the promotion of cognitive health, little is known regarding how to optimize acute exercise prescriptions in order to maximize its beneficial effects. The current literature provides the rationale for investigating the differential effects of acute MICE and HIIE on various domains of cognition, given that prior research indicates that the relationship between acute exercise and cognitive performance may be moderated by exercise intensity. Therefore, examining how these two modes of exercise may exert transient influences on inhibitory control, working memory, and long-term memory, which are critical cognitive functions in everyday life, is warranted.

Aims and Hypotheses

Aim 1: To replicate the observed effects of acute MICE on inhibitory control, working memory, and long-term memory in young adults (Coles &Tomporowski, 2008; Kamijo et al., 2007; O'Leary et al., 2011; Roig et al., 2013).

Hypothesis 1: Following a single bout of MICE, the performance during all three cognitive tasks was predicted to improve compared to the inactive control condition. These improvements were likely to be larger on task conditions requiring greater amounts of inhibitory control and working memory (O'Leary et al., 2010; Weng et al., 2015). The improvements in long-term memory were likely to be selective in the primacy and recency position in the free recall list (Coles & Tomporowski, 2008).

Aim 2: To investigate the effects of acute HIIE on inhibitory control, working memory, and long-term memory relative to MICE and inactive control conditions.

Hypothesis 2: Following a single bout of HIIE, the performance on all three cognitive tasks was predicted to improve compared to the inactive control condition. The improvements following a single bout of HIIE were hypothesized to be larger compared to a single bout of MICE (Chang et al., 2012; Ferris et al., 2007; Winter et al., 2007).

Aim 3: To investigate the effects of acute MICE on neuroelectric mechanisms underlying performance during inhibitory control and working memory tasks.

Hypothesis 3: A single bout of MICE was predicted to increase the amplitude of P3 and decrease the latency of P3 during the flanker task (Hillman et al., 2003; Kamijo et al., 2007; O'Leary et al., 2010). A single bout of MICE was also predicted to increase iCNV and tCNV amplitude during the Sternberg task (Kamijo et al., 2004).

Aim 4: To investigate the effects of acute HIIE on neuroelectric mechanisms during tasks assessing inhibitory control and working memory and to investigate whether these effects differed from those induced by MICE.

Hypothesis 4: Following a single bout of HIIE, P3 amplitude during the flanker task was predicted to show no change compared to the inactive control, and decrease compared to MICE (Kamijo et al., 2007). HIIE was predicted to show reduced P3 latency compared to the inactive control (Kao et al., 2017). Following a single bout of HIIE, iCNV and tCNV amplitude during the Sternberg task was predicted to show no change compared to the inactive control condition and decrease compared to the MICE (Kamijo et al., 2004).

CHAPTER 2: REVIEW OF LITERATURE

To better understand why acute bouts of MICE and HIIE may exert differential effects on inhibitory control, working memory, and long-term memory, it is necessary to review the existing literature on these three aspects of cognition, their neuroelectric indices, and MICE- and HIIE-induced changes in cognitive function. First, the role of acute exercise to counteract the consequence of physical inactivity is discussed to provide an overview for the significance of acute exercise to public health. Second, the literature on the three aspects of cognition, and their relationships with neuroelectric indices, is reviewed to provide a background for how to investigate these domains of cognition in response to acute exercise. Finally, the existing literature on the effects of acute MICE and HIIE on behavioral and neuroelectric indices of inhibitory control, working memory, and long-term memory processes is examined to provide justification for the present investigation.

Physical Activity and Acute Exercise

Physical activity is defined as any bodily movement produced by skeletal muscles that results in energy expenditure (Caspersen, Powell, &Christenson, 1985). Although it has been widely accepted for many years that physical activity promotes various health outcomes (Department of Health and Human Services, 1996), physical inactivity has prevailed in the past decades (Carlson, Densmore, Fulton, Yore, & Kohl, 2009; Troiano et al., 2008). Such a prevalence of physical inactivity may be attributed to the increasing accessibility of

technology in progressively industrialized society (Ng &Popkin, 2012), leading to decreases in occupation-related and leisure time physical activity (Church et al., 2011; Crespo, Keteyian, Heath, & Sempos, 1996). According to the most recent statistics, 23% of adults and 80% of adolescents around the world were considered physically inactive (World Health Organization, 2010c, 2010d). In the United States, 35.5% of adults and 82.9% of adolescents failed to achieve daily-recommended levels of physical activity in 2011 (Centers for Disease Control and Prevention, 2010). Despite governmental agencies promoting physical activity, a continued unhealthy trend was reported in 2014, with 48.4% of adults and 72.9% of adolescents failing to meet daily recommendations for physical activity (Centers for Disease Control and Prevention, 2014).

The secular trend of physical inactivity is a public health concern because it has been identified as the fourth leading risk factor for multiple causes of death, chronic morbidity, and disability (World Health Organization, 2010b). Research has shown that an insufficient amount of physical activity is known to increase the risk of non-communicable diseases (e.g., cardiovascular disease, diabetes, cancer) and shorten life expectancy (Lee et al., 2012). In contrast, participation in physical activity has been associated with the prevention of several chronic diseases and premature death (Li & Siegrist, 2012; Warburton, Nicol, & Bredin, 2006). Besides physical health, physical activity has important implications for mental health, such as depression (Conn, 2011), anxiety (Petruzzello, Landers, Hatfield, Kubitz, & Salazar,

1991), and quality of life (Bize, Johnson, & Plotnikoff, 2007). More importantly, emerging evidence has suggested that physical activity may be associated with structural and functional changes in brain, in turn leading to enhanced brain and cognitive health, particularly important for the optimization of cognitive development and the attenuation of age-related cognitive decline (Erickson, Hillman, & Kramer, 2015; Hillman et al., 2008). Given the importance of physical activity to public health, research has aimed to determine means for increasing physical activity in order to counteract the development of physical inactivity and its consequences on health outcomes (Heath et al., 2012).Of the various means, acute exercise has been proposed as a promising approach for increasing physical activity. Acute exercise refers to a short bout of physical activity with prescribed exercise mode, intensity, and duration. The current guidelines suggest that multiple short bouts of physical activities, at least 10 minutes each, spread throughout the week could be accumulated to meet the weekly recommendation (World Health Organization, 2010a). In addition to physical activity volume, evidence has suggested that one single bout of acute exercise could cause short-term positive effects on health outcomes, such as insulin resistance (Henriksen, 2002), affective response (Reed & Ones, 2006), anxiety (Petruzzello et al., 1991), cigarette craving and tobacco withdrawal symptoms (Roberts, Maddison, Simpson, Bullen, & Prapavessis, 2012), and cognition (Chang et al., 2012). Among these exercise-induced transient benefits, the relationship between acute exercise and cognition is of interest in the current investigation.

Thus, the following literature review will focus on the effects of acute exercise on various domains of cognition, including cognitive control and memory.

Cognitive Control

Cognitive control (also known as 'executive control') refers to a collection of cognitive operations involved in the recruitment, modulation, evaluation, and disengagement of top-down control processes in response to current cognitive demands (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Norman & Shallice, 1986). These processes allow for the selection, scheduling, coordination, and maintenance of computational processes, which optimize the stimulus identification, response selection, and action production that achieve goal-directed behavior (Meyer & Kieras, 1997). Convergent evidence from cognitive neuroscience has suggested that cognitive control processes are mediated by the prefrontal cortex (PFC), which is an interconnected brain region that synthesizes the diverse range of information and exerts top-down influences on a wide range of brain processes through its connectivity with sensory and motor systems and subcortical structures (Miller, 2000). Within this neural network, the lateral PFC and anterior cingulate cortex (ACC) have been identified as two closely interacting, but anatomically dissociable components, which are responsible for the dynamic implementation of cognitive control (Badre & Wagner, 2004; MacDonald, Cohen, Stenger, & Carter, 2000). The lateral PFC acts as a hub, enabling flexible top-down implementations of control process through shifting of its connectivity

with various task-relevant regions (Cole, Yarkoni, Repovš, Anticevic, & Braver, 2012; Koechlin, Ody, & Kouneiher, 2003), whereas activation in the ACC is associated with conflict monitoring (Botvinick et al., 2001; Ridderinkhof, Ullsperger, & Crone, 2004). Cognitive control has also been described by a dual-mechanisms framework, which suggests two temporarily dissociable components within the lateral PFC – proactive control and reactive control (Braver, 2012). Proactive control has been described as active maintenance of representations for continuous adjustments and biased anticipation toward task-relevant information, which optimizes the completion of a goal-directed behavior and is associated with extended activation of the lateral PFC (Cohen et al., 1997). On the other hand, reactive control is driven by a bottom-up mechanism in which task goals are reactivated each time as needed, resulting in transient activation in the lateral PFC and other brain regions such as the ACC (Botvinick et al., 2001; Braver, 2012). The core cognitive processes underlying cognitive control consist of inhibitory control, working memory, and cognitive flexibility (Diamond, 2013; Miyake et al., 2000). Of these processes, inhibitory control and working memory have been most studied in the acute exercise literature (Hillman et al., 2009; Hillman et al., 2003; McMorris et al., 2011; O'Leary et al., 2011; Pontifex et al., 2009, 2013). Inhibitory control refers to the ability to regulate impulse and interference at perceptual, cognitive, and behavioral levels (Diamond, 2013). This ability is dissociable into two conceptually distinct but statistically correlated behavioral interference control components

and one completely independent cognitive inhibition component (Friedman & Miyake, 2004). These inhibition-related functions are central to selective, focused, and sustained attention, and allow control over impulse action (Diamond, 2013). Among various cognitive tasks assessing inhibitory control (Hallett, 1978; Li, Huang, Constable, & Sinha, 2006; Simmonds, Pekar, & Mostofsky, 2008; Simon & Wolf, 1963; Stroop, 1935), the Eriksen flanker task (and modified versions of the task) has been widely used to investigate the relationship between acute exercise and inhibitory control (Drollette et al., 2014; Hillman et al., 2009; Hillman et al., 2003; O'Leary et al., 2011; Pontifex et al., 2013). The flanker task requires the discrimination of a centrally presented target stimulus amid lateral flanking stimuli, through manipulating the congruency of target-noise arrays that impose variable amounts of inhibitory control (Eriksen & Eriksen, 1974). In the incongruent array (e.g., <<><< or HHSHH), the target and flanking stimuli are mapped to opposing action-schemas (Eriksen & Schultz, 1979), resulting in longer and less accurate response relative to the congruent array (e.g., <<<<< or HHHHH), where less interference occurs due to identical directionality of target and flanking stimuli (Eriksen & Schultz, 1979). Given that the incongruent array simultaneously results in correct (elicited by the target) and incorrect (elicited by the flanking stimuli) response activations before the completion of stimulus evaluation, greater amounts of interference control are required to inhibit the incorrect and execute the correct response (Ridderinkhof, 2002).

Working memory is another sub-discipline of cognitive control that refers to the ability of concurrent maintenance and manipulation of information (Baddeley, 1992). This ability consists of a central executive system and two independent slave sub-systems: the phonological loop and the visuospatial sketchpad (Baddeley, 1992). The coordination of these systems supports inhibitory control, selective and focused attention, language comprehension, learning, and reasoning (Baddeley, 1992; Diamond, 2013). Research has shown that the PFC is activated by tasks that rely on working memory (Cohen et al., 1994), particularly the middle frontal gyrus (McCarthy et al., 1996). This PFC activity and its connectivity with parietal and perceptual regions also play a role in working memory (Cohen et al., 1997; Courtney, Ungerleider, Keil, & Haxby, 1997). PFC activity has been associated with both maintenance and manipulation aspects of working memory (D'Esposito, Postle, Ballard, & Lease, 1999), and is sensitive to working memory load (Barch et al., 1997; Rypma, Prabhakaran, Desmond, Glover, & Gabrieli, 1999). Although both working memory maintenance and manipulation have been examined in response to acute exercise, existing findings suggest more consistent positive effects on working memory maintenance (Hsieh et al., 2015; Hwang et al., 2016; Pontifex et al., 2009). The Sternberg task (Sternberg, 1966), is one of the commonly used paradigms in acute exercise research to assess working memory maintenance (Hsieh et al., 2015; Pontifex et al., 2009). This task employs a visual S1-S2 paradigm in which a warning signal (S1) is presented followed by an imperative stimulus (S2)

that requires a response. In this task, warning signals consist of a letter or digit array, which requires individuals to remember for later recall. Imperative signals serve as a probe, which requires a response to determine whether they were present or absent in the preceding warning signal. This paradigm allows evaluation of memory encoding following warning signals and memory maintenance, search, and match following imperative signals (Veltman, Rombouts, & Dolan, 2003). The load of working memory maintenance can be manipulated through the varying length of arrays presented during warning signals, with greater working memory maintenance being required by longer array length, as reflected by decreased task performance such as longer RT (Pontifex et al., 2009; Veltman et al., 2003).

Long-Term Memory

Under the overarching set of the memory system, long term memory is a core component that is divided into two major sub-systems: non-declarative memory and declarative memory (Gazzaniga, Ivry, & Mangun, 2014). The former indicates memory without conscious awareness encompassing procedural memory, priming, classical conditioning, and non-associative learning (Squire, 1992a). The latter indicates memory with conscious awareness, including episodic and semantic memory, with the episodic memory being specific and context-dependent and semantic memory being general and context-independent (Tulving, 1972). Memory process is temporally dissociable according to three major stages, including encoding, consolidation, and retrieval (Gazzaniga et al., 2014).

The encoding of memory creates memory traces through the filtering out of unnecessary perceptual stimuli while keeping useful information for further processing. Memory consolidation refers to processing in which temporally encoded information stabilizes to create a stronger representation for further storage. Memory retrieval describes the processing involved in accessing stored information for creating a conscious representation or executing learned mental operations and behavior (Gazzaniga et al., 2014). The anatomy of these processes during declarative memory has been associated with a widely distributed network of brain regions (Buckner, Kelley, & Petersen, 1999), including the prefrontal, temporal, parietal, occipital, and cerebellar cortices as well as the hippocampal formation (Andreasen et al., 1999; Buckner, Logan, Donaldson, & Wheeler, 2000; Demb et al., 1995; Dolan & Fletcher, 1997; LaBar & Phelps, 1998; Murray & Ranganath, 2007; Nyberg, Mclntosh, Houle, Nilsson, & Tulving, 1996; Wagner, Desmond, Glover, & Gabrieli, 1998). Within this neural network, the hippocampus is particularly crucial for memory encoding, consolidation, and retrieval (Alvarez & Squire, 1994; Carr, Jadhav, & Frank, 2011; Eldridge, Knowlton, Furmanski, Bookheimer, & Engel, 2000; Manns, Hopkins, & Squire, 2003; Ranganath et al., 2004; Squire, 1992b). In addition, the PFC and parietal cortex also contribute to the processing of memory encoding and retrieval (Cabeza, 2008; Daselaar et al., 2009; Leshikar & Duarte, 2012; Nyberg, Cabeza, & Tulving, 1996). On the other hand, non-declarative

memory is associated with activity in the basal ganglia, cerebellum, amygdala, and reflex pathways (Seger & Spiering, 2011; Squire & Zola, 1996; Yin & Knowlton, 2006).

