# The neural correlates of human cognition during aerobic exercise

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# TABLE OF CONTENTS

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*“How vain it is to sit down to write when you have not stood up to live!”*

*– Thoreau*

# 1 INTRODUCTION

## 1.0 Summary

The intuition that cognitive performance can improve during aerobic exercise is by no means revolutionary. As was extolled by Pliny the Younger before the end of the 1st century C.E., "…it is a wondrous thing how the mind is stirred up by the agitation and movement of the body" (Edwards, 2008). In the late 19th century, the psychologist and existentialist Freidrich Nietzsche similarly espoused the concurrent benefit that aerobic activity can have on the mind. Seizing on the claim of his contemporary Gustav Flaubert that "one cannot think and write except while sitting down", Nietzsche retorted "Here I have got you, nihilist! A sedentary life is the real sin against the Holy Spirit. Only those thoughts that come while walking have any value." (Nietzsche 2018).

This long-standing notion has attracted a growing community of present-day cognitive scientists and psychologists, who have produced a concerted effort to better understand the functional bases of how various forms of aerobic activity might influence cognitive performance. Indeed, engaging in aerobic exercise has been indicated by several meta-analyses to have a small positive effect on concurrent cognitive performance, with low to moderate cardiovascular workloads most frequently providing benefits, of which speeded processing is most prevalent (Chang, Labban, Gapin, & Etnier, 2012; Lambourne & Tomporowski, 2010; Ludyga, Gerber, Brand, Holsboer-Trachsler, & Pühse, 2016; McMorris & Hale, 2012). Nevertheless, the neurocognitive underpinnings of these effects have rarely been investigated while exercise has taken place. This can be largely attributed to the sensitivity of conventional neurocognitive measures to both motion and myographic artifacts, leading a vast majority of researchers to only monitor neural correlates before and/or after periods of aerobic effort, rather than immediately during. However, over the past decade, the advent of compact, mobile electroencephalographic (EEG) recording devices, along with advancements in signal processing such as independent-component analysis (ICA), have rendered the collection of robust event-related potentials (ERPs) possible, even during full body motion (see De Sanctis Butler, Green, Snyder, & Foxe, 2012; Gramann, Gwin, Bigdely-Shamlo, Ferris, & Makeig, 2010; Gwin, Gramman, Bigdely-Shamlo, Ferris, & Makeig, 2010; Nathan & Contreras-Vidal, 2016; Reis, Hebenstreit, Gabsteiger, von Tscharner, & Lochmann, 2014). Therefore, the intent of the doctoral project outlined in this dissertation was to investigate the influence acute aerobic exercise can have on concurrent cognitive performance, both overtly in terms of behavioural measures, but also covertly as referenced by well-established ERP indices.

The proceeding sections of this introductory chapter will detail the physiological basis of the exercise-cognition interaction to elucidate how and why cognitive performance might be modulated during aerobic activity, then review the state of current findings to this regard. An original study will be presented in each of the following two chapters, both of which combine behavioural and EEG measures to investigate performative aspects of visual cognition during aerobic exercise. The study presented in chapter 2 explores the influence of moderate-intensity exercise within two postural modalities (sitting and standing) on the performance of a visual working memory (VWM) retro-cue task, testing the ability of observers to briefly maintain then accurately recall visual information. Behaviourally, both moderate-intensity exercise and standing were found to elicit faster responding (as compared to resting or sitting), while standing additionally enhanced response accuracy. Further, the neural origins of the speeded responding could be temporally isolated using lateralized ERPs, which reflected expedited processing specifically between the cognitive stages of accessing working memory and selecting an appropriate motor response. The study presented in chapter 3 investigates the effect of both low and moderate-intensity exercise on attentional processing, using an additional-singleton paradigm (ASP) visual search task to examine the executive control of attentional selection. In addition to response times becoming gradually faster with increasing cardiovascular workload, ERPs reflected enhanced goal-driven attentional processing specifically during low-intensity exercise. Finally, in chapter 4, a concluding discussion will then examine the results of these experiments and their implications for future studies.

## 1.1 Cognitive resources during aerobic exercise

Executive functions and the neural mechanisms subserving them are considered to be both resource-limited and resource-competitive, their performative scope and/or efficiency becoming taxed when processing demands exceed resource availability (Broadbent, 1958; Franconeri, Alvarez, & Cavanagh, 2013; Miller & Cohen, 2001). For example, the simultaneous engagement of multiple cortical networks could induce resource competition, resulting in a degraded performance of one or several networks at the expense of another. This basic principle informs the reticular activating hypofrontality (RAH) theory, which predicts reduced executive performance during exercise (Dietrich & Audiffren, 2011). Mechanistically, the theory suggests that during exercise, networks governing implicit functions such as motor-control are afforded the resources necessary to do so at the expense of frontal networks governing explicit functions such as executive control. Importantly, this theory assumes the global cache of neural resources to remain relatively static, or to at the very least not be significantly modulated during exercise, therefore inducing a highly competitive reallocation of resources between networks. For example, the theory would suggest that maintaining coordinated bodily movements when running down a steep hillside should likely take precedence over maintaining peak attentional control or working memory capacity, and thus motor control should be supplemented at the expense of executive control.

However, various lines of evidence indicate that the assumption of a static pool of neural resources may not hold during physical activity. As such, resource competitions between the executive control and motor networks may not always pose as substantial a threat to cognitive performance as the RAH would assume. While the absolute volume of neuronal populations can indeed be considered acutely fixed, the global and local availability of haemodynamic, metabolic, and endocrinological factors fuelling neuronal function are shown to be dynamically modulated across various cardiovascular workloads (Hellstrom, Fischer-Colbrie, Wahlgren, & Jogestrand, 2017; Rooks, Thom, McCully, & Dishman, 2010; Secher, Seifert, & van Lieshout, 2008). In other words, the concentration and rate at which various neuronal resources are delivered and/or produced can both increase and decrease from a resting baseline, depending on their systemic availability and utilisation. The dynamic influence acute aerobic exercise can have on concurrent cognitive performance is generally regarded as being driven by these modulations, although the precise dynamics of this relationship remain largely unexplored (Chmura, Nazar, & Kaciuba-Uscilko, 1994; Kashihara, Maruyama, Murota, & Nakahara, 2009; McMorris, Tomporowski, & Audiffren, 2009; McMorris, Davranche, et al., 2009; Secher et al., 2008). The following subsections will provide an overview of the resource modulations observed during exercise across both the cerebral haemometabolic and endocrinological domains.