Considerable evidence suggests that memory encoding, consolidation, and retrieval are modulated by changes in arousal and endogenous stress hormones (Cahill & Alkire, 2003; Kuhlmann, Kirschbaum, & Wolf, 2005; Kuhlmann &Wolf, 2006; LaBar & Phelps, 1998). Given that these changes correspond with the psychological and physiological responses to acute bouts of exercise (Ekkekakis & Petruzzello, 1999; Vega et al., 2006; Winter et al., 2007), research has aimed to investigate the effects of acute exercise on memory (Roig et al., 2013). In the acute exercise literature, the free recall paradigm has been used to evaluate the exercise-induced effects on the declarative aspect of long-term memory (Coles & Tomporowski, 2008; Pesce et al., 2009). In this task, following the study of a list of items (i.e., nouns), an immediate spoken or written recall of the studied items in any order is prompted. Subsequently, a distraction period is interpolated between the final studied item and the start of the delayed recall. The recall periods typically last a few minutes. The number of correct items recalled during the immediate and delayed recall periods served as an index of free recall memory. Further investigation into free recall tasks indicated primacy and recency effects as reflected by the disproportionally higher probability of corrected recall for the initial and terminal items in the study list compared to those in the middle. The primacy

effect is believed to reflect long-term memory, whereas the recency effect may be indicative of short-term memory during the immediate recall task (Murdock, 1962).

Neuroelectric Indices of Cognition

The examination into cognition beyond overt behavioral performance during task operations may be achieved more precisely using electroencephalogram (EEG). EEG is a digitalized and graphic representation of the difference in voltage between two scalp locations over time (Olejniczak, 2006). EEG signals are generated by summed activity of post-synaptic potentials when a large number of pyramidal neurons simultaneously fire in similar orientation (Speckman, Elger, & Altrup, 1993). The average of EEG segments time-locked to specific internal or external events is defined as event-related potentials (ERPs). ERPs refer to manifestations of neuroelectric activities that occur in response to, or in preparation for, a stimulus or response (Fabiani, Gratton, & Federmeier, 2007). The stimulus-locked ERP consist of a series of positive (P) and negative (N) peaks, which are subjected to a variety of measurement operations (Fabiani et al., 2007). These peaks define a number of components by assessing the amplitude of the peaks in microvolts and their latency in milliseconds. Such high temporal resolution of ERP offers a comprehensive means for assessing the dynamics of obligatory responses to perceived stimuli (exogenous) and endogenous processing elicited in the absence of an external eliciting event (Fabiani et al., 2007).

The P3 (P3b) is a positive-going deflection occurring approximately 300 to 800 milliseconds after stimulus presentation. This positive component is believed to be generated, in part, by the medial temporal-parietal junction (Knight, Scabini, Woods, & Clayworth, 1989; Smith et al., 1990; Verleger, Heide, Butt, & Kompf, 1994), with a topographical distribution centered at parietal electrode sites (Polich & Kok, 1995). P3 is one of the major endogenous components that reflects the updating of a mental representation as the result of incoming stimuli (Donchin, 1981). Based on the context-updating theory, studies utilizing dual-task paradigms to test the association between P3 and resource allocation have consistently found that P3 amplitude in a secondary task decreases when the difficulty of the primary task increased (Isreal, Chesney, Wickens, & Donchin, 1980; Kramer, Wickens, & Donchin, 1985; Wickens, Kramer, Vanasse, & Donchin, 1983). These findings were interpreted to suggest that P3 amplitude is a reflection of attentional resource allocation (Polich, 2007). On the other hand, P3 latency is believed to index speed of information processing, particularly processing related to stimulus classification and evaluation (Kutas, McCarthy, & Donchin, 1977), suggesting that P3 latency may play a role in bridging perceptual and response processing (Verleger, Jaskowski, & Wascher, 2005). P3 has been widely used in research of the effect of physical activity on cognition (Hillman, Kamijo, & Scudder, 2011), given that it may be more sensitive to the exercise-induced acute effects on cognition than overt behavioral responses (Hillman et al., 2003). Additionally, the P3

amplitude has been found to associate with acute exercise intensity in an inverted-U fashion (Kamijo et al., 2004, 2007), which makes P3 a useful neuroelectric index to investigate the cognitive effects of acute exercise characterized across different intensities.

Contingent negative variation (CNV) is a response-locked ERP component that stems from a cortico-striatal-thalamo-cortical circuit (Meck, Penney, & Pouthas, 2008), including supplementary motor area, somatomotor cortex, cingulate cortex, thalamus, and basal ganglia (Bares & Rektor, 2001; Cui et al., 2000; Nagai et al., 2004). CNV is a slow negative wave elicited during the preparatory interval between a warning signal (S1) and an imperative stimulus (S2) that requires a response (Walter et al., 1964), and is thought to reflect expectancy, mental priming, association, and attention when individual's behavior is directed toward a planned action in response to a sequence of events (Donchin, Ritter, & McCallum, 1978; Rohrbaugh & Anthony, 1983). CNV is dissociable into two distinct components, an initial wave following S1 with a frontocentral distribution and a terminal wave following S2 located pre-centrally (Gaillard, 1976). It is believed that the initial CNV (iCNV) is associated with orienting to a warning signal, whereas the terminal CNV (tCNV) is related to stimulus anticipation or response preparation (Loveless & Sanford, 1974; Weerts & Lang, 1973). Studies have indicated the association of CNV with cardiorespiratory fitness and physical activity, particularly during working memory tasks (Hillman, Weiss, Hagberg, & Hatfield, 2002; Kamijo et al., 2011, 2010). Further, the acute exercise literature has demonstrated an

inverted-U relationship between exercise intensity and both iCNV and tCNV amplitude (Kamijo et al, 2004). Taken together, these findings suggested that CNV modulation is a relevant neuroelectric index of cognition in relation to exercise and may serve as a tool to understand the transient effects of exercise on preparatory processes underlying cognitive performance.

Acute Continuous Exercise, Cognitive Control, and Memory

The current literature suggests that acute exercise has positive effects on cognitive outcomes, with disproportionally larger benefits when specific exercise protocols are used and particular domains of cognition are assessed (Chang et al., 2012). For the most part, MICE has been considered one of the most effective types of physical activity to facilitate cognition (Chang et al., 2012). This type of acute exercise typically consists of 20-30 minutes of physical activity at moderate intensity, and had beneficial effects on inhibitory control, with disproportionally larger benefits when greater amounts of inhibitory control are required (Hillman et al., 2009; Kamijo et al., 2009, 2007; O'Leary et al., 2011; Pontifex et al., 2013). Further, such exercise-induced positive effects on inhibitory control may be greater in response to continuous exercise at higher intensities (Ferris et al., 2007). However, some studies revealed no effect of acute MICE on performance during inhibitory control tasks (Gothe et al., 2013; Hillman et al., 2003; Themanson & Hillman, 2006; Weng et al., 2015). In addition to differences in experimental design, this discrepancy was interpreted to suggest

that the effects of acute MICE may not be as apparent in behavioral measures of performance compared to changes in brain function (Weng et al., 2015). This explanation is supported by Hillman et al. (2003) who indicated unchanged behavioral performance paralleled with larger P3 amplitude and decreased P3 latency interference (incompatible – neutral condition during a flanker paradigm) following acute MICE compared to a control condition. Although Themanson and Hillman (2006) reported no effect of acute MICE on flanker task performance and ERP components, P3 was not examined in that study. Collectively, these findings suggest that P3 may be a sensitive neuroelectric index to reflect the transient effect of MICE on inhibitory control. In addition, research has proposed an inverted-U shaped relationship between P3 amplitude and exercise intensity, with MICE resulting in the largest increase in P3 amplitude (Kamijo et al., 2007). Through further investigations into acute MICE, studies have indicated increased performance in a flanker task accompanied by larger P3 amplitude or shorter P3 latency, suggesting that acute MICE may facilitate inhibitory control and its underlying brain function as characterized by increased attentional resource allocation and faster information processing speed (Hillman et al., 2009; Kamijo et al., 2009, 2007; O'Leary et al., 2011; Pontifex et al., 2013).

In addition to inhibitory control, existing evidence has suggested that working memory may be affected by acute MICE (McMorris et al., 2011; Roig et al., 2013). Research examining working memory in response to a single bout of MICE has revealed improved

performance during tasks requiring variable amounts of working memory (Chen et al., 2014; Hogan et al., 2013), with particularly significant benefits for individuals with lower working memory capacity (Sibley & Beilock, 2007) and under task conditions requiring greater demands for working memory (Weng et al., 2015). Studies also indicated enhanced working memory, particularly for maintenance, following acute bouts of high-intensity continuous exercise (Hwang, Castelli et al., 2016; Pontifex et al., 2009). Specifically, Pontifex et al. (2009) investigated the effects of high-intensity continuous exercise and resistance exercise on working memory using a modified Sternberg task, and indicated improved RT following high-intensity continuous exercise compared to baseline. Additionally, the beneficial effect of high-intensity continuous exercise on RT was disproportionally larger in the task condition requiring a larger amount of temporal information storage. Similar positive effects following an acute bout of high-intensity continuous exercise were observed for performance during a delayed matching task (Hwang, Castelli, et al., 2016). Collectively, existing evidence suggests that acute MICE has beneficial effects on the manipulation aspect of working memory, and continuous exercise at higher intensity was found to improve the maintenance aspect of working memory. However, neuroelectric underpinnings of such beneficial effects on the behavioral indices of working memory have not yet be explored.

The positive effect of acute continuous exercise on long-term memory has also been documented (Roig et al., 2013). Coles and Tomporowski (2008) examined vocabulary free

recall memory before and after an acute bout of 40-minnute MICE in young adults, and indicated that MICE maintained free recall memory in the primacy and recency portions while memory retention decreased following control conditions. Labban and Etnier (2011) indicated a similar positive effect on delayed memory only when exercise was performed prior to, but not after, memory encoding. In children, acute bouts of physical activity (i.e., circuit activities, team exercise, PE class) were found to facilitate learning and delayed recall memory compared to inactive control conditions (Etnier et al., 2014; Pesce et al., 2009). Hötting et al. (2016) further examined the modulatory influences of exercise intensity on the process of memory consolidation in response to acute exercise. Their findings showed that only an acute bout of 20-min high-intensity (80% HR_{max}), but not low-intensity (< 57% HR_{max}), continuous exercise enhanced memory retention after a delay of 24 hours. In addition to declarative memory, a series of studies has demonstrated the facilitating effects of acute exercise on non-declarative memory such as procedural motor memory (Roig et al., 2012; Skriver et al., 2014; Thomas, Beck, et al., 2016; Thomas, Johnsen, et al., 2016). Thomas, Johnsen, et al. (2016) found that 20 minutes of both low- (45% HR_{max}) and high-intensity (90% HR_{max}) continuous exercise following motor skill acquisition improved memory retention at a delay of 7 days. Their results also showed that high-intensity continuous exercise exhibited additional improvements in memory retention after a one-day delay and a larger enhancement of memory retention after a delay of 7 days compared to low-intensity

continuous exercise. Further, research indicated that exercise performed prior to and after motor memory acquisition facilitated memory retention (Roig et al., 2012; Skriver et al., 2014), with selective facilitation when the temporal proximity of exercise was close to memory acquisition (Thomas, Beck, et al., 2016). Taken together, these findings suggest that acute continuous exercise may facilitate long-term memory through enhanced processing related to memory encoding and consolidation in a time-dependent fashion. Importantly, exercise intensity may play a role in maximizing this exercise-induced facilitation on memory processes.

Acute HIIE, Cognitive Control, and Memory

Besides traditional continuous exercise, emerging evidence has indicated that acute bouts of HIIE may be a feasible approach for facilitating cognitive functioning. HIIE is defined as repeated bouts of short to moderate duration exercise at an intensity that is greater than the anaerobic threshold, separated by inactive breaks or light recovery exercise (Gibala & McGee, 2008; Laursen & Jenkins, 2002; Weston, Wisløff, & Coombes, 2014). Although HIIE was originally developed from the field of athletic training (Laursen & Jenkins, 2002), there is an increasing interest in the application of HIIE due to its possible impact on public health (Biddle & Batterham, 2015), as research has indicated various health benefits of participation in HIIE (Costigan, Eather, Plotnikoff, Taaffe, & Lubans, 2015; Gibala, Gillen, & Percival, 2014; Weston et al., 2014; Whyte, Gill, & Cathcart, 2010). In addition to physical

health, studies have shown positive effects of chronic participation in HIIE on cognition (Costigan et al., 2016; Drigny et al., 2014).

Similar, yet transient, cognitive benefits were found through engagement in acute bouts of HIIE (Alves et al., 2014; Kao et al., 2017; Tsukamoto et al., 2016; van Dongen et al., 2016). Tsukamoto et al. (2016) adopted a HIIE protocol with four 4-min high-intensity cycling bouts interspersed by 3-min active recovery periods, and indicated decreased RT interference scores during a Stroop task immediately and 30 min following HIIE compared to the baseline level. With a smaller volume dose, Kao et al. (2017) indicated that three sets of high-intensity running for 1.5 min (90% HR_{max}) improved overall RT and response accuracy under a condition requiring upregulation of inhibitory control. Further, Alves et al. (2014) indicated improved inhibitory control following an acute bout of HIIE consisting of ten 1-min high-intensity cycling bouts separated by 1-min active recovery period while HIIE did not affect maintenance aspect of working memory, as indexed by unchanged performance during a digit span test. However, it should be noted that the absence of HIIE-induced effects on performance during the digit span test might be due to insufficient task difficulty as well as a lack of RT measures, which are considered more sensitive to modulations in cognitive processes in adults (Davidson, Amso, Anderson, & Diamond, 2006), particularly exercise-induced modulations of processing related to working memory (McMorris et al., 2011). Collectively, these findings suggest that HIIE may result in a transient facilitation of

the inhibitory aspect of cognitive control. On the other hand, the effect of acute HIIE on the working memory would require further investigation to measure RT during tasks that tap greater amounts of working memory.

Evidence of the relationship between acute HIIE and long-term memory is limited. A recent study adopted a HIIE protocol with four bouts of 4-min high-intensity cycling, separated by 3-min active recovery immediate following or at a 4-hour delay after memory encoding (van Dongen et al., 2016). The findings revealed that performance in a cued recall task at 48 hours after initial encoding was greater when HIIE was performed at 4-hour after initial encoding compared to a control condition. Further, the enhanced delayed recall memory was paralleled with increased hippocampal activity during correct memory retrieval. However, no such positive effects were observed when HIIE was immediately performed following initial encoding. Although this study provides initial evidence that properly timed HIIE may benefit mnemonic processes related to consolidation and retrieval (van Dongen et al., 2016), more research is needed to advance the understanding of the effect of HIIE on other memory-related processes such as memory encoding during a free recall task.

Gaps in the Literature

Despite the fact that literature has indicated the beneficial effects of acute MICE and HIIE on cognition, several knowledge gaps exist. First, although prior research has demonstrated the effects of MICE on ERP indices of inhibitory control tasks (i.e., flanker

tasks), the neuroelectric mechanisms underlying the exercise-induced changes in working memory performance have not yet been investigated. For instance, given the significance of CNV to preparatory processing during working memory tasks (Kamijo et al., 2010; Kamijo et al., 2011), the examination into CNV may provide new insight into the effects of acute exercise on working memory. Secondly, comparison between acute MICE and HIIE on their effectiveness for facilitating cognition is limited in the existing literature. To date, only two studies exist that compared the effects of acute MICE and HIIE on inhibitory control (Kao et al., 2017; Tsukamoto et al., 2016). Tsukamoto and colleagues found that four bouts of 4-min high-intensity cycling with a total exercise duration of 40 minutes is as effective as 40 minutes of MICE in facilitating inhibitory control as indexed by a reduced RT interference score in Stroop task. Specifically, such a positive effect was sustained for only 30 min following HIIE, accompanied by larger and more sustained increases in serum lactate, suggesting an additional benefit on inhibitory control following HIIE compared to MICE possibly through a shift in brain metabolism from glucose to lactate (Tsukamoto et al., 2016). Further, Kao et al. (2017) advanced the understanding of the differential effects of HIIE and MICE on cognition through examining neuroelectric mechanisms underlying the process related to inhibitory control. The findings indicated improved RT during a modified flanker task following exercise, but only HIIE selectively improved response accuracy under the task condition requiring greater amounts of inhibitory control. Concurrent with these differential

behavioral outcomes, the patterns of brain function underlying cognitive performance differed following the two exercise protocols. That is, to support inhibitory control operations, MICE increased attentional resource allocation as indexed by increased P3 amplitude, while HIIE resulted in a faster speed of stimulus identification with a smaller amount of attentional engagement as indexed by decreased P3 latency and amplitude. However, it is important to note that the duration of HIIE was less than half the duration of MICE, making the differences observed following these two protocols confounded between the duration, intensity, and volume of exercise. Thus, further research employing duration-matched MICE and HIIE is warranted to corroborate and extend the previously observed differential effects of MICE and HIIE on inhibitory control and other aspects of cognition such as working memory and long-term memory.

Purpose

Given that the literature suggests possible differential effects of acute MICE and HIIE on various domains of cognition, this dissertation aimed to compare the acute effects of MICE and HIIE on three aspects of cognition in a young adult population. Inhibitory control, working memory, and long-term memory were assessed by a modified flanker task, a modified Sternberg task, and a free recall task, respectively. Further, as the differential modulations of neuroelectrical activity induced by MICE and HIIE are less known, the

present investigation employed ERPs to examine neuroelectric mechanisms underlying cognitive performance in response to acute MICE and HIIE.

Rationale

As the impact of physical inactivity on cognitive health has become a public health concern, examination into means to counteract this unhealthy trend and its consequences on cognition is necessary. Despite convergent findings indicating a beneficial effect of acute exercise on cognition, empirical evidence is lacking to determine the modulating role of exercise intensity. Given that HIIE has been found effective and feasible for facilitating cognitive function not only in the laboratory but also real-world environments, the present investigation examined post-exercise cognitive performance using HIIE as a high-intensity exercise protocol for acute exercise to compare with MICE. The results of this investigation may serve to inform the public regarding whether MICE and HIIE are both feasible modes of exercise for enhancing cognition and whether HIIE may be an alternative approach for increased cognitive facilitation.

Hypotheses

Empirical evidence has shown that inhibitory control may benefit more from acute HIIE compared to MICE (Kao et al., 2017; Ferris et al., 2007; Tsukamoto et al., 2016). This differential benefit may be manifested by differences in allocation of attentional resource and information processing speed as indexed by P3 amplitude and latency, respectively (Kamijo

et al., 2007; Kao et al., 2017; Tsukamoto et al., 2016). Working memory may benefit from both acute MICE and high-intensity exercise (Chen et al., 2014; Hogan et al., 2013; Hwang, Castelli, et al., 2016; Pontifex et al., 2009; Weng et al., 2015). Such similar effects may be manifested by preparatory processing as indexed by the amplitude of initial and terminal CNV components. Although research has shown that long-term memory benefits from both acute MICE and high-intensity exercise (Coles & Tomporowski, 2008; Etnier et al., 2014; Labban & Etnier, 2011; Pesce et al., 2009; van Dongen et al., 2016), the beneficial effect may be larger following HIIE (Hötting et al., 2016; Thomas, Johnsen et al., 2016; Winter et al., 2007). All in all, a meta-analysis indicated that acute bouts of exercise at high-intensity may result in larger facilitation on cognitive performance irrespective of cognitive domains during the post-exercise period compared to MICE (Chang et al., 2012). Accordingly, the first purpose of this investigation was to replicate and extend the observed effects of acute MICE on behavioral performance during tasks requiring inhibitory control, working memory, and long-term memory in young adults, relative to seated rest. It was predicted that:

- Following a single bout of MICE, the performance in all three cognitive tasks was predicted to improve compared to the inactive control condition. The improvements are predicted to be larger on task conditions requiring greater amounts of inhibitory control and working memory (O'Leary et al., 2010; Weng et al., 2015). The

improvements in long-term memory were likely to be selective in the primacy and recency position in the free recall list (Coles & Tomporowski, 2008).

The second purpose of this investigation was to determine the effects of acute HIIE on behavioral indices of cognition during the performance of tasks requiring inhibitory control, working memory, and long-term memory in young adults, relative to seated rest and MICE. It was predicted that:

- Following a single bout of HIIE, the performance on all three cognitive tasks was predicted to show improvements compared to the inactive control condition. The improvements following a single bout of HIIE were hypothesized to be larger compared to that following a single bout of MICE (Chang et al., 2012; Ferris et al., 2007; Winter et al., 2007).

The third purpose of this investigation was to examine neuroelectric indices underlying MICE-induced changes in the performance during tasks requiring inhibitory control and working memory, relative to seated rest. It was predicted that:

- A single bout of MICE was predicted to increase P3 amplitude and decrease P3 latency during the flanker task (Hillman et al., 2003; Kamijo et al., 2007; O'Leary et al., 2010). A single bout of MICE was also predicted to increase iCNV and tCNV amplitude during the Sternberg task (Kamijo et al., 2004).

The fourth purpose of this investigation was to examine neuroelectric indices underlying HIIE-induced changes in the performance during tasks requiring inhibitory control and working memory, relative to seated rest and MICE. It was predicted that:

- Following a single bout of HIIE, P3 amplitude during the flanker task was predicted to show no change compared to the inactive control, and decrease compared to MICE (Kamijo et al., 2007). HIIE was predicted to show reduced P3 latency compared to the inactive control (Kao et al., 2017). Following a single bout of HIIE, iCNV and tCNV amplitude during the Sternberg task was predicted to show no change compared to the inactive control condition and decrease compared to the MICE (Kamijo et al., 2004).

CHAPTER 3: METHODOLOGY

The effects of a single bout of MICE and HIIE on the modulations in inhibitory control, working memory, and long-term memory in healthy young adults were investigated using a sample from the East Central Illinois region. Each participant underwent a behavioral assessment during the completion of a modified flanker task, a modified Sternberg task, and a free recall task following 20 minutes of MICE, 20 minutes of HIIE, and 20 minutes of seated rest. Neuroelectric activity was assessed during the flanker and Sternberg tasks.

Participants and Recruitment

A total of 36 young adults (male = 18) between the ages of 18 and 30 years old were recruited to participate. This sample size was determined based on the *a priori* power analysis (alpha = .05, power = 0.80) to detect a small-to-moderate effect (Cohen's $d = 0.44$) of acute MICE on P3 amplitude according to previous research (O'Leary et al., 2011). All participants were asked to provide written consent in accordance with the Institutional Review Board of the University and Illinois at Urbana-Champaign. All participants were asked to complete a Health History & Demographic Questionnaire (HHDQ), Physical Activity Readiness Questionnaire (PAR-Q; Thomas, Reading, & Shephard, 1992), and Edinburgh Handedness Inventory (Oldfield, 1971).

Exclusionary Criteria

Any participant outside of the 18-30 year old age range was excluded. Any participant who was not capable of performing exercise based on PAR-Q and/or the cardiovascular section of HHDQ was excluded from the investigation for their safety. All participants had a normal or corrected-to-normal vision based on the minimal 20/20 standard in order to complete the computerized cognitive tasks. Participants were excluded from this investigation if diagnosed with any neurological disease.

Cognitive Tasks

Free Recall Task

Participants completed a visual free recall task using Neuroscan Stim2 software (Compumedics, Charlotte, NC) to assess the declarative aspect of long-term memory. This task was previously used in acute exercise research on long-term memory in young adults (Coles & Tomporowski, 2008). A set of 160 words was collected from the MRC Psycholinguistic Database (Coltheart, 1981). Words were selected based on the following criteria: number of letters (3-8), written frequency (2-60: Kucera & Francis, 1982), concreteness (500-700), familiarity (300-600), and age of acquisition (100-600). Words were then being randomly assigned to four non-overlapping word lists. In this task, following an attentional cue (i.e., "+") the 40-item word list was presented in the center of the computer screen, with each word presented individually for 5s in 48-point Arial font. A 100-s

consolidation period was provided following the last word from the list. During the consolidation period, participants were allowed, but not specifically instructed, to rehearse the list. After the consolidation period, a sentence presented on the computer screen instructed participants to recall as many words, in any order, as possible for 100s. Participants were instructed to perform a delayed recall approximately 12 min after the first recall. The number of correct words recalled in the primacy and recency position (first 10 and last 10 words) and middle position (middle 20 words) during the immediate and delayed recall tests served as indices of memory. Recalled words were considered correct with minor pronunciation errors and plural – singular substitutions ignored (Coles & Tomporowski, 2008).

Modified Flanker Task

Participants completed a modified version of the Eriksen flanker task (Eriksen & Eriksen, 1974) to assess inhibitory control. Five 3-cm tall white arrows were presented focally on a black background of a computer screen at a distance of ~1m. Congruent and incongruent trials required participants to respond based on the direction of the centrally presented arrow. Congruent trials consisted of an array of five arrows pointing in the same direction, while incongruent trials consisted of the four flanking arrows pointing in the opposite direction of the middle target arrow. After receiving task instructions, participants were given opportunities to ask questions and then practiced the task prior to the start of

testing. During 20 practice trials, the experimenter observed the participant to ensure that they understood the task and responded correctly. Subsequently, each participant performed two blocks of 100 trials with equiprobable congruency and directionality. The stimuli were presented for 100 ms with a variable inter-stimulus interval (1000, 1200, and 1400ms). Thus, each block lasted ~ 4 minutes. Participants received a brief rest between each block. Total task time duration was approximately 10 minutes. This task allowed for measures of response accuracy and response time, as well as ERP.

Modified Sternberg Task

The Sternberg paradigm was chosen as an assessment of working memory because it not only affords the examination on exercise-induced changes in working memory performance but also the underlying modulation of CNV, allowing a direct comparison with behavioral (Pontifex et al., 2009) and CNV (Kamijo et al., 2004) findings from previous studies. In this task, a warning signal (S1) required participants to encode a memory set containing an array of three, five, or seven letters, followed by a probe (S2) requiring participants to decide whether the single probe letter in S2 was present in the preceding encoded array. The memory sets were comprised of all capitalized consonants and contained no alphabetical consonant strings (e.g., JKLMN), whereas the probe letters were lowercase consonants, bilaterally flanked by one, two, or three ‘‘?’’ to match the memory set in physical size and visual content. The variation in the number of letters within each array allows for modulation

in task difficulty by changing the amounts of information temporarily maintained in mind. A probe was defined as “positive” if it was present, whereas a probe was called “negative” if it was absent. The presentation of positive and negative probes with equal probability generates an uncertain mental representation, which requires searching and matching processes in a previously presented letter array while the information from the memory set is maintained. Accordingly, the Sternberg task used in the present investigation might reflect both maintenance and manipulation aspects of working memory, with working memory maintenance possibly having a greater contribution than working memory manipulation to task performance. Stimulus-response mapping was counterbalanced, such that half of the participants were instructed to make a right thumb press for a positive probe and a left thumb press for a negative probe, whereas another half were instructed to respond in the opposite fashion. Probes presence/absence occurred with equal probability, and participants were instructed to respond to the probe letters as quickly and accurately as possible. Three blocks of 72 trials counterbalanced with 24 trials in each set size were presented focally on a computer monitor at a distance of 1m. All stimuli were 7-cm tall white letters presented on a black background for 2000 ms (encoded array) and 200 ms (probe letter), with a 1500-ms response window. A fixed inter-stimulus interval of 2500 ms was used throughout the task block with a 1700-ms inter-trial interval.