### 1.1.1 Cerebral haemometabolic effects of exercise

Despite having a primarily oxidative metabolism, neurons do not store their own glycogen, therefore requiring a constant supply of oxygen ($O_2$) and other energetic substrates in order to maintain metabolic activity (Inoue, Matsukado, Goto, & Miyamoto, 1988). These metabolic requirements of the brain are by no means miniscule; even in a resting state, approximately 20% of all $O_2$, and 20-25% of all glucose available in the cerebral blood flow (CBF) are consumed (Clarke & Sokoloff, 1999; Mink, Blumenschine, & Adams, 1981). As neuronal populations become active, regional CBF can be elevated by up to 30%, increasing the local blood-oxygen saturation ($sO_2$) to compensate for greater metabolic demands (Fox & Raichle, 1986; Gusnard & Raichle, 2001; Villringer, Them, Lindauer, Einhäupl, & Dirnagl, 1994). It is thus reasonable to predict that neuronal populations would be relatively sensitive to systemic haemometabolic modulations (e.g., the rate of blood flow and concentration of metabolites therein), and as one might expect, such modulations are found to occur during exercise (Secher et al., 2008).

Although at least partially due to greater cortical activity, the majority of the systemic haemometabolic response during exercise is due to muscular recruitment. As such, the potential for a neurometabolic surplus may arise when this response "overshoots" physiological demands, or in other words, when a greater volume of resources is made available in the CBF than are otherwise systemically consumed or cortically necessary. This indeed seems to be the case, although the presence of a neurometabolic surplus may be largely dependent on whether cardiovascular workloads are maintained within a sub-maximal range of aerobic intensities. The CBF increases by up to 30% during exercise workloads falling between the aerobic and anaerobic ventilatory thresholds (VT1 & VT2; also referred to as the inter-threshold area, or *ITA*). Conversely, during higher-intensity workloads ranging from VT2 to the maximal aerobic capacity ($VO_2$ max), there is a general “oxygen debt” in the bloodstream, as muscular demands exceed the available supply. This results in a substantial compensatory breathing rate increase, gradually reducing the concentration of carbon dioxide ($CO_2$) in the blood, which in turn instigates cerebral vasoconstriction, causing the CBF to decrease (Bain & Ainslie, 2014; González-Alonso et al., 2004; Querido & Sheel, 2007; Willie et al., 2012). Similarly, the $sO_2$ of the prefrontal cortex (PFC) shows a quadratic response to incremental exercise, exceeding neural demands during workloads within the ITA, but then rapidly decreasing from VT2 onwards (Rooks et al., 2010). These findings demonstrate that while both the CBF and $sO_2$ of the PFC are elevated during ITA workloads, this surplus is generally exhausted during cardiovascular demands exceeding the anaerobic turning point (VT2). Regardless, both the oxygen extraction fraction (OEF) and metabolic rate of oxygen (CMRO2) for cerebral tissue increase during moderate exercise, providing some evidence for the presence of enhanced neurometabolic utilisation capacity when the suggested surplus is available (Smith & Ainslie, 2017).

An accumulation of lactate in the blood during exercise may provide an additional source of neurometabolic supplementation. At rest, the cerebral metabolic ratio (CMR; defined as the ratio of $O_2$ to glucose + ½ lactate uptake) is ~6:1, indicating resting neuronal metabolism to be almost entirely glucose dependent, as complete glucose oxidation requires six $O_2$ per glucose (Bélanger, Allaman, & Magistretti, 2011; Hyder et al., 2006; Ide, Schmalbruch, Quistor, Horn, & Secher, 2000; Rasmussen, Wyss, & Lundby, 2011; Zhang et al., 2014). However, lactate concentrations subtly rise to between 2 – 3 mmol/dl during workloads within the ITA, and beyond VT2, can exponentially increase to as high as 30 mmol/dl (Goodwin, Harris, Hernández, & Gladden, 2007). Because the neuronal uptake of lactate is proportional to its arterial concentration, this causes the CMR to gradually decrease when peripheral lactate begins to accumulate in the blood. This results in a CMR of ~3:1 during exercise within the ITA, and as low as 1.7:1 during physical efforts above VT2 – indicating that as lactate is introduced to the CBF, it is increasingly utilized as a neurometabolic resource (Boumezbeur et al., 2010; Dalsgaard & Secher, 2007; Gallagher et al., 2009; Rasmussen et al., 2011; Secher et al., 2008; Van Hall et al., 2009; Volianitis, Rasmussen, Seifert, Nielsen, & Secher, 2011). This has led to the suggestion that neurons may somewhat preferentially metabolise lactate during exercise, even when being abundantly supplied with $O_2$ (Magistretti & Allaman, 2015; Rasmussen et al., 2011; Wyss, Jolivet, Buck, Magistretti, & Weber, 2011). However, it is important to note that anaerobic respiration is markedly less energetically efficient than aerobic respiration. As such, it may be that a heightened blood-lactate concentration can only produce neuronal benefits prior to the $sO_2$ beginning to decline. This is at least somewhat evidenced by the finding that a greater neurometabolic utilization of both $O_2$ and lactate has been shown specifically under workloads where a concurrent increase in the $sO_2$ and lactate concentrations of the CBF was present (González-Alonso et al., 2004).

### 1.1.2 Cerebral endocrinological effects of exercise

Another avenue through which exercise is suggested to influence cognitive performance is by inducing a heightened state of arousal, or in other words, the level of psychological and physiological preparedness to perform cognitive tasks (Revelle & Loftus, 1990). Importantly, it has long been hypothesised that cognitive performance demonstrates an "inverted-U" pattern in response the present state of arousal – with performance being reduced during low and high states, but enhanced during more moderate states (Hebb, 1955). As engaging in aerobic exercise is considered one of the most potent "arousal-inducing" factors, the pattern of cognitive performance in response to incremental exercise has been predicted following this same inverted-U pattern (Cooper, 1973; Davey, 1973; Kashihara et al., 2009, Oxendine, 1984, Raglin & Hanin, 2000).