Neuroelectric Assessment

Electroencephalographic (EEG) activity was recorded from 64 electrode sites arranged according to the international 10-10 system using a Neuroscan Quick-Cap (Compumedics, Charlotte, NC). All electrodes maintained impedance < 10kΩ prior to EEG recordings. Continuous data was referenced online using a midline electrode between Cz and CPz with AFz electrode serving as the ground. Additional electrodes were placed above and below the left orbit and outer canthus of each eye to monitor electrooculographic (EOG) activity. Continuous data was digitalized at a sampling rate of 500Hz, amplified 500 times with a DC to 70Hz filter, and a 60-Hz notch filter was applied using a Neuroscan SynAmps2 amplifier. Matlab (R2014a, Mathworks Inc.), EEGLAB toolbox (version 13.4.4, Delorme & Makeig, 2004), and ERPLAB toolbox (version 4.0.2.3, Lopez-Calderon & Luck, 2014) were used for offline data processing. Continuous data was re-referenced to averaged mastoids (M1, M2), followed by Independent Component Analysis (ICA). Prototypical ICA components representing eye movements and blinks were removed after corroborating their consistency and temporal match with the ocular artifacts in continuous EEG data. EEG epochs during the flanker task were created from -100 to 1000 ms around the stimulus, baseline-corrected using -100 to 0 ms pre-stimulus period, filtered using a zero-phase shift low-pass filter at 30 Hz (12dB/oct), and then subjected to a linear-detrend procedure. EEG epochs during the Sternberg task were created from -100 to 4500 ms around S1, baseline-corrected using the

-100 to 0 ms period prior to S1 onset, and filtered using a zero-phase shift band-pass filter from 0.05 to 10 Hz (12dB/oct). Subsequently, epochs during both the flanker and Sternberg tasks were rejected if a response error occurred or an identified artifact exceeded ±75 μV. Artifact-free data that was accompanied by correct responses were averaged for each congruency trial type during the flanker task (M = 90.5 ± 8.4 accepted trials). Given that not every participant had enough trials to be averaged separately for each letter condition due to the number of response errors and the noise in the EEG signal, ERP measured during Sternberg task were averaged across the different letter sizes (M = 137.1 ± 72.6 accepted trials). The P3 component was evaluated as the mean amplitude within a 50 ms window surrounding the largest positive-going peak within a 250 – 700 ms latency window following stimulus presentation. The CNV components were evaluated as the mean amplitude calculated in two different windows, from 500 - 1000 ms after S1 offset for initial CNV and from -500 - 0 ms prior to S2 onset for terminal CNV (Kamijo et al., 2011).

Cardiorespiratory Fitness Testing

Maximal oxygen consumption (VO2max) was measured using a computerized indirect calorimetry system (ParvoMedics True Max 2400) with averages for oxygen uptake (VO2) and respiratory exchange ratio (RER; VCO2/VO2) assessed every 20s. A modified Balke protocol (American College of Sports Medicine, 2014) used a motor-driven treadmill at a constant speed with a 2.5% grade increase every 2 min until volitional exhaustion. A Polar

heart rate monitor (Polar WearLink +31, Polar Electro, Finland) was used to measure heart rate throughout the test, and ratings of perceived exertion (RPE) were assessed every 2 min (Borg, 1970). Relative maximal oxygen consumption was expressed in ml/kg/min and its confidence level was recorded according to the following criteria: (1) a plateau in oxygen consumption resulting in an increase of less than 2 ml/kg/min with an increase in workload, (2) a peak heart rate ≥ age-predicted HRmax (220 - age); (3) RER ≥ 1.1; and/or (4) RPE ≥ 17. Age and gender matched percentile values were derived from normative values (Shvartz & Reibold, 1990).

Exercise Conditions

Individual maximum heart rate was estimated using 220 – age. The MICE protocol consisted of 20 minutes of walking on a treadmill at 70% of their maximum heart rate (*M* = 70.0 ± 3.1% HR_{max}). This protocol has been previously shown to serve as an effective exercise dose to elicit changes in brain function and task performance (Hillman et al., 2009; O'Leary et al., 2011; Pontifex et al., 2013). The HIIE protocol consisted of a 2 min warm-up, 16 min interval exercise, and 2 min cool-down. Participants performed the warm-up and cool-down at a self-determined speed. During HIIE, participants repeated 8 bouts of 1 min running at a target work rate of an individual's 90% estimated maximum HR (*M* = 88.6 ± 3.7% HR_{max}), separated by 1 min walking at a self-determined pace. Twenty minutes of seated rest served as an inactive control condition. Participants sat on a chair placed on a

treadmill and remained quiet for 20 minutes with conversation kept to a minimum (*M* = 34.0 ± 4.9% HR_{max}). During each condition, HR was recorded every two minutes. The mean energy expenditure of MICE and HIIE protocols were 133.9 ± 4.0 and 153.8 ± 8.6 kcal, respectively. The dynamic change of HR over the course of each exercise condition is shown in Figure 3.1.

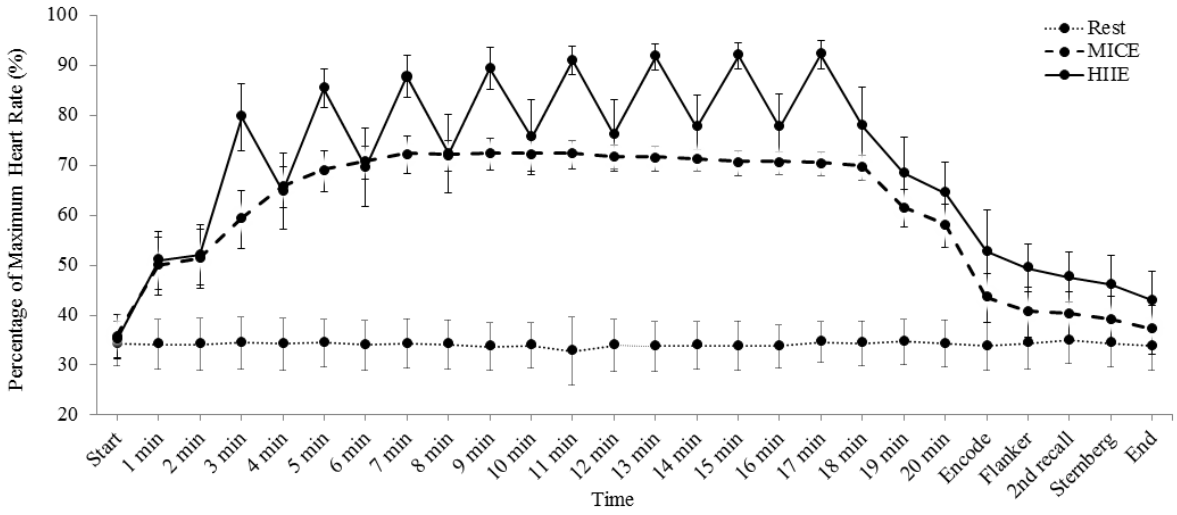

Figure 3.1. Mean HR (± 1 *SD*) over the course of each experimental condition.

Procedure

Using a within-subject design, participants visited the laboratory on four separate days in which they were informed not to participate in physical activity prior to each laboratory visit. During the first visit, participants were provided a detailed explanation of the purpose of the research and its potential risks and were given the opportunity to ask questions prior to obtaining informed written consent from the participants. Following the completion of informed consent, participants completed the HHDQ, PAR-Q, and Edinburgh Handedness Inventory, followed by practice runs of each cognitive task. Finally, participants were fitted with a HR monitor, had their height and weight measured, and completed a VO_{2max} test.

Participants were then assigned to one of six session orders such that the experimental sequence effect was accounted for through counterbalancing (mean days between visits, 4.7 ± 3.0 days; mean time of day difference, 0.3 ± 0.6 hours). During each visit, participants were equipped with a HR monitor and a Neuroscan Quik Cap in accordance with the guidelines of the Society for Psychophysiological Research (Picton et al., 2000). Participants' HR was monitored throughout the testing session and EEG was recorded during the modified flanker and Sternberg tasks. After preparation for neuroelectric measurement, participants performed 20 minutes of MICE, HIIE, or seated rest. A five-minute break was given prior to the encoding phase of the free recall task, followed by a consolidation period and then the immediate free recall test. Following the immediate free recall, participants performed 20

practice trials and two blocks of a modified flanker task, followed by a delayed free recall task at 12 minutes after the completion of the immediate free recall test. Finally, participants performed 20 practice trials and three blocks of a modified Sternberg task. Upon completion of this study, participants were briefed on the purpose of the experiment and receive $80 remuneration ($10/hour) for their involvement in the experiment.

Statistical Analysis

All statistical analyses were conducted using SPSS (SPSS v. 22, Chicago, IL) with a significance level of $p = .05$, and analyses with three or more within-subjects levels used the Pillai's Trace statistic with subsidiary univariate ANOVAs and Bonferroni-corrected *t* tests for post hoc comparisons. Prior to hypothesis testing, a preliminary analysis was conducted to examine the experiment session order to ensure that observed effects are not due to specific experimental orders. This analysis employed an additional between-subject factor with six levels (Session Order: rest-MICE-HIIE, rest-HIIE-MICE, MICE-rest-HIIE, MICE-HIIE-rest, HIIE-rest-MICE, HIIE-MICE-rest) to the analyses described below for each dependent measure.

Analysis of free recall task measures (number of correct recalled words) was conducted using a 3 (Condition: rest, MICE, HIIE) × 2 (Time: immediate, delayed) × 2 (Position: middle, primacy and recency) multivariate repeated-measures ANOVA.

Analysis of flanker task measures (mean RT and response accuracy) were conducted using a 3 (Condition: rest, MICE, HIIE) × 2 (Congruency: congruent, incongruent) multivariate repeated-measures ANOVA. Secondary one-way multivariate repeated-measures ANOVAs (Condition: rest, MICE, HIIE) were conducted to examine RT and response accuracy interference scores. Additional analysis was conducted separately for P3 amplitude and latency using a 3 (Condition: rest, MICE, HIIE) × 2 (Congruency: congruent, incongruent) × 6 (site: Fz, FCz, Cz, CPz, Pz, POz) multivariate repeated-measures ANOVA.

Analysis of Sternberg task measures (mean RT and response accuracy) was conducted using a 3 (Condition: rest, MICE, HIIE) × 3 (Size: 3-letter, 5-letter, 7-letter) multivariate repeated-measures ANOVA. Additional analyses were conducted separately for initial and terminal CNV amplitude using a 3 (Condition: rest, MICE, HIIE) × 6 (site: Fz, FCz, Cz, CPz, Pz, POz) multivariate repeated-measures ANOVA.

CHAPTER 4: RESULTS

Participant characteristics are provided in Table 4.1. Preliminary analyses were conducted to ensure that the observed effects related to exercise condition were not due to specific experimental session orders. Findings revealed that Session Order did not result in any main effects or interactions involving Condition for any of the outcome variables, Fs (2, 33) ≤ 1.8, ps ≥ 0.083, $\eta_p^2 \leq 0.30$. Thus, further analyses were collapsed across Session Order.

Table 4.1. *Participant demographic values (± 1 SD).*

Measure	Mean (*SD*)	Range
N	36 (18 females)	–
Age (years)	21.5 ± 3.1	18 – 30
Body mass index (kg/m^2)	23.4 ± 3.0	18.4 – 29.1
VO_{2max} (ml/kg/min)	46.6 ± 10.1	30.8 – 69.7
VO_{2max} percentile (%)	56.9 ± 35.1	3.0 – 97.0

Note: VO_{2max} percentile was adjusted for age and sex based on Shvartz and Reibold (1990).

Task Performance

Free Recall Task

Analyses revealed a main effect of Condition, F (2, 33) = 11.5, $p < 0.001$, $\eta_p^2 = 0.40$. Post hoc tests revealed a decreased number of correctly recalled words for rest (7.1 ± 0.4) relative to MICE (8.2 ± 0.5), $t(35) = 2.8$, $p = 0.008$, $d = 0.47$, and HIIE (8.8 ± 0.5) conditions, $t(35) = 4.8$, $p < 0.001$, $d = 0.80$), see Figure 4.1. No difference in number of correctly recalled words was observed between MICE and HIIE, $t(35) = 1.7$, $p = 0.090$, $d = 0.29$. Planned t tests were performed based on an *a priori* hypothesis for the effect of acute exercise specific to primacy and recency words based on previously published research (Coles & Tomporowski, 2008). Findings revealed that MICE did not exhibit more correctly recalled words based on primacy and recency position order, $t(35) = 2.0$, $p = 0.049$, $d = 0.34$, nor middle position order after Bonferroni correction, $t(35) = 1.8$, $p = 0.085$, $d = 0.29$, while HIIE demonstrated an increase in the number of correctly recalled words across for both the middle position as well as the primacy and recency order compared to rest, ts (35) ≥ 2.9, ps < 0.006, ds ≥ 0.48. A main effect of Position was also observed, F (2, 33) = 18.9, $p < 0.001$, $\eta_p^2 = 0.35$, with an increased numbers of correctly recalled words for the primacy and recency positions (8.9 ± 0.5) compared to the middle position (7.1 ± 0.5).

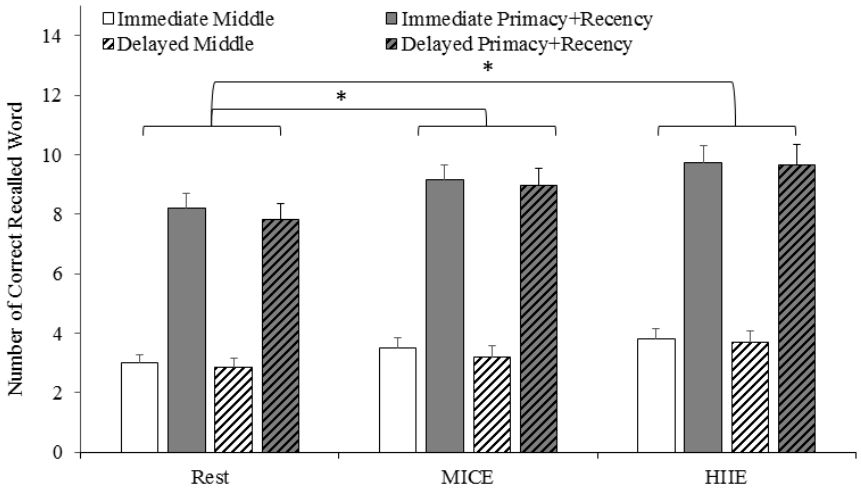

Figure 4.1. Mean number of correctly recalled words (± 1 *SE*) during the free recall task following each experimental condition.