The term "arousal" is in essence only descriptive of an affective mental state. Mechanistically however, the cognitive effects described as arousal are driven by modulations to the availability and concentration of endocrinological factors; that is, hormonal neurotransmitters such as norepinephrine, dopamine, and serotonin. Accordingly, acute aerobic exercise has been shown to increase the endocrine production of these neurotransmitters in both humans and animals alike (McGaugh, 1983; McMorris, Tomporowski, et al., 2009; McMorris, Davranche, et al., 2009; Meeusen, Piacentini, & De Meirleir, 2001). The cerebral concentration of norepinephrine and dopamine metabolites have also been found in animal studies to be elevated both during and following exercise, indicating their neurometabolic processing to have increased (Gerin & Privat, 1998; McMorris, Tomporowski, et al., 2009; McMorris, Davranche, et al., 2009). Further, the PFC in humans demonstrates an inverted-U pattern of performative modulation in response to the concentration of these catecholamines, with moderate increases promoting efficient functioning of the dorsolateral PFC in particular (Arnsten, 2011).

Although it remains to be determined whether the increased cortical and circulatory availability of endocrinological factors observed during exercise directly influences executive control, an inverted-U relation between cardiovascular workload and cognitive performance has been established meta-analytically (McMorris & Hale, 2012). Further, speeded performance during low to moderate intensity exercise has been correlated with moderately increased concentrations of norepinephrine, adrenaline, and corticotrophin in the bloodstream (Chmura et al., 1994; McMorris & Graydon, 2000; McMorris, Tomporowski, et al., 2009; McMorris, Davranche, et al., 2009). Moreover, improved memory consolidation – a process subserved by norepinephrine, dopamine, and serotonin pathways – has also been related to moderate levels of arousal (Nielson & Powless, 2007). As such, it is reasonable to suspect that the cerebral endocrinological effects of exercise should influence cognitive performance similarly to any other arousal-inducing factor, with benefits likely being most prominent during ITA workloads.

## 1.2 Cognitive performance during exercise

Although the aforementioned haemometabolic and endocrinological modulations suggest a likely facilitation of cognitive performance particularly during ITA workloads, the actual findings between individual studies have proven somewhat conflicting. For example, Dietrich and Sparling (2004) used the paced auditory serial-addition task (PASAT) to provide evidence in support of the RAH, finding working memory (WM) performance to be *reduced* during moderate exercise, whereas the performance of tasks requiring less substantial executive control remained unaffected. By contrast, other studies using the same PASAT paradigm have shown both children and young adults to effectively maintain equivalent levels of WM performance between rest and moderate exercise (Drollette et al., 2014;

Komiyama et al., 2015), while others still have shown performance of the PASAT to *improve* during moderate workloads (Martins et al., 2013). Further examples of reported cognitive benefits include expediated goal-driven attentional orienting (Pesce, Cereatti, Forte, Crova, & Casella, 2011; Pesce, Tessitore, Casella, Pirritano, & Capranica, 2007), enhanced feature selection in the lateral periphery (Hüttermann, Memmert, & Simons, 2014), and speeded responding in a sustained attention task (González-Fernández, Etnier, Zabala, & Sanabria, 2017), each alluding to a facilitation of top-down attentional control. Conversely, Davranche and colleagues found the magnitude of the Simon effect to increase during exercise, suggesting that executive control as referenced by response inhibition may have become impaired (Davranche & McMorris, 2009).

Several studies have employed EEG to monitor the neural correlates of performative enhancements *following* bouts of aerobic exercise, demonstrating, for example, enhanced CNV amplitudes reflecting better WM performance (Ludyga et al., 2018), and increased P3 amplitudes with improved response inhibition (Hillman et al., 2015). Still, only a handful of prior studies have employed EEG to monitor individual processing events *during* exercise (e.g., Bullock, Cecotti, & Giesbrecht, 2015; de Sanctis, Butler, Malcolm, & Foxe, 2014; Grego et al., 2004; Olson et al., 2016; Pontifex & Hillman, 2007; Yagi, Coburn, Estes, & Arruda, 1999). These have almost exclusively focused on non-lateralized ERP waves, and as was the case for the behavioural findings mentioned above, electrocortical effects have also proven inconsistent across cardiovascular workloads and cognitive tasks.

For example, the visual P3 is well suited to investigating the influence of aerobic exercise on executive performance, as its magnitude is thought to reflect attentional resource allocation, and its latency the speed at which visual objects are classified (Polich, 2007). I the performance of a visual odd-ball task during high-intensity exercise (≈ VT2), Yagi and colleagues (1999) found speeded responding to be compromised by reduced accuracy, which was reflected by a speeded but reduced P3 wave. This finding would suggest that due to a reduction of attentional resources during exercise, attentional performance degraded despite faster object classification speeds, resulting in an exercise-induced speed-accuracy trade-off. By contrast, Pontifex & Hillman (2007) found moderate-intensity exercise (≈ ITA-median) to enhance the P3 during the performance of a flanker task, which would instead suggest that the allocation of attentional resources had increased. Bullock and colleagues (2015) also found differential electrocortical effects between conditions low (≈ VT1) and moderate exercise (≈ ITA-median) within a single experiment. Compared to rest, exercise was found to induce an earlier P3a relative to infrequent distractors and P3b relative to distractors during both exercise workloads. However, sensory processing as indexed by the P1 component (Woldorff et al., 1997) demonstrated a more rapid onset for targets, and a greater magnitude for frequent non-targets exclusively during low-intensity exercise, which was suggested to represent a workload-specific facilitation of sensory gain control.

## 1.3 Considerations for the present studies

Both the behavioural and electrocortical discrepancies between studies detailed above are likely a product of inconsistencies across several moderator variables also indicated in meta-analyses, including the age and cardiorespiratory fitness of individual participants, the duration and modality of exercise, and the cognitive domain being tested (Chang et al., 2012; Lambourne & Tomporowski, 2010; Ludyga et al., 2016; McMorris & Hale, 2012). Thus, it becomes evident that any observed or potential benefits of exercise are likely to reside within specific combinations of physiological and cognitive constraints, and that particular care should be taken to acknowledge those conditions in studies of this nature. Even so, the weight of both physiological and behavioural evidence points to a general propensity for cognitive benefits to be elicited within ITA workloads, providing a rational for comparing performance during these workloads to both rest and higher-intensity exercise.

Controlling for the cardiorespiratory fitness of individual participants is also of particular concern. It should be no surprise the cardiorespiratory fitness can be highly variable between individuals, and so normalising physiological efforts between individuals of different fitness levels can be challenging. Even between individuals of comparable age and fitness, cardiorespiratory parameters such as maximum heart rate (MHR), resting heart rate (RHR), systolic and diastolic blood pressure, and the oxygen carrying capacity of blood can differ substantially. Although some cognitive researchers have employed more physiologically sophisticated methodologies to standardizing workloads between subjects, the vast majority rely on much simpler measures, such as selecting a target percentage of

MHR. The dilemma with using solely MHR is that it is often estimated rather than directly tested, and entirely disregards the functional range of potential heart rates an individual can achieve. This range is referred to as the heart rate reserve (HRR), calculated as the difference between MHR and RHR. Relying on a percentage of HRR (% HRR) as determined per-individual will provide more comparable efforts than % MHR can alone (ACSM 2013). An even more sophisticated methodology would be to utilize spirometry to identify the unique respiratory thresholds of each participant, then target heart rates relative to those thresholds. However, because a spirometry system had not yet been acquired by our lab at the time, the experiments detailed in the following chapter relied on the % HRR methodology.

## 1.4 Central question

As stated previously, the intent of this dissertation was to investigate both the behavioural and neurocognitive influences acute aerobic exercise can have on concurrent cognitive performance. Of primary interest was to determine if performative benefits could be elicited within ITA workloads, while also exploring whether neurocognitive indices might elucidate the physiological basis of these benefits or illuminate more covert effects that would be otherwise inaccessible behaviourally. This was accomplished by recording EEG signals while participants performed well established visual working memory and attentional control tasks, both at rest and during bouts of acute aerobic exercise within the ITA. In each of the studies in following two chapters, the pertinent background information regarding visual working memory and attentional control, as well as the tasks utilized, will be provided respectively.

# 2 ELECTROENCEPHALOGRAPHIC EVIDENCE FOR IMPROVED VISUAL WORKING MEMORY PERFORMANCE DURING STANDING AND EXERCISE[1]

Gordon Dodwell, Hermann J. Müller, and Thomas Töllner

## 2.0 Abstract

While a substantial body of research has investigated the effects of aerobic exercise on cognitive performance, few have monitored exercise-concurrent cognitive processes via electroencephalography (EEG), and fewer still using an event-related potential (ERP) approach. As such, little is known regarding how the temporal dynamics of cognitive processing are influenced during aerobic activity. Here, we aimed to elucidate the influence of aerobic exercise on the temporal dynamics of concurrent visual working-memory (VWM) performance. Participants performed a VWM retro-cue task at rest and during aerobic exercise across two postural modalities: seated (using a stationary bicycle) and standing upright (using a treadmill). Three consecutive phases of the VWM processing pipeline were assessed by means of lateralized ERPs: access of VWM representations (CDA), response selection (sLRP), and response execution (rLRP). Aerobic exercise and upright posture were found to have significant effects on VWM performance, facilitating processing speed in the retro-cue task. This facilitation arose primarily at an intermediary stage between the phases of accessing VWM representations and response selection. Our findings hold implications not only for understanding the influence of aerobic activity on VWM, but also for contemporary models of VWM that are built exclusively on data recorded during stationary, seated conditions.

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[1] © 2018 The British Psychological Society. This is the accepted version of the following article: Dodwell, G., Müller, H. J., & Töllner, T. (2019). Electroencephalographic evidence for improved visual working memory performance during standing and exercise. *British Journal of Psychology*, 110(2), 400–427., which has been published in final form at [https://doi.org/10.1111/bjop.12352]. This article may be used for non-commercial purposes in accordance with the Wiley Self-Archiving Policy [http://www.wileyauthors.com/self-archiving].

## 2.1 Introduction

Acute aerobic exercise has been found to influence cognitive performance both subsequently and concurrently. While early reviews concluded this relationship to exhibit a small beneficial trend (e.g., Brisswalter, et al., 2002; Tomporowski, 2003), individual studies have yielded inconsistent results, leading to some obscurity surrounding the conditions under which effects are both present and positive. Following acute aerobic exercise, meta-analyses have indicated executive function-based cognitive control systems (e.g., working memory) to be particularly benefited, especially in terms of processing speed (Chang et al., 2012; Ludyga et al., 2016; McMorris & Hale 2012; Verburgh et al., 2013). Ludyga and colleagues (2016), for example, found exercise-induced executive facilitation following exercise to be independent of the cognitive domain measured, with a greater influence conferred by moderate aerobic workloads. However, the influence on executive performance during acute exercise is less clear, with several accounts providing contradictory theory and evidence regarding the direction of effects.

Mechanistically, the influence of acute aerobic exercise on cognitive performance is thought to originate from exercise-induced modulations to the cortical concentration, allocation, and utilization of haemodynamic and endocrinological resources (Chmura et al., 1994; Kashihara et al., 2009; McMorris et al., 2009; Secher et al., 2008), although the dynamics of when and how these modulations influence cognitive processing, particularly during exercise, remains uncertain. Meta-analyses have revealed exercise intensity to be a particularly significant moderator of these effects, though the duration and postural modality of activity hold additional influence, as well as individual cardiorespiratory fitness (Chang et al., 2012; Labelle et al., 2013; Lambourne & Tomporowski, 2010; McMorris & Hale, 2012). Across a range of incremental increases in exercise intensity, concurrent cognitive benefits have been found to be most prominent during efforts at or near the aerobic threshold (VT1), with an optimal range from just below VT1 up to the lactate or anaerobic threshold (VT2). Below this range, performance tends to remain unchanged or show a slight decline, while above this range, performance generally degrades from VT2 to maximal aerobic capacity (VO2 max) (Kashihara et al., 2009, Rooks et al., 2010) (see table 1 for a classification of these terms).

**Table 1**. Example classification scale of exercise intensities, detailing relative comparisons between per cent max heart rate (% MHR), per cent maximal aerobic capacity (VO2 max), per cent heart rate reserve (% HRR), and perceived effort (on a scale from 1 to 10), categorized into 'exercise zones' additionally identified by their relation to effort-level and ventilatory benchmarks. This has been adapted by the author from previous such models (see Allen & Coggan, 2012; Garber et al., 2011; Karvonen & Vuorimaa, 1988)

| *Workload* | *% MHR* | *% $vO_2$ max* | *% HRR* | *Perceived Effort (1 – 10)* |
|---|---|---|---|---|
| Zone 0<br>'Rest'<br>$vO_2$ rest | < 57 | < 37 | < 30 | ≤ 2 |
| Zone 1<br>'Light'<br>Recovery | 57 – 63 | 37 – 45 | 30 – 39 | 2 – 3 |
| Zone 2<br>'Moderate'<br>Endurance | 64 – 76 | 46 – 63 | 40 – 59 | 4 – 5 |
| Zone 3<br>'Vigorous'<br>> VT1 | 77 – 95 | 64 – 90 | 60 – 89 | 6 – 7 |
| Zone 4<br>'Near-Maximal'<br>> VT2 | ≥ 96 | ≥ 91 | ≥ 90 | 8 – 9 |
| Zone 5<br>'Maximal'<br>$vO_2$ max | ≥ 99 | ≥ 99 | ≥ 99 | ≥ 9 |