Flanker Task

Reaction Time

Analysis revealed main effects of Condition, $F(2, 33) = 8.0$, $p = 0.001$, $\eta_p^2 = 0.32$, and Congruency, $F(1, 34) = 422.9$, $p < 0.001$, $\eta_p^2 = 0.92$, which were superseded by an interaction of Condition × Congruency, $F(2, 33) = 3.4$, $p = 0.044$, $\eta_p^2 = 0.17$. Decomposition of this interaction revealed a Condition main effect for both congruent and incongruent trials, Fs$(2, 33) \geq 6.4$, ps ≤ 0.004, $\eta_p^2 \geq 0.27$, with longer RT for rest (419.8 ± 7.1 ms) relative to MICE (396.0 ± 7.8 ms) and HIIE (397.3 ± 9.3 ms) conditions, see Figure 4.2. Post hoc tests examined the Congruency effect for each Condition and revealed a significant Congruency main effect for all Condition, ts$(35) \geq 17.1$, ps < 0.001, ds ≥ 2.86, with longer RT for incongruent (431.2 ± 7.9 ms) relative to congruent (377.5 ± 6.6 ms) trials. However, the rest condition exhibited a disproportionally larger congruency effect relative to HIIE, which was confirmed by a significant Condition effect for the RT interference score, $F(2, 33) = 3.4$, $p = 0.044$, $\eta_p^2 = 0.17$, with less interference following HIIE (49.9 ± 2.8 ms) compared to the rest (57.8 ± 3.4 ms) condition, $t(35) = 2.6$, $p = 0.012$, $d = 0.44$. RT interference scores following MICE (53.2 ± 2.9 ms) did not differ between HIIE and rest conditions, ts$(35) \leq 1.7$, ps ≥ 0.107, ds ≤ 0.28, see Figure 4.3.

Response Accuracy

Analyses revealed a main effect of Congruency, $F(1, 34) = 38.1$, $p < 0.001$, $\eta_p^2 = 0.52$, with increased response accuracy for congruent (98.1 ± 0.3 %) relative to incongruent (92.3 ± 1.1 %) trials. No main effects or interactions involving Condition were observed for response accuracy, Fs$(2,33) \leq 1.5$, ps ≥ 0.239, $\eta_p^2 \leq 0.08$. Further, no significant findings were observed for response accuracy interference scores, $F(2, 33) = 0.4$, $p = 0.658$, $\eta_p^2 = 0.24$.

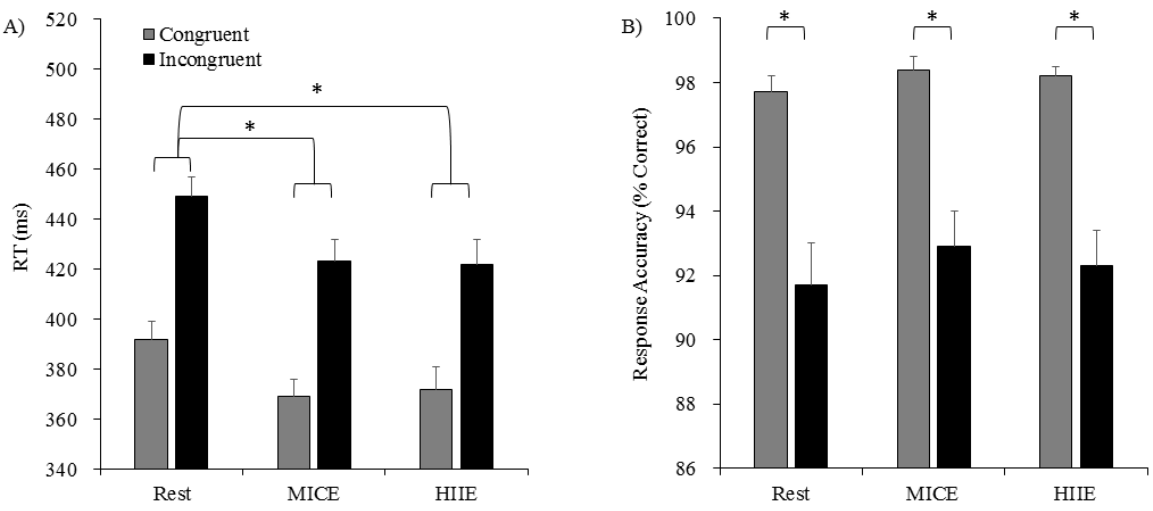

Figure 4.2. Mean (± 1 *SE*) RT (A) and response accuracy (B) during the modified flanker task following each experimental condition.

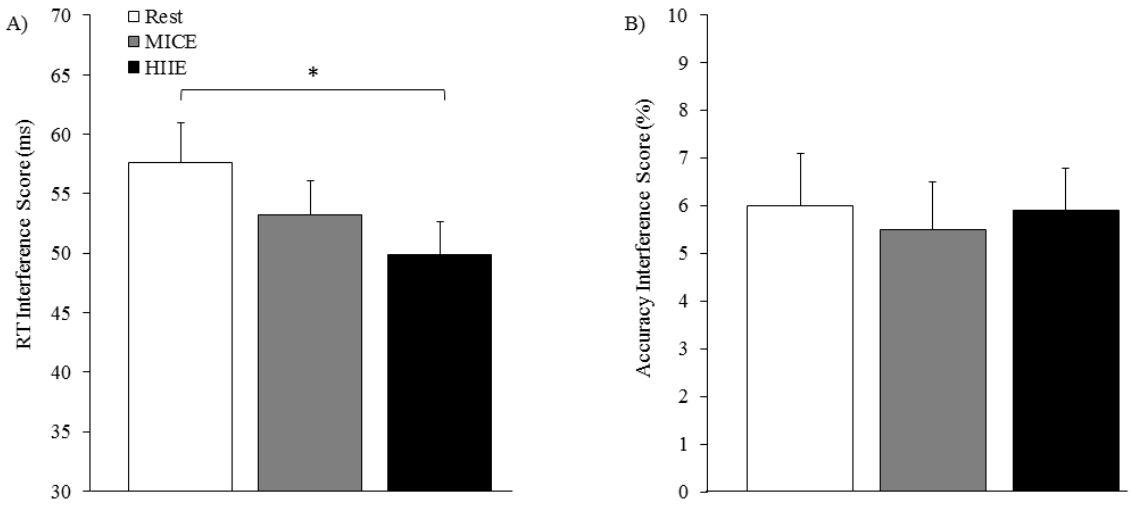

Figure 4.3. Mean (± 1 *SE*) RT (A) and response accuracy (B) interference scores during the modified flanker task following each experimental condition.

Sternberg task

Reaction Time

Analyses revealed a main effect of Condition, $F(2, 33) = 3.7$, $p = 0.035$, $\eta_p^2 = 0.18$. Post hoc tests revealed longer RT for rest (767.0 ± 16.4 ms) relative to HIIE (736.8 ± 15.7 ms), $t(35) = 2.7$, $p = 0.011$, $d = 0.45$, see Figure 4.4. MICE exhibited no differences in RT compared to the rest and HIIE conditions, $ts(35) \leq 1.8$, $ps \geq 0.076$, $ds \leq 0.30$. A main effect of Size was also observed, $F(2, 33) = 98.5$, $p < 0.001$, $\eta_p^2 = 0.85$. Post hoc tests revealed shorter RT for 3-letter (696.8 ± 14.2 ms) compared to 5-letter (750.1 ± 14.6 ms) and 7-letter (804.4 ± 17.2 ms) trials, $ts(35) \geq 11.1$, $ps < 0.001$, $ds \geq 1.78$. Shorter RT was also observed for 5-letter compared to 7-letter trials, $t(35) = 10.3$, $p < 0.001$, $d = 1.71$.

Response Accuracy

Analysis revealed a main effect of Size, $F(2, 33) = 90.3$, $p < 0.001$, $\eta_p^2 = 0.84$. Post hoc tests revealed increased response accuracy for 3-letter (92.4 ± 1.2 %) relative to 5-letter (88.2 ± 1.4 %) and 7-letter (77.2 ± 1.7 %) trials, $ts(35) \geq 7.4$, $ps < 0.001$, $ds \geq 1.24$. Increased response accuracy was also observed for 5-letter compared to 7-letter trials, $t(35) = 11.9$, $p < 0.001$, $d = 1.98$. No main effects or interactions involving Condition were observed for response accuracy, $Fs(2,33) \leq 1.4$, $ps \geq 0.129$, $\eta_p^2 \leq 0.19$.

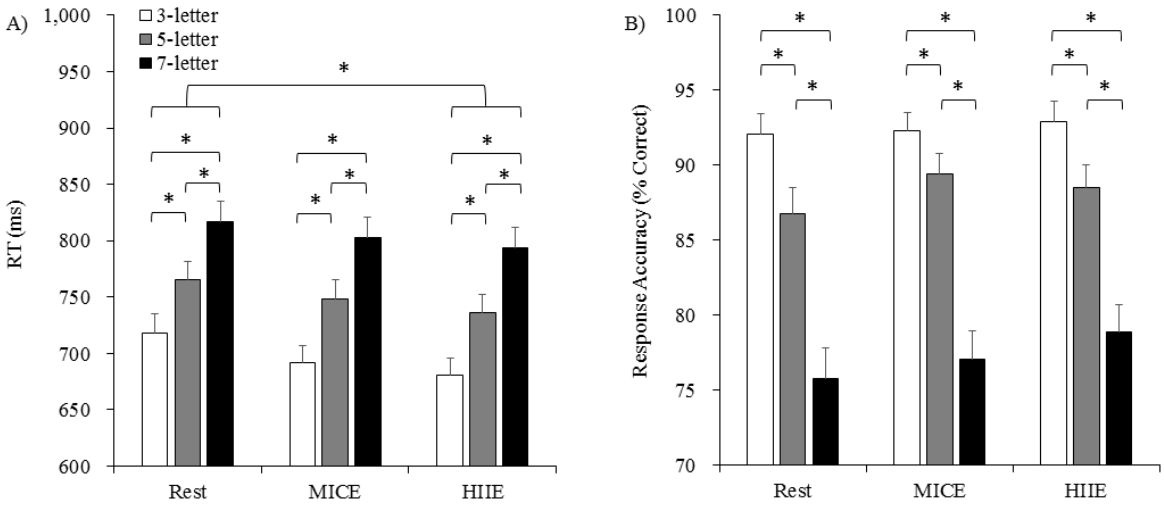

Figure 4.4. Mean (± 1 *SE*) RT (A) and response accuracy (B) during the modified Sternberg task following each experimental condition.

Event-Related Potentials

Flanker Task Elicited P3

Amplitude

Analyses revealed a main effect of Condition, $F(2, 33) = 4.8$, $p = 0.015$, $\eta_p^2 = 0.22$. Post hoc tests revealed that P3 amplitude following MICE (7.7 ± 0.4 μV) was increased compared to rest (7.0 ± 0.5 μV), $t(35) = 2.6$, $p = 0.012$, $d = 0.44$, and HIIE (6.8 ± 0.4 μV) conditions, $t(35) = 2.7$, $p = 0.011$, $d = 0.45$. No differences were observed between HIIE and rest conditions, $t(35) = 0.6$, $p = 0.531$, $d = 0.11$. Findings also revealed main effects of Congruency, $F(1, 34) = 21.1$, $p < 0.001$, $\eta_p^2 = 0.38$, and Site, $F(5, 30) = 7.2$, $p < 0.001$, $\eta_p^2 = 0.54$, which were superseded by a Congruency × Site interaction, $F(5, 30) = 6.5$, $p < 0.001$, $\eta_p^2 = 0.51$. Post hoc test revealed increased P3 amplitude for incongruent than congruent trials at Fz, FCz, Cz, and CPz, ts$(35) \geq 3.2$, ps ≤ 0.003, ds ≥ 0.53, while no such Congruency effect was observed at Pz and POz after Bonferroni correction, ts$(35) \leq 2.5$, ps ≥ 0.017, ds ≤ 0.42. See Figure 4.5 for the grand average stimulus-locked ERP waveforms and Figure 4.6 for topographical scalp distribution of P3 amplitude.

Latency

Analyses revealed a main effect of Condition, $F(2, 33) = 4.0$, $p = 0.027$, $\eta_p^2 = 0.19$. Post hoc tests revealed shorter P3 latency following HIIE (406.7 ± 8.8 ms) compared to rest (425.1 ± 9.2 ms), $t(35) = 2.8$, $p = 0.008$, $d = 0.47$. No differences in P3 latency were observed for

MICE (419.3 ± 10.7 ms) relative to HIIE, $t(35) = 1.7$, $p = 0.101$, $d = 0.28$, and rest conditions, $t(35) = 0.8$, $p = 0.434$, $d = 0.13$. Findings also revealed main effects of Congruency, $F(1, 34) = 21.0$, $p < 0.001$, $\eta_p^2 = 0.38$, and Site, $F(5, 30) = 10.8$, $p < 0.001$, $\eta_p^2 = 0.64$, which were superseded by a Congruency × Site interaction, $F(5, 30) = 4.7$, $p = 0.003$, $\eta_p^2 = 0.43$. Post hoc test revealed shorter P3 latency for congruent than incongruent trials at Cz, CPz, Pz, and POz, $ts(35) \geq 4.8$, $ps < 0.001$, $ds \geq 0.80$, while no such Congruency effect was observed at Fz and FCz after Bonferroni correction, $ts(35) \leq 0.7$, $ps \geq 0.500$, $ds \leq 0.11$.

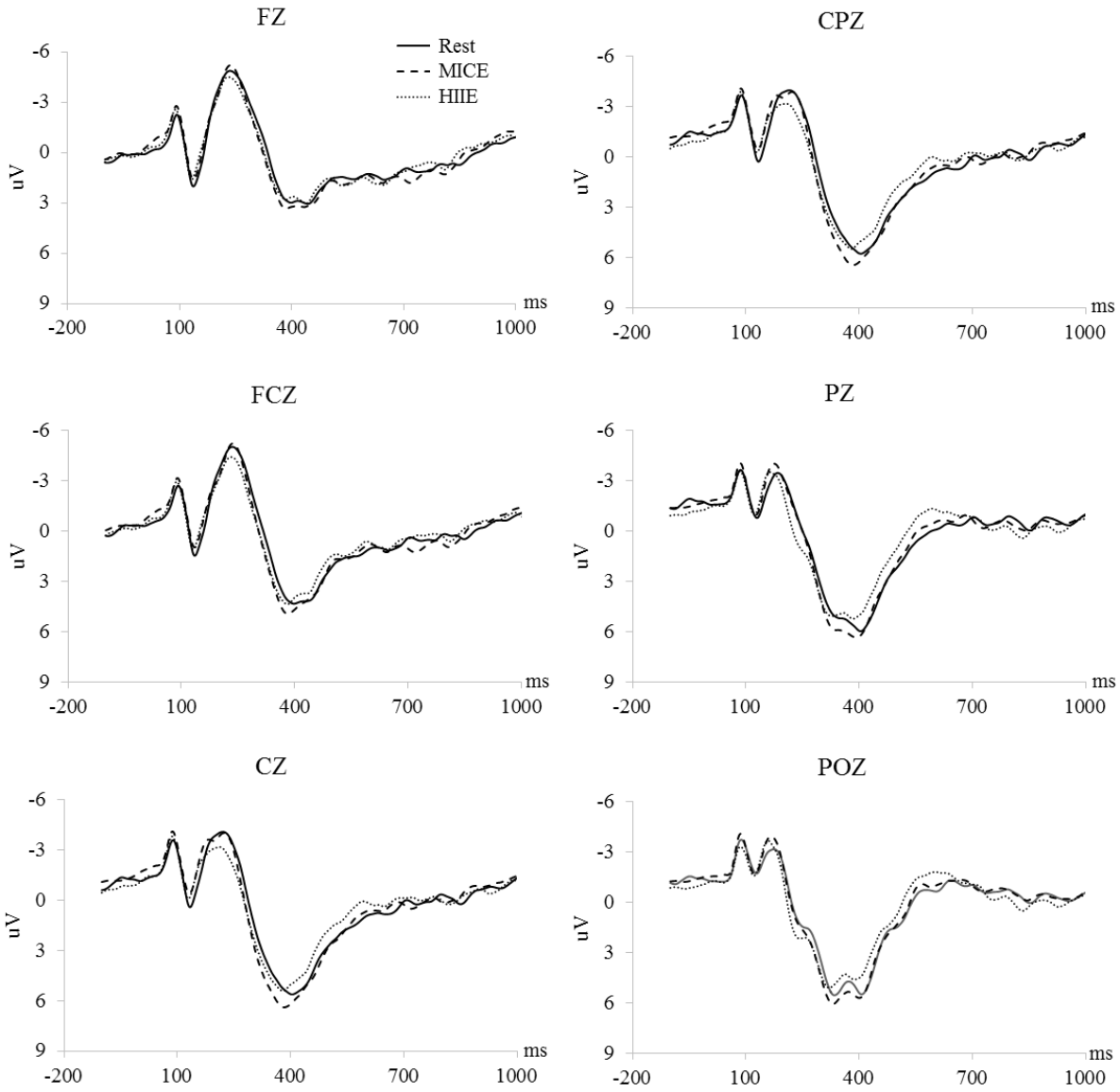

Figure 4.5. Grand-averaged waveforms of the P3 component at each electrode site collapsing across congruent and incongruent trials during a modified flanker task following each experimental condition.

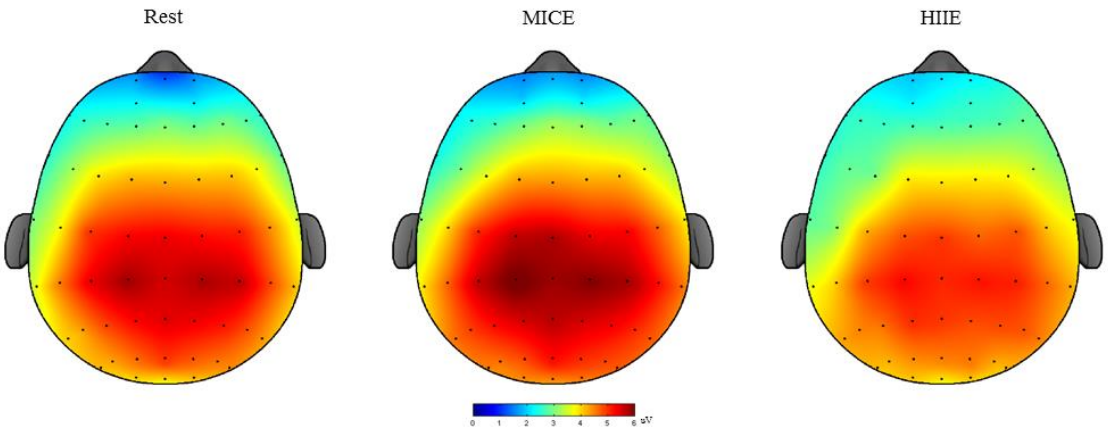

Figure 4.6. Topographical scalp distribution of P3 amplitude at averaged latency across Fz, FCz, Cz, CPz, Pz, and POz during congruent and incongruent trials of the modified flanker task following each experimental condition.

Sternberg Task Elicited CNV

Initial CNV

Analyses revealed a significant main effect of Site, $F(5, 30) = 4.9$, $p = 0.002$, $\eta_p^2 = 0.44$, which was superseded by a Condition × Site interaction, $F(5, 30) = 2.3$, $p = 0.047$, $\eta_p^2 = 0.46$. Decomposition of this interaction revealed a significant Condition effect at Fz and FCz, Fs$(2, 33) \geq 4.6$, $p \leq 0.017$, $\eta_p^2 \geq 0.21$, but not at the remaining sites, Fs$(5, 30) \leq 3.0$, ps ≥ 0.061, $\eta_p^2 \leq 0.15$. Post hoc test revealed larger iCNV amplitude at Fz and FCz following HIIE (Fz: -0.5 ± 1.3 μV, FCz: -1.5 ± 1.4 μV) relative to rest (Fz: 3.5 ± 0.6 μV, FCz: 2.2 ± 0.5 μV), ts$(35) \geq 2.6$, ps ≤ 0.015, ds ≥ 0.43. The amplitude of iCNV following MICE (Fz: 1.1 ± 093 μV, FCz: 0.4 ± 0.8 μV) was not differed from HIIE and rest conditions after Bonferroni correction, ts$(35) \leq 2.3$, ps ≥ 0.027, ds ≤ 0.38. See Figure 4.7 for CNV grand average stimulus-locked ERP waveforms and Figure 4.8 for topographical scalp distribution of iCNV amplitude.

Terminal CNV

Analysis revealed a significant main effect of Site, $F(5, 30) = 2.6$, $p = 0.048$, $\eta_p^2 = 0.29$, which was superseded by a Condition × Site interaction, $F(5, 30) = 2.4$, $p = 0.037$, $\eta_p^2 = 0.48$. Decomposition of this interaction revealed no significant Condition effect at any site, Fs$(5, 30) \leq 2.6$, ps ≥ 0.086, $\eta_p^2 \leq 0.13$. See Figre 4.9 for topographical scalp distribution of tCNV amplitude.

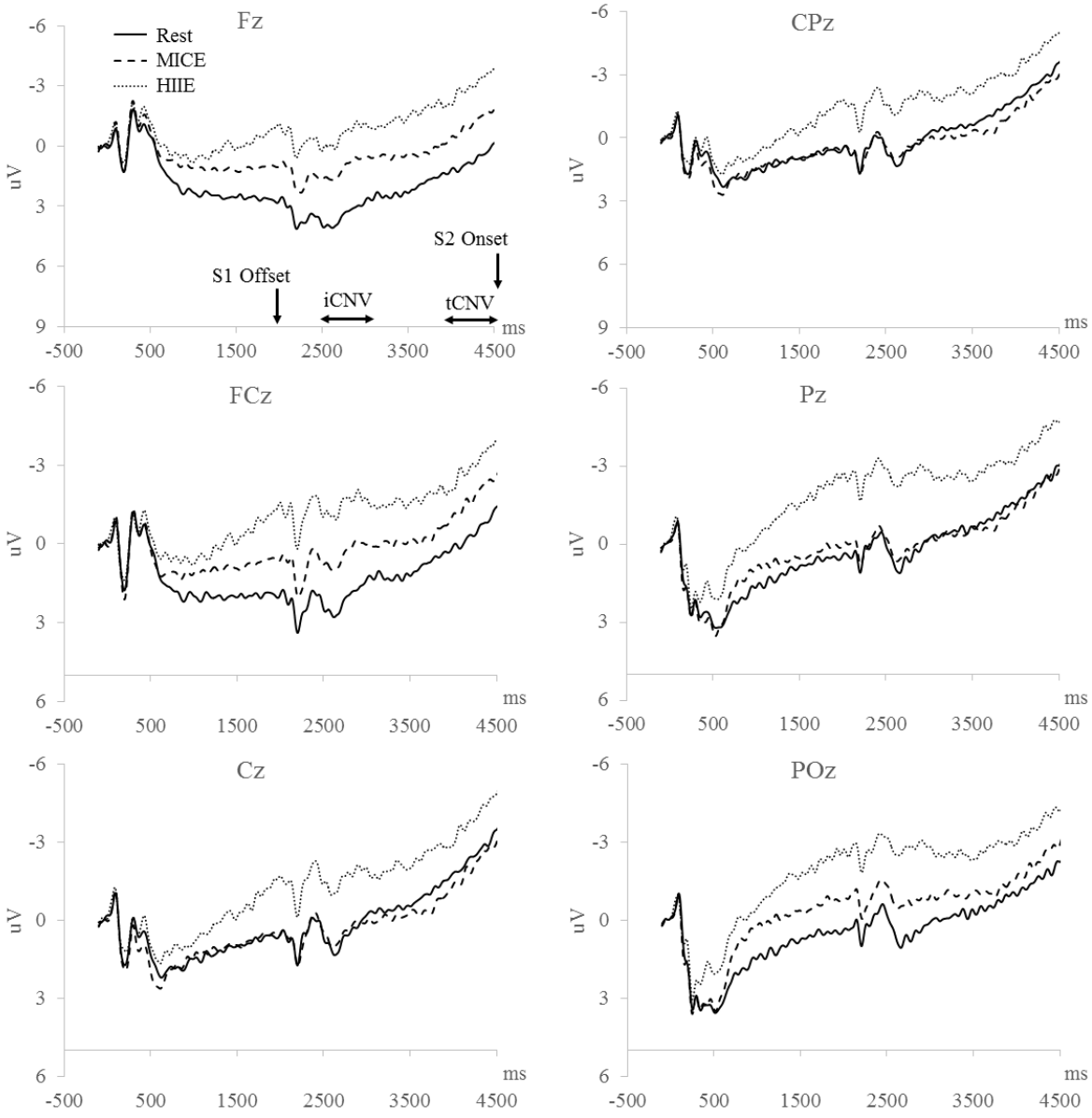

Figure 4.7. Grand-averaged waveforms of CNV at each electrode site collapsing across 3-, 5-, and 7-letter trials during the modified Sternberg task following each experimental condition.

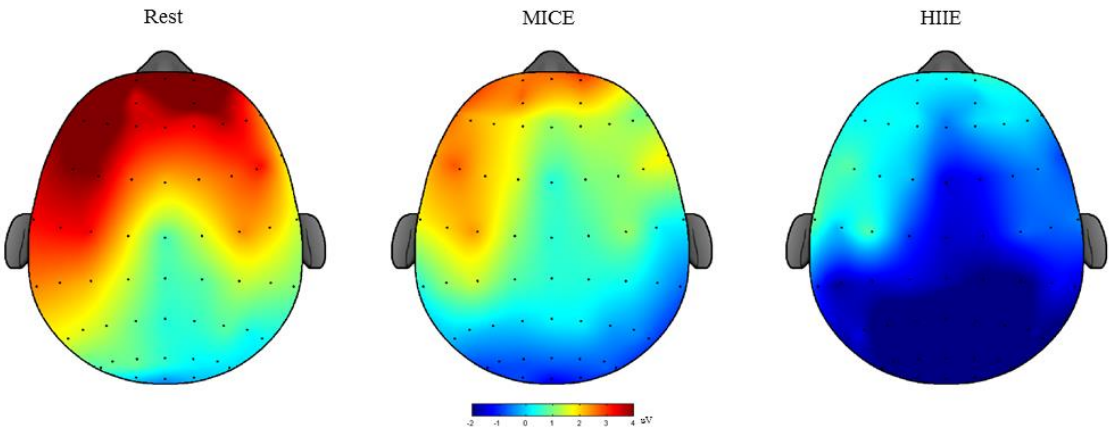

Figure 4.8. Topographical scalp distribution of initial CNV amplitude at the 500-1000 ms window after S1 offset collapsing across 3-, 5-, and 7-letter trials during the modified Sternberg task following each experimental condition.

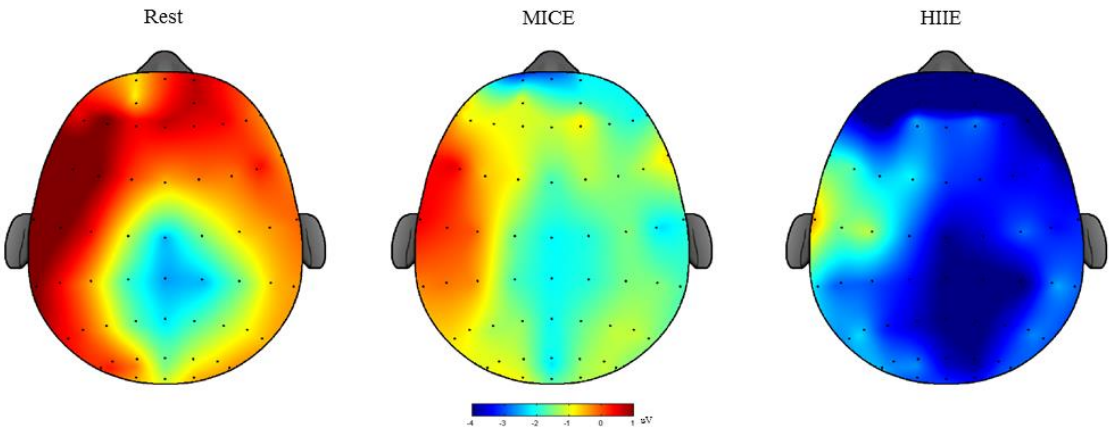

Figure 4.9. Topographical scalp distribution of terminal CNV amplitude at the 500-0 ms window prior to S2 onset collapsing across 3-, 5-, and 7-letter trials during the modified Sternberg task following each experimental condition.