The present study aimed to investigate the performance of an executive control process, namely the access to visual working memory (VWM), during two separate postural modalities of moderate aerobic exercise: seated (on a stationary bicycle) and standing upright (on a treadmill). We were particularly interested in what effect concurrent aerobic exercise and postural modality might have on both processing speed and response accuracy in a VWM task. In addition, ERPs corresponding to discrete stages of the cognitive processing pipeline were monitored to identify at what stage of processing these effects might occur, refining our understanding of the spatiotemporal nature of these interactions. Before we develop the precise question of the present study, we provide a brief review of (i) cognition during exercise and standing, (ii) the hemodynamic-metabolic perspective, (iii) the endocrinological perspective, and (iv) neuro-cognitive measures during exercise. Such a comprehensive overview appears warranted, given that we draw on a part of the literature that is hitherto only rarely represented in standard psychology work.

### 2.1.1 Cognition during exercise and standing

Given a finite pool of neural resources, information processing in the brain can be considered both resource-limited and resource-competitive (Broadbent, 1958). As cognitive workload increases, these resources must be allocated more widely, potentially giving rise to performance limitations (i.e., in speed or accuracy) (Franconeri, 2013). Following this logic, the reticular-activating hypofrontality (RAH) model (Dietrich, 2006; Dietrich & Audiffren, 2011) suggests that during exercise, the reallocation of neural resources towards networks involved in implicit functions such as motor-control (e.g., the reticular-activating system) may lead to a resource-limitation-driven inhibition of frontal and prefrontal networks involved in executive functions. This is proposed as an evolutionary means to maximize the efficiency of more automatic and movement-critical processes subserved by implicit systems, while downregulating frontal and pre-frontal networks less involved in maintaining movement, preventing performative interference via resource competition. The RAH model therefore predicts the performance of more implicitly driven stimulus-detection and motor-decision-based tasks to improve during exercise, while the performance of tasks requiring more explicitly driven executive functions would deteriorate. The latter includes systems such as VWM, requiring cognitive control to govern the selection, scheduling, and coordination of computational events (Meyer & Kieras, 1997; Norman & Shallice, 1986; Pontifex et al., 2009). The extent of frontal inhibition is suggested to depend on a 3-way interaction between muscle mass, exercise duration, and most importantly exercise intensity – where performance detriments are most prominent at or near the anaerobic threshold (VT2).

The predictions of the RAH have been supported in studies where executive performance deteriorated during acute aerobic exercise (e.g., Audiffren et al., 2009; Davranche & McMorris, 2009; Del Giorno et al., 2010; Dietrich & Sparling, 2004; Pontifex & Hillman, 2007). Dietrich and Sparling (2004), for example, demonstrated reduced working-memory performance in the paced auditory serial-addition task (PASAT) during moderate aerobic exercise, whereas no detriments were observed in tasks not heavily involving frontal or prefrontal networks, providing some evidence of localized inhibition. However, preadolescents have been found to produce equivalent performance during rest and exercise in working memory and inhibitory control (Drollette et al., 2014), as have young adults, even when performing under moderately hypoxic conditions (Komiyama et al., 2015).

A lack of inhibited performance does not necessarily rule out the possibility of hypofrontality, as it could be argued that the intensity or duration of exercise did not sufficiently effectuate resource competition. However, acute aerobic exercise has also been shown to enhance concurrent executive performance. Contrasting the findings of Dietrich and Sparling, Martins and colleagues (2013) found improved working-memory performance in the PASAT and Starnberg tasks during moderate aerobic exercise (Martins et al., 2013). Prior research has further demonstrated exercise-concurrent enhancements to additional executive functions, including enhanced cognitive flexibility and expedited task switching (Pesce & Audifferen, 2011), improved and speeded goal-directed attentional orienting (Cereatti et al., 2009), and more accurate feature-selective attentional allocation in the periphery (Hüttermann & Memmert, 2014). In contrast to the inhibition predicted by the RAH model, these findings suggest that during aerobic exercise, efficient deployment of both implicit motor control and explicit executive control can be either unimpeded or even facilitated. As such, aerobic exercise may hold the potential to maintain or even expand the pool of available neural resources.

The postural modality of exercise may also influence cognitive performance. A meta-analysis by Lambourne and Tomporowski (2010) indicated that while cognitive facilitation was observed following both treadmill running and stationary cycling, exercise-concurrent benefits tended to be cycling-specific (Lambourne & Tomporowski, 2010). This discrepancy was considered to result from the more pronounced dual-task costs of maintaining balance during upright as compared to seated posture. Indeed, sustained upright posture requires constant attentional engagement (Woollacott & Shumway-Cook, 2002), and the dorsolateral prefrontal cortex (DLPFC) has been indicated to play an important role in maintaining balance (Mihara et al., 2008). As with physical activity, however, research regarding the influence of upright posture on cognitive performance has produced mixed results (for reviews see Kelly et al., 2012; Schaefer & Schumacher, 2011).

The heterogeneity of findings in this area may be driven in part by spatial versus non-spatial processing demands. Kerr and colleagues (1985) found reduced visuospatial working-memory accuracy during sustained upright balance compared to sitting, but no effect for a non-spatial task, suggesting that visuospatial working memory and sensorimotor systems may overlap (Kerr et al., 1985). This proposal has been supported more recently by research elucidating the same dissociation, while additionally revealing selectively reduced fronto-parietal network (FPN) oxygenation during the spatial task via functional near-infrared spectroscopy (fNIRS) (Chen et al., 2018). Overlapping activation in brain areas governing visuospatial working-memory and sensorimotor processes has also been described via functional magnetic-resonance imaging (fMRI), particularly within the DLPFC and inferior parietal lobules (Anguera et al., 2010). Meanwhile, upright posture has been shown to improve performance in nonspatial tasks such as the Stroop paradigm, enhancing both processing speed and attentional selectivity (Rosenbaum et. al, 2017). Thus, it has been suggested that active spatial processing during increased postural control may generate greater dual-task interference for cognitive tasks involving spatial components (Fuhrmann et al., 2015).

### 2.1.2 The hemodynamic-metabolic perspective

Neurons do not maintain stores of glycogen; rather, having a primarily oxidative metabolism, they require a continuous supply of oxygen (O2) and other energetic substrates to ensure constant neurometabolic activity (Inoue et al., 1988). The resting brain consumes ~20% of O2 (Clarke & Sokoloff, 1999) and 20-25% of glucose (Mink et al., 1981) in the cerebral blood flow (CBF). Neuronal activation rapidly increases regional demand for and utilization of metabolic resources, elevating regional CBF (rCBF) by up to 30% and producing localized changes in blood-oxygen saturation (sO2) (Fox & Raichle, 1986; Gusnard & Raichle, 2001; Villringer et al., 1994). Thus, acute modulations to haemodynamic content and delivery influence cognitive performance, as is evident at rest under high-altitude hypoxia (Shukitt-Hale et al., 1994).

Astrocytes do however maintain glycogen stores, being metabolically driven by anaerobic glycolysis (Brown & Ransom, 2007; Dalsgaard et al., 2007). These stores act as a supplementary energetic reserve for neuronal metabolism. In response to neural activation, astrocytes convert glycogen to lactate, which is transferred to neurons by way of an astrocyte-neuron lactate shuttle, preserving neurometabolic function when energetic demands are high (Mächler et al., 2016; Mangia et al., 2009; Pellerin, 2005; Proia et. al., 2016). This is reflected by the cerebral metabolic ratio (CMR), defined as the ratio of O2 to glucose + ½ lactate uptake (Ide et al., 2000). The resting CMR is ~6:1 (Rasmussen et al., 2011), indicating that resting neuronal metabolism is almost exclusively dependent on glucose (a complete glucose oxidative reaction includes six O2 per glucose) (Bélanger et al., 2011; Hyder et al., 2006; Zhang et al., 2014). However, lactate increasingly serves as a neuronal metabolic resource as it becomes available in the CBF (Boumezbeur et al., 2010; Gallagher et al., 2009; Van Hall et al., 2009), having an uptake proportional to its arterial concentration (Rasmussen et al., 2011; Secher et al., 2008). As such, the CMR begins to decrease during exercise following peripheral lactate release (Secher et al., 2008). Although lactate from astrocytes can only briefly sustain neuronal function before glycogen depletion (Secher et al., 2008), it has been proposed that even in the presence of abundant oxygen, lactate may be the preferred energetic substrate for neuronal metabolism (Magistretti, & Allaman, 2015; Rasmussen et al., 2011; Wyss et al., 2011).

Aerobic exercise modulates cerebral hemodynamic and metabolic factors irrespective of neural activity. Mean CBF increases gradually during sub-maximal exercise (below VT2) by up to 20-30%, coupled with an increase in cerebral vascular conductance, whereas during more intense exercise (at or above VT2), CBF begins to decrease (Hellström et al. 1996; Ide et al. 1998; Secher et al., 2008). Similarly, cerebral sO2 in the prefrontal cortex (PFC) shows a quadratic response to incremental exercise, rising substantially from VT1 to VT2, then falling at intensities above VT2 and nearing VO2 max (Rooks et al., 2010). Below VT2, these increases far exceed neural demands (Obrig et al., 1996), preventing O2 supply from becoming a resource-limiting factor (Young & Reeves, 2002). While the plasma concentration of glucose typically remains relatively consistent between rest and exercise (Coggan, 1991), lactate levels follow a more exponential function, increasing gradually until VT2, after which increases as high as 30 mmol/dl can occur (Goodwin et al., 2007). As such, The CMR can decrease to below 3:1 during whole-body exercise (Dalsgaard & Secher, 2007), and as low as 1.7:1 during physical efforts above VT2

(Volianitis et al., 2008), indicating a substantial decrease in glucose oxidation due to the systemic presence of and neurometabolic supplementation by lactate (Rasmussen et al., 2011). Increased arterial sO2 as well as concentrations of glucose and lactate also induce increased neuronal metabolism (González-Alonso et al., 2004), suggesting the presence of these additional substrates may propagate increased activation.

Evidence for the hemodynamic-metabolic influence of exercise on cognitive performance has been growing recently, particularly through investigations employing fNIRS. Following sub-maximal aerobic exercise, improved Stroop performance has been correlated with exercise-induced increases in oxygenation of the DLPFC (Byun et al., 2014; Yanagisawa et al., 2010), a finding replicated in both upright and recumbent body postures (Faulkner et al., 2016). Given the indicated pattern of prefrontal sO2 during aerobic exercise (Rooks et al., 2010), similar facilitations might be expected during cardiovascular workloads between VT1 and VT2.

### 2.1.3 The endocrinological perspective

Arousal is a core concept in cognitive performance, defined here as the state of preparedness for stimulus detection and response dependent on physiological and psychological activation (Revelle & Loftus, 1990). Arousal is thought to adopt an "inverted-U" pattern, where under- and over-arousal decrease performance, while moderate arousal propagates optimal performance (Hebb, 1955). Considering exercise as an arousal-stimulating factor (Cooper, 1973; Davey, 1973; Kashihara et al., 2009), this "inverted-U" pattern has predicted cognitive performance during exercise (Oxendine, 1984; Raglin & Hanin, 2000), and has been proposed as a potential mechanistic underpinning to observed exercise-concurrent modulations in oddball task performance (Bullock et al., 2015). This pattern may be perturbed, however, in athletes with a high level of cardiovascular fitness, who show a maintenance of benefits even at higher workloads (e.g., efforts above VT2) (Hüttermann & Memmert, 2014).

Arousal describes an affective mental state mechanistically driven by endocrinological factors. Acute aerobic exercise has been shown in both human and animal studies to increase endocrine production of hormonal neurotransmitters, particularly norepinephrine, dopamine, and serotonin (McGaugh, 1983; McMorris et al., 2009; Meeusen & De Meirleir, 1995). While the interaction may be limited, peripheral release of catecholamines also promotes the availability of analogous neurotransmitters in the brain (Genuth, 1998). Animal studies have indicated elevated cerebral concentrations of catecholamine metabolites both during and following activity (Gerin and Privat, 1998; McMorris et al., 2009), suggesting increased neurometabolic processing of noradrenaline and dopamine. Similarly, plasma concentrations of catecholamines such as norepinephrine, adrenaline, and dopamine rapidly increase following shifts from supine or seated positions to an upright standing posture (Jacob et al., 1998; Smith et al., 1994). As such, posture-induced arousal has been claimed to be the second-most significant physical stressor to propagate catecholamine release, besides active exercise (Robertson et al., 1979).