CHAPTER 5: DISCUSSION

The purpose of the present investigation was to compare exercise-induced effects on inhibitory control, working memory, and long-term memory during the recovery period following MICE and HIIE relative to a seated rest control condition. After a short delay following acute bouts of 20 minutes of MICE and HIIE, there was an increase in the number of words correctly recalled from the free recall lists during both the immediate and delayed tests compared to following seated rest. Performance during the modified flanker task was improved following MICE and HIIE compared to seated rest, as indexed by improved overall RT across task conditions requiring varying amounts of inhibitory control. Additionally, HIIE resulted in an additional improvement on RT interference scores compared to seated rest. The behavioral facilitation during the flanker task was paralleled by exercise-induced modulation in the P3 component, with HIIE decreasing P3 latency relative to seated rest and MICE increasing P3 amplitude relative to HIIE and seated rest. Further, HIIE improved the behavioral and neuroelectric indices of performance during a modified Sternberg task compared to seated rest, as reflected by shorter overall RT and increased iCNV amplitude, regardless of working memory load. Taken together, these findings suggest that acute bouts of MICE and HIIE may have similar, yet differential, facilitating effects on performance related to multiple aspects of cognition and their underlying neural mechanisms.

Long-Term Memory - Free Recall Task

Replicating previous investigations (Roig et al., 2013), the current findings indicated enhanced long-term memory following a single bout of MICE. Specifically, the number of correctly recalled words in the free recall task increased during the recovery period within 20 minutes following MICE relative to seated rest. Such benefits were not selective for the time of memory retrieval nor the position of words in the free recall list, suggesting a general facilitation on memory. When primacy and recency words and middle words were examined separately based on our *a priori* hypothesis stemming from Coles and Tomporowski (2008), only a marginal facilitating effect was observed for each position, confirming that general improvements in memory following MICE were driven by all positions of words, despite a trend for a larger positive effect in primacy and recency words ($p = 0.049$, $d = 0.34$) than middle words ($p = 0.085$, $d = 0.29$). These findings failed to corroborate prior research reporting that acute MICE specifically maintained the number of correctly remembered primacy and recency words from pre- to post-exercise while the number of correctly recalled words in these positions decreased from pre- to post-inactive control conditions (Coles & Tomporowski, 2008). According to the literature, the absence of the interaction between exercise and word position is not uncommon (Tomporowski, Ellis, & Stephens, 1987). One possibility for this inconsistency is the difference in experimental and task designs. For instance, Coles and Tomporowski (2008) found that participants recalled significantly more

words when tested during the immediate recall than delayed recall following a task that taps substantial cognitive resources for information storage. Such memory-related processing required in a distraction task may impair performance during subsequent delayed recall due to the disturbed consolidation of items encoded from the free recall list, particularly the middle items (Cohen & Sandber, 1977; Engle, Tuholski, Laughlin, & Conway, 1999). However, the current study administered the distraction using an inhibitory control task, which has less distracting effects on memory formation. This argument is supported by the unchanged performance from immediate to delayed recall test across conditions. Furthermore, in Coles and Tomporowski's study, participants encoded one free recall list before and a different list after acute exercise. This pre-post design might lead to increased task difficulty during post-test due to the distraction caused by words encoded during pre-test, as indicated by impaired performance during the post-test in that study. Therefore, the absence of a pre-test condition and a different distraction task employed in the current investigation might partially explain the lack of exercise-induced effect to specific serial positions in the free recall list.

Novel to this investigation, however, was the examination into HIIE-induced effects on long-term memory and a direct comparison with the effect of MICE. The findings indicated that one session of HIIE increased the overall number of correctly recalled words that was attributed to more remembered words in the middle position as well as primacy and recency

positions. Such findings replicated previous research indicating enhanced memory consolidation following one session of HIIE (van Dongen et al., 2016; Winter et al., 2007). However, only a marginal trend for more correctly recalled words was observed following HIIE compared to MICE ($p = 0.090$). This suggests that HIIE and MICE had similar beneficial effects on memory. These findings do not perfectly replicate prior research showing larger benefits of high-intensity exercise than MICE on learning and memory (Etnier et al., 2016; Winter et al., 2007). Specifically, Winter et al. (2007) found faster vocabulary learning following two short bouts of high-impact running compared to one bout of continuous aerobic running. Further, Etnier et al. (2016) found that the largest benefits on long-term memory at 24 hours following maximal intensity exercise compared to following exercise at lower intensities. One possible explanation for the discrepant findings between previous studies and the current investigation is the nature of experimental design. For instance, Winter et al. (2007) employed a high-intensity exercise protocol that was much shorter than the MICE protocol, while in the current study the duration of HIIE and MICE was matched. Further, Etnier et al. (2016) indicated an additional beneficial effect of high-intensity exercise after a much longer delay compared to the current study (after 24 hours versus within 20 minutes). However, despite the absence of a significant difference between MICE and HIIE, further examination into the effect size indicated a greater beneficial effect following HIIE ($d = 0.80$) compared to MICE ($d = 0.47$). Taken together,

findings from the free recall task are consistent with the current hypothesis that acute MICE and HIIE have benefits on long-memory, with HIIE exhibiting a larger beneficial effect than MICE.

Inhibitory Control – Flanker Task

In addition to serving as a distractor to interrupt memory consolidation, performance during the flanker task was interesting on its own, as it demonstrated beneficial effects of single bouts of HIIE and duration-matched MICE on inhibitory control assessed approximately 10 minutes following the cessation of exercise. As predicted, overall RT was reduced following both MICE and HIIE compared to seated rest. Similar exercise-induced improvement has been found in prior research, suggesting a general facilitation on the speed of information processing associated with inhibitory control (Kamijo et al., 2009; Kamijo et al., 2007; Kao et al., 2017; O'Leary et al., 2011). Alternatively, no difference in response accuracy was observed between exercise conditions, suggesting that the improvement in RT was not a result of a speed-accuracy tradeoff. Moreover, following acute HIIE RT interference scores decreased compared to following seated rest, while MICE did not exhibit any such changes, suggesting facilitation of interference control selectively induced by HIIE. These findings replicate previous studies indicating the benefit of acute HIIE on interference control (Alves et al., 2014) and additional benefits following HIIE compared to traditional MICE (Kao et al., 2017; Tsukamoto et al., 2016).

Specifically, Tsukamoto et al. (2016) adopted a HIIE protocol with four 4-minute high-intensity cycling bouts separated by 3-minute active breaks and a volume-matched 40 minutes of MICE. The findings indicated improved interference control immediately following both HIIE and MICE. Further, these two types of exercise began showing differential effects after a delay following the cessation of exercise, such that improvements diminished over time following MICE but sustained for 30 minutes following HIIE. Similarly, Kao et al. (2017) found shorter overall RT following 9 minutes of HIIE and 20 minutes of MICE with larger amounts of exercise volume, while only HIIE exhibited facilitating effects on response accuracy compared to rest, as indexed by smaller interference scores as well as increased rate of corrected responses during the task condition requiring greater inhibitory control. Although such selective facilitation for response accuracy following HIIE was inconsistent with a selective benefit on RT observed in Tsukamoto et al. (2016) and the present investigation, these discrepant findings might be due to the variability across exercise protocols. That is, to test the hypothesis that HIIE is more efficient than MICE relative to transient cognitive benefits, Kao et al. (2017) did not match exercise duration nor exercise volume. Specifically, the duration of the HIIE protocol employed in that study was less than half of the HIIE protocol used in present investigation. Thus, it is plausible that the presence of the HIIE-induced benefit on response accuracy in that study might be due to the combination of shorter exercise duration and smaller exercise volume. Taken together, the

current findings along with existing literature suggest that acute HIIE and MICE have similar beneficial effects on inhibitory control, while HIIE may lead to additional facilitation when the requirement of inhibitory control is upregulated.

A more precise understanding of the differential effects of HIIE and MICE on inhibitory control may be provided through the assessment of ERP components underlying behavioral performance during the flanker task. One such component that reflects specific cognitive operations is the P3 (Donchin, 1981), whose amplitude and latency are thought to reflect attentional resource allocation during stimulus engagement and stimulus classification speed, respectively (Polich, 2007). In addition to improvements in behavioral performance, findings from the present investigation revealed increased P3 amplitude across congruency conditions following MICE compared to seated rest. Such an effect following MICE replicates several prior reports, and indicates that increases in attentional resources were invested to support cognitive processing during performance of the flanker task, suggesting that MICE at this intensity may not only be beneficial for behavioral outcomes but also attentional processes during inhibitory control operations (Hillman et al., 2003; Kamijo et al., 2007, 2009; Kao et al., 2017; O'Leary et al., 2011).

On the other hand, following HIIE P3 amplitude was unchanged compared to seated rest and decreased compared to MICE. Interestingly, the maintained P3 amplitude following HIIE does not exactly replicate the findings of Kao et al. (2017) who observed decreased P3

amplitude following HIIE compared to seated rest. However, it is important to note that a number of methodological factors may be responsible for the discrepant findings from the present investigation. That is, administration of multiple cognitive tasks along with a smaller sample size might introduce more variance into the analysis, leaving less power to detect the HIIE-induced decrease in P3 amplitude compared to seated rest. Despite these differences in experimental design, the findings from the present investigation are consonant with the inverted-U shaped relationship between acute exercise intensity and P3 amplitude (Kamijo et al., 2007), suggesting that HIIE, like seated rest, did not alter the availability of attentional resources in support of task performance requiring varying amounts of inhibitory control.

Despite a lack of difference in P3 amplitude, a general reduction in P3 latency across congruency conditions was observed following HIIE relative to seated rest, while no such latency effect was observed following MICE. The unchanged P3 latency following MICE relative to seated rest is inconsistent with some prior research (Hillman et al., 2003; Kamijo et al., 2007, 2009), but it is possible that such a discrepancy is the result of differences in task design (Kao et al., 2017; O'Leary et al., 2011). That is, when a shorter and varied inter-stimulus interval pairs with a shorter stimulus duration, increases in task difficulty may diminish the observed effect of MICE on the modulation of P3 latency (Kao et al., 2017; O'Leary et al., 2011). However, despite the presence of this diminishing effect possibly related to task design, the reduction in P3 latency following HIIE remained evident. As such,

it is plausible that this effect might be more robust for HIIE than MICE. Given that P3 latency reflects processing speed associated with stimulus evaluation and classification (Polich, 2007), faster P3 latency concurrent with unchanged P3 amplitude suggests that HIIE may lead to more efficient neuroelectric activation as manifested by faster stimulus identification without the need for additional engagement of attentional resources to support goal-directed cognitive operations. Support for improved neural efficiency may also be found through decreased RT interference following HIIE, suggesting a lowered threshold in the upregulation of attentional resources in response to less perceived interference. Notably, although the argument of superior neural efficiency related to exercise has been proposed in the literature (Kao et al., 2017; Malinowski, 2013; Moore et al., 2012; Pontifex et al., 2011; Voss et al., 2011), the improved neural efficiency following single bouts of exercise should be distinguished from that induced by chronic participation in physical activity. That is, long-term exercise or exercise-induced improvement in physical fitness may be associated with neural adaptations that redistribute neural resources to efficiently accomplish goal-directed behavior during cognitively demanding tasks (Malinowski, 2013; Moore, et al., 2012; Pontifex et al., 2011; Voss et al., 2011), while acute exercise may result in a transient implementation of greater efficiency in brain function (Kao et al., 2017). The findings of the current investigation corroborated the latter argument, indicating that acute HIIE improved

behavioral performance, paralleled with brain functioning characterized by a faster processing speed without additional cost of attentional resources.

However, it is important to acknowledge the alternative explanation of the differential modulations in P3 following HIIE and MICE. Namely, it is possible that P3 and behavioral measures during the flanker task are two independent exercise-induced outcomes supported by different mechanisms, given that a paucity of evidence indicating an association between neuroelectric and behavioral indices following acute exercise. Thus, future research is warranted to determine whether P3 and behavioral performance are simply unrelated or their association is modulated by other factors such as individual differences, exercise parameters, or exercise-induced brain metabolism.

Collectively, the current findings are consistent with predicted outcomes, suggesting that acute HIIE and MICE may have similar beneficial effects on behavioral indices of inhibitory control, while HIIE may lead to additional facilitation when the requirement of inhibitory control was upregulated. Such differential benefits were concurrent with differential patterns of neuroelectrical activities in the brain, with MICE relating to increased attentional resource allocation and HIIE relating to improved speed of information processing.

Working Memory – Sternberg Task

Investigation of the exercise-induced effects on working memory revealed that performance during a modified Sternberg task improved following HIIE compared to seated

rest, while such improvement was only trended following MICE. Contrary to the meta-analysis that indicated a moderate-positive effect on performance during a variety of working memory tasks in response to acute MICE (Roig et al., 2013); findings from this investigation did not reveal facilitation of response accuracy or RT during the Sternberg task following MICE. Such finding also contradicts several empirical studies indicating facilitated working memory performance during n-back tasks following acute MICE (Chen et al., 2014; Hogan et al., 2013; Weng et al., 2015). However, it is important to note that Sternberg and n-back tasks have been used to assess maintenance and manipulation aspects of working memory, respectively, and been found to result in distinct functional activation in the brain (Veltman et al., 2003). That is, the Sternberg task employed in the present investigation may demand larger amounts of working memory maintenance, but minimum amounts of working memory manipulation, compared to n-back paradigms used in prior research (Chen et al., 2014; Hogan et al., 2013; Weng et al., 2015). Thus, the unchanged performance during the Sternberg task following MICE suggests that exercise at moderate intensity may have a weaker effect on the maintenance aspect of working memory. Such speculation is supported by a smaller effect size (d = 0.30) observed in this study compared to others employing tasks primarily tapping working memory manipulation (d = 0.67; Weng et al., 2015). In other words, the present investigation may be underpowered to detect the MICE-induced effects on the maintenance aspect of working memory. Additionally, the lack of behavioral modulation

during the Sternberg task in response to MICE might also be the mixed results of exercise intensity and the temporal relation of task administration relative to exercise. That is, it is plausible that exercise at 70% of HR_{max} was potentially an insufficient exercise intensity to induce a sustained performance enhancement at a delay from 25 -50 minutes following the cessation of exercise.