Whether cortical endocrinological modulations during exercise directly affect human cognition remains uncertain. However, an exercise-concurrent increase in cortical and circulatory availability of endocrinological factors is apparent. Both norepinephrine and dopamine modulate prefrontal-cortex functioning in an inverted-U pattern such that moderately increased cortical concentrations facilitate activity, with the DLPFC being particularly reactive (Arnsten, 2011). Meta-analysis has also confirmed an inverted-U relationship between aerobic exercise and executive functions, indicating speeded performance during moderate aerobic workloads (McMorris & Hale, 2012), which in parallel has been correlated with increased circulatory concentrations of norepinephrine, adrenaline, and corticotrophin (Chmura et al., 1994; McMorris & Graydon, 2000; McMorris et al., 2009). Further, increased limbic activity due to stressors such as exercise has been related to improved memory consolidation (Nielson & Powless, 2007), a process sub-served by norepinephrine, dopamine, and serotonin pathways.

### 2.1.4 Neuro-cognitive measures during exercise

Due to the susceptibility of most neuro-cognitive measures to motion-based artefacts, prior attempts to better understand the mechanistic basis of cognitive effects during exercise have been somewhat limited. Most have opted to investigate neural correlates of this relationship in static, seated positions before and after periods of exercise (Gwin et al., 2010; Tomporowski, 2003). Several such studies have employed electroencephalography (EEG), demonstrating, for example, improved working-memory performance in the Sternberg item-recognition task with increased CNV amplitudes (Ludyga et al., 2018), increased flanker task accuracy coupled with decreased P3 latency and N2 amplitudes (Drollette et al., 2014), and improved response inhibition and cognitive flexibility with increased P3 amplitudes (Hillman et al., 2015). While these findings provide insight into the potential for an exercise-induced facilitation of the cognitive networks involved, how these indices might differ if monitored during exercise remains largely unexplored.

Fortunately, advancements in signal processing techniques and hardware now make exercise-concurrent EEG viable (see Nathan & Contreras-Vidal, 2016; Reis et al., 2014). For example, independent component analysis (ICA) can effectively extract not only blinks and saccades, but also motion artefacts (such as rhythmic body movements) from otherwise unusable cortical signals (Gwin et al., 2010; Lau et al., 2012). Mobile brain-imaging (MoBi) EEG systems have also been shown to produce typical ERP components between seated rest and during self-generated full-body motion such as walking (De Sanctis et al., 2012; Gramann, et al., 2010). Several studies have employed exercise-concurrent EEG to elucidate time-frequency modulations during exercise; however, monitoring the temporal dynamics of individual processing events is largely excluded in frequency-based approaches (Bullock et al., 2015), while an ERP-based approach is far better suited to investigating the temporal and characteristic nature of regionally specific cognitive processing events.

Studies employing an ERP-based approach during exercise have focused on the analysis of non-lateralized ERP waves, including the P1, N2, and P3 (e.g., Bullock et al., 2015; De Sanctis et al., 2014; Grego et al., 2004; Olson et al., 2016; Pontifex & Hillman, 2007). A recurrent finding has been expedited cognitive task performance during exercise coupled with increased P3b amplitude, suggesting a facilitation of later processing stages (De Sanctis et al., 2014; Grego et al., 2004; Olson et al., 2016; Pontifex & Hillman, 2007). However, a reduction in N2b amplitude has been identified in parallel, potentially sub-serving some observed decreases in response inhibition and error-monitoring performance (De Sanctis et al., 2014; Pontifex & Hillman, 2007). Faster reaction time in an oddball task during exercise has also been indicated to coincide with increased P1 amplitude and reduced P1 and P3a latency, considered as potential indicators of facilitated sensory gain and attentional engagement, respectively (Bullock et al., 2015). These findings illuminate dynamic shifts in processing that may underlie the directionally heterogenous and aspect-specific nature of observed effects on performance. However, no studies to date regarding the influence of acute exercise on concurrent cognitive performance have investigated the covert temporal dynamics of latent executive control processes such as VWM.

Because the visual and motor systems are largely organized contralateral to the hemifield or side of the body they monitor and control, several ERPs involved with this activity show greater activation in the hemisphere contralateral to the hemifield or side of the body where the target event or motor response occurred. Referred to as an event-related lateralization (ERL), several such components have been identified in relation to visual and motor activity and are often employed to investigate mental chronometry in 2-alternative forced-choice tasks. Two such ERL components are particularly informative for the present study: the contralateral delay activity (CDA), and the lateralized readiness potential (LRP). CDA serves to viably measure various aspects of VWM (Luria et al., 2016), likely originating from specific portions of the intraparietal sulcus (Robitaille et al., 2010). For instance, CDA can indicate the process of accessing visual target representations held in VWM (Dell'Aqua et al. 2010; Eimer & Kiss, 2010; Kuo et al. 2009). The LRP serves as an indication of lateralized motor preparation, such as preparing to produce a response with the left thumb (Coles, 1989), where the LRP is computed as either stimulus-locked (sLRP) or response-locked (rLRP) (Wiegand et al., 2013). The onset latency of the sLRP indicates the point in time at which a response has been selected by executive processes (Eimer, 1998; Töllner et al., 2012), while the rLRP onset reflects the amount of time needed by the motor system to produce this response (Miller et al., 1998).

### 2.1.5 Rationale of the present study

The aim of the present study was to investigate the influence of moderate acute aerobic exercise and body posture on the temporal dynamics of concurrent VWM performance. To this end participants performed a VWM retro-cue task adopted from Töllner et al. (2014, 2015) concurrently during conditions of rest and exercise across two postural modalities: seated on or pedalling a stationary bicycle, as well as standing or walking on a treadmill. Along with behavioural data, EEG was recorded with a focus on segregating and isolating three temporally consecutive and functionally distinct stages of the VWM processing pipeline: accessing actively held target representations (CDA), selecting a motor response (sLRP), and executing the selected motor response (rLRP) – providing a means to discern when and where exercise-driven cognitive modulations may occur (see figure 1 for an illustration of the processing pipeline).