On the other hand, the duration-matched HIIE protocol resulted in a general improvement of RT compared to seated rest, suggesting a facilitating effect on the processing speed associated with working memory operation. Despite a prior meta-analysis indicating a strong beneficial effect of acute exercise on response speed along with a low-to-moderate detrimental effect on response accuracy during a variety of working memory tasks (McMorris et al., 2011), the observed reduction in overall RT in the present investigation following HIIE was not accompanied by a decrease in response accuracy, suggesting that HIIE facilitated speed of information processing at no consequence to other behavioral indices of working memory performance. Further, the findings from the present investigation mirrored results from previous studies using not only a similar modified Stenberg task (Pontifex et al., 2009) but also a different working memory paradigm (delayed match-to-sample task; Hwang, Castelli, et al., 2016). Specifically, Pontifex and colleagues found a general reduction in RT immediately and at 30-minute following a single bout of high-intensity continuous exercise. Because working memory was assessed pre- and post-exercise, their results further indicated

a selective improvement in relative RT [(post-exercise RT – pre-exercise RT) / pre-exercise RT] during task conditions requiring greater amounts of working memory maintenance. Importantly, the observed facilitation on working memory was sustained for at least 30 minutes following exercise cessation. These findings from Pontifex et al. (2009) echoed the speculation that exercise intensity may be an important intervention component of sustained facilitation on working memory maintenance after a longer delay during the post-exercise period.

In addition to behavioral indices, the process of cognitive preparation during working memory operation was assessed through the examination of CNV between S1 and S2 during the Sternberg task. Research on CNV has indicated an inverted-U relationship between CNV amplitude and arousal level (Tecce, 1972). Empirical evidence also replicated similar association of CNV amplitude with arousal level and behavioral performance using measures of HR, eye-blink rate, and RT during a short-term memory task (Tecce, Favignano-Bowman, & Meinbresse, 1976). Specifically, smaller CNV amplitude, along with increased HR, eye-blink rate, and RT, were observed in the task condition that required maintenance of information compared to those conditions which did not. These findings were interpreted to suggest that the demand of maintaining information in mind tends to elevate arousal levels, and heightened arousal levels might result in impaired behavioral performance and underlying cognitive preparation, as indexed by decreased CNV amplitude. Similar

associations among CNV, arousal, and cognitive performance were observed in acute exercise research (Kamijo et al., 2004), with larger amplitude for both iCNV and tCNV amplitude following MICE compared to inactive control and continuous exercise at other intensities, particularly high-intensity exercise. Although such differential modulations in CNV amplitude did not couple with differences in response accuracy and RT during the cognitive task, the lack of behavioral changes was interpreted as the result of simplicity of the task. Findings from that study suggested that the process of stimulus orienting and motor preparation may be enhanced at an optimized arousal level following a single bout of MICE.

However, instead of replicating Kamijo's findings, the current investigation indicated no changes in iCNV nor tCNV amplitude following MICE, while HIIE resulted in increased amplitude of frontal iCNV, but not tCNV, compared to seated rest. Given that iCNV has been closely related to arousal process (Tecce, 1972), such selective increases in iCNV amplitude at frontal regions following HIIE suggested a more optimized arousal level that was associated with enhanced stimulus orienting processes. Further, this HIIE-induced iCNV modulation might be in favor of behavioral performance, as a reduced overall RT was observed. Although the lack of CNV modulation following MICE was opposite to predictions of the present investigation, such unexpected findings may be related to the length of delay prior to the administration of the Sternberg task. In the current investigation, the Sternberg task began after approximately a 25-minute delay and was not completed until 50 minutes

following exercise cessation. Thus, it is possible that arousal levels following MICE already subsided and returned to a level that was lower than optimal. In contrast, although arousal levels might be excessive immediately following HIIE, it may have returned to the optimized zone to support performance during the Sternberg task. This argument was supported by the HR data, as the HR after completion of the Sternberg task following HIIE remained as elevated as the HR prior to the first cognitive task following MICE (see Figure 3.1).

Despite the finding that HIIE induced an optimal arousal state for cognitive preparation, modulation in tCNV activity was not observed. The functional significance of tCNV has been thought to reflect various processes such as attentional anticipation, motor preparation, and information retention for a pending stimulus (Ruchkin, Johnson, Grafman, Canoune, & Ritter, 1997; Tecce, 1972). Therefore, one possibility of the unchanged tCNV paired with increased iCNV amplitude is that HIIE may selectively affect arousal processes but not influence other preparatory processes during the foreperiod prior to S2 and following S1. This possible interpretation appears appropriate given that the exercise-induced increase in tCNV amplitude was observed during a monotonous simple RT task, which did not require various complexed controlled processes (Kamijo et al., 2009). In contrast, the Sternberg task employed in the present investigation required individuals to maintain temporarily stored letter arrays and compare letter in each array with the subsequent target probe letter. The

complexity of such working memory operation may attenuate the modulations of tCNV as a function of exercise-induced changes in arousal.

In sum, findings from the Sternberg task suggest that acute HIIE, but not MICE, facilitated working memory maintenance assessed 25-50 minutes following exercise cessation. Such improvements following HIIE were coupled with increased iCNV amplitude, suggesting an optimal level of arousal that is beneficial for the orienting process related to working memory operation.

Mechanisms

Accumulating evidence from animal and human studies has explored the association between the peripheral biomarkers in response to acute exercise and exercise-induced facilitation on cognitive performance. Specifically, McMorris, Turner, Hale, and Sproule (2016) have proposed a catecholamine hypothesis to explain the interaction between acute exercise and cognition. That is, acute exercise, as a stressor, affects cognition through activating the reticular-formation, a set of interconnected nuclei that play a crucial role in the arousal system located throughout the brainstem. When exercise induces substantial increases in the concentration of circulating catecholamines such as norepinephrine (NE), NE can cross the blood-brain barrier to initiate a series of interactions that stimulate the locus coeruleus (LC), the principal site for brain synthesis of NE within the reticular formation. Such LC stimulation of the reticular formation may facilitate cognitive performance through improved

attention and vigilance (Kinomura, Larsson, Gulyas, & Roland, 1996). In addition to the arousal-mediated general facilitation on cognition, LC-induced NE activity may exert a potent modulatory effect on cognitive performance relying on the PFC and hippocampus (Berridge & Waterhouse, 2003). Accordingly, McMorris et al. (2016) argued that exercise-induced increases in catecholamine activity may benefit attentional/perceptual, working memory, and memory processing. However, this argument has been challenged given that most of the evidence supporting cellular and molecular cascades in response to acute exercise are from animal studies (McMorris, 2016), and that some human studies have failed to find correlations between exercise-induced changes in catecholamines and cognitive performance (McMorris, Collard, Corbett, Dicks, & Swain, 2008, Winter et al., 2007). Furthermore, researchers argued that the catecholamine hypothesis should be mainly used to interpret cognition during exercise because exercise-induced increases in catecholamines returned to baseline rapidly (Dietrich & Audiffren, 2011). Nevertheless, it is important to note that exercise at higher intensities typically results in greater elevation in catecholamines, and such increases might be sustained during the recovery period up to 2 hours following exercise cessation (Børsheim et al., 1998), indicating that intensity-dependent catecholamine modulation may play a role in the observed larger and longer cognitive improvements following HIIE compared to MICE within the present investigation. Clearly, future studies on the relationship between catecholamine activity and cognition in response to acute exercise

are necessary before concluding catecholamines are a mechanism to interpret the beneficial effects of acute exercise on human cognition.

Another possible mechanism underlying enhancement in cognition following exercise is the increase in brain-derived neurotrophic factors (BDNF) that accompany exercise participation. The role of BDNF in supporting the survival of existing neurons and the growth and differentiation of new neurons and synapses is well established (Bekinschtein, Cammarota, Izquierdo, & Medina, 2008). Acute exercise research has indicated that a single bout of exercise increased peripheral concentration of BDNF (Ferris et al., 2007; Griffin et al., 2011; Hwang, Brothers et al., 2016; Lee et al., 2014; Skriver et al., 2014; Winter et al., 2007). In addition, the release of BDNF in the brain contributes to 70-80% of exercise-induced increases of peripheral BDNF (Rasmussen et al., 2009), which could be sustained for up to 60 minutes following exercise (Knaepen, Goekint, Heyman, & Meeusen, 2010), and were paralleled by enhanced performance during a variety of tasks assessing cognitive control and memory (Ferris et al., 2007; Griffin et al., 2011; Hwang, Brothers, et al., 2016; Skriver et al., 2014; Winter et al., 2007). Furthermore, research indicated that exercise-induced BDNF concentration predicted cognitive performance during PFC-dependent (Hwang, Brothers, et al., 2016) and hippocampal-dependent tasks (Skriver et al., 2014; Winter et al., 2007), suggesting the possibility that exercise-induced peripheral BDNF concentration may be associated with facilitation on cognition post-exercise. Moreover, exercise at higher

intensities was associated with larger elevations of BDNF concentrations (Ferris et al., 2007; Vega et al., 2006; Winter et al., 2007), as well as greater facilitation on cognition (Ferris et al., 2007; Lee et al., 2014; Skriver et al., 2014; Winter et al., 2007), particularly when cognitive demand increased (Ferris et al., 2007). This suggests that HIIE may result in disproportionally larger facilitation on cognition via greater exercise-induced BDNF responses compared to MICE.

In addition, studies have suggested the possibility of serum lactate as a possible candidate to explain the effects of acute exercise on cognitive function. Tsukamoto et al. (2016) found that enhanced inhibitory control was paralleled by increased serum lactate following both MICE and HIIE relative to baseline. Specifically, HIIE exhibited larger and longer lasting increases in blood lactate, which coincided with a prolonged improvement in inhibitory control compared to MICE. Similarly, other research has indicated that high-intensity exercise resulted in increased blood lactate and decreased P3 amplitude compared to MICE (Kamijo et al., 2004, 2007). Given that the brain shifts energy sources from glucose to lactate due to exercise-induced decreases in cerebral glucose uptake (van Hall et al., 2009; Rasmussen, Wyss, & Lundlby, 2011), exercise-induced accumulation of serum lactate may affect brain metabolism, particularly in the frontal cortical regions, as a function of exercise intensity (Kemppainen et al., 2005). Further, evidence from animal studies also indicated the importance of brain lactate to ensuring energy availability during

the process of memory formation (Steinman, Gao, & Alberini, 2016; Suzuki et al., 2011). Thus, it is plausible that the observed differential effects of HIIE and MICE on cognitive performance and the neuroelectric underpinnings are the result of the differential effects of these two types of exercise on lactate production and metabolism.

Lastly, modulations in cerebral blood flow (CBF) in response to exercise may serve as a possible mechanism accounting for exercise-induced changes in cognitive performance. Dietrich (2003; 2006) has proposed a transient hypofrontality hypothesis to explain impaired performance in executive control tasks during exercise. This hypothesis argued that redistribution of metabolic resources during exercise, as reflected by CBF, would cause reduced activation in PFC, resulting in impaired performance during PFC-dependent tasks. However, after a delay following the cessation of exercise, studies have shown that a single bout of MICE increased dorsolateral PFC activation as measured by near-infrared spectroscopy (NIRS, Byun et al., 2014; Yanagisawa et al., 2010). Such increased frontal activation corresponded with enhanced performance on PFC-dependent tasks requiring operations of central executive processing (Byun et al., 2014; Yanagisawa et al., 2010). Moreover, Lambrick, Stoner, Grigg, and Faulkner (2016) indicated that improved inhibitory control following intermittent exercise was related to activation over PFC, while MICE only resulted in smaller improvements that were unassociated with prefrontal activation. Accordingly, these findings suggest that increased blood flow and oxygenation in the PFC

may be associated with acute exercise, especially the additional benefit of interval exercise verses continuous exercise, on cognitive function.

Limitation

Despite the findings of the present investigation being well-supported by the aforementioned mechanisms, the presence of certain limitations is worth noting. First, given the fixed order of cognitive tasks, the observed changes in performance of each cognitive domain following exercise were confounded by the temporal relation of task administration to exercise cessation. For instance, improved performance during free-recall and flanker tasks, but not the Sternberg task, following MICE was not necessarily indicative of selective facilitation on long-term memory and inhibitory control, as working memory might be improved if the Sternberg task was performed at an earlier time point following MICE. Future research will need to address this limitation to determine the effects on the various cognitive domains. Second, the lack of a pretest prior to each condition limits the interpretation of exercise-induced changes in cognition within each condition. For instance, Pontifex et al. (2015) indicated that following MICE, P3 amplitude was sustained relative to pretest whereas the non-exercise condition resulted in decreased P3 amplitude compared to pretest. The findings were interpreted to suggest that the allocation of attentional resources was maintained rather than increased following a single bout of exercise. Thus, future research should endeavor to assess cognition before and after acute exercise bouts to account

for time-related variation in behavioral and neuroelectric measures. Third, the age range of the participants in the present investigation was restricted from 18 – 30 years old. As a paucity of studies directly comparing the effects of HIIE versus MICE on cognition outside of this age range, future research is warranted to examine additional age groups, particularly children and older adults, whose cognitive function and brain health may benefit more from exercise due to the rapid brain development and age-related cognitive decline in these populations. Lastly, as the ultimate goal of this investigation was to optimize the exercise prescription, the observed effects of HIIE and MICE in well-controlled laboratory setting require further examination for the purpose of facilitating learning, productivity, and rehabilitation in the real-life environment.

Conclusion

In conclusion, although existing literature has suggested the beneficial effects of acute exercise on cognition, less well-known is how to maximize such benefits through optimizing the prescription of exercise. Thus, the present investigation aimed to determine whether HIIE could be an alternative acute exercise prescription for enhancing cognitive function during the recovery period following exercise. The findings indicated that HIIE resulted in similar, yet differential, improvements of behavioral performance during tasks assessing inhibitory control, working memory, and long-term memory compared to MICE. Such differential effects were coupled with different patterns of brain implementation, with the neuroelectric

activity following MICE characterized by increased allocation of attentional resources while HIIE led to more efficient fashion of brain activation as indexed by faster processing speed and enhanced cognitive preparation. Collectively, the results of this investigation added to the literature by not only corroborating the importance of exercise intensity as a possible modulator of the relationship between acute exercise and cognition, but also substantiating HIIT as a feasible approach for generating transient benefits on cognition beyond that following traditional MICE. Accordingly, the present findings may serve to inform the public that HIIE might be an alternative approach for gaining transient beneficial effects on cognition.

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