Targeting an executive function such as VWM in this manner allows us to test the predictions of the RAH model, according to which concurrent aerobic exercise should produce a resource-limitation-driven inhibition of explicit processes governed by frontal neural networks, thus impairing VWM performance. However, if the pool of available resources is increased during exercise, the predicted inhibition might be reduced, negated, or even reversed towards facilitation. Further, if facilitations can be isolated to explicit processes executed by frontal neural networks, the predictions of the RAH model would be challenged under the conditions of the present study. Therefore, our first hypothesis was that during aerobic exercise targeting an optimal cardiovascular workload, the net pool of available resources should increase beyond neural demands, leading to a facilitation of frontal neural networks involved in executive processing, culminating in speeded VWM task performance and allowing these improvements to be temporospatially isolated via ERLs.

We additionally looked for differential performance between separate postural modalities of aerobic exercise while maintaining comparability with static, seated positions, allowing us to assess the potential for interference between the neural mechanisms governing posture regulation and spatial VWM while standing. In this regard, our second hypothesis was that increased processing interference between spatial aspects of VWM and sensorimotor systems during upright posture may result in identifiable deficits.

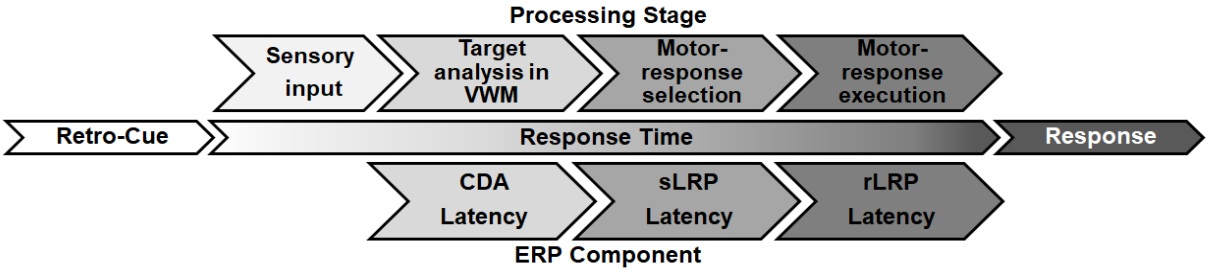

**Figure 1.** Schematic illustration of the cognitive processing pipeline for the retro-cueing task. Top row: stage of cognitive processing. Bottom row: ERP components which are used to represent the corresponding processing stage. Abbreviations: CDA – contralateral delay activity; sLRP – stimulus locked lateralized readiness potential; rLRP – response-locked lateralized readiness potential; ERP – event-related potential.

## 2.2 Materials and Methods

### 2.2.1 Participants

24 adult volunteers were paid to participate. 6 datasets were excluded from analysis: two due to sub- or supra-threshold heart rates (outside the targeted range), two due to high error rates (>20%), and two due to poor wireless signal quality. 18 participants (8 females, age = 24.5 ± 2.6, 2 left-handed, 1 ambidextrous) were included in the analysis. All participants provided written informed consent, reported normal or corrected-to-normal vision, and indicated they had no sign of neurological, cardiorespiratory, or neuromuscular illnesses. In addition, each participant was rated per an 11-point scale intended to predict functional aerobic capacity without direct testing (Jackson et al, 1990) (see table 2).

Participants were asked to be well rested, and to refrain from consuming alcohol the night before, or any tobacco or caffeine for at least 2 hours prior to the experiment. Their resting heart rate (RHR) was recorded during ~5 minutes of seated rest, while their maximum heart rate (MHR) was estimated using a standard formula [MHR = 220 – age] (Tanaka et al., 2001). These values were used to determine individual heart-rate reserve (HRR). HRR represents the difference between MHR and RHR (MHR – RHR), providing a metric of cardiovascular capacity that can serve as a relative measure of exercise intensity (Karvonen, & Vuorimaa, 1988). Targeting an active heart rate equal to a percentage of HRR added to RHR (% HRR) is particularly useful when standardizing efforts across individuals, as this accounts for variabilities in cardiovascular capacity and fitness (Swain & Leutholtz, 1997) (demographic information can be found in table 3).

**Table 2.** This 11-point scale is intended to predict a participants' functional aerobic capacity without direct fitness testing (Jackson et al., 1990). Participants were asked about their exercise habits and ranked per the categorizations listed here

| *Scale* | *Exercise Intensity* | *Exercise Frequency* | *Exercise Duration* |
|---|---|---|---|
| 0 | No Exercise | None | None |
| 1 | Occasional Light Exercise | Once Every 2 Weeks | Under 15 Minutes |
| 2 | | | 15 – 30 Minutes |
| 3 | | Once A Week | ~ 30 Minutes |
| 4 | | | ~ 45 Minutes |
| 5 | Regular Exercise | 2 – 3 Times A Week | 45 Min – 1 Hour |
| 6 | | | 1 – 3 Hours |
| 7 | | 3 – 5 Times A Week | 3 – 7 Hours |
| 8 | | Almost Daily | 7 – 11 Hours |
| 9 | Intense Exercise | Daily | 11 – 15 Hours |
| 10 | | | Over 15 Hours |

**Table 3**. Demographic information regarding participants, including means of age, resting heart rate (RHR) in beats per minute, max heart rate (MHR) in beats per minute, heart rate reserve (HRR) in beats per minute, fitness rating per the scale defined in Table 2, height in cm, weight in kg, and body mass index (BMI). Separate columns for each sex (n = 10 males, eight females) are present as well as a combined column for the entire sample of n = 18 participants

| *Measure* | *Male* | *Female* | *All* |
|---|---|---|---|
| Age | 25.0 ± 2.9 (22-30) | 23.9 ± 2.2 (20-26) | 24.5 ± 2.6 |
| RHR (BPM) | 60 ± 9.2 (45-70) | 54 ± 6.8 (45-65) | 57.5 ± 8.3 (45-70) |
| MHR (BPM) | 195 ± 2.9 (190-198) | 196 ± 2.2 (194-200) | 196 ± 2.6 (190-200) |
| HRR (BPM) | 135 ± 9.23 (126-150) | 142 ± 5.8 (132-150) | 138 ± 8.0 (126-150) |
| Fitness | 5.5 ± 1.4 (3-7) | 5.1 ± 1.6 (2-7) | 5.3 ± 1.5 (2-7) |
| Height (cm) | 176.3 ± 3.6 (173-183) | 163 ± 5.4 (155-170) | 170.4 ± 8.4 (155-183) |
| Weight (kg) | 72.8 ± 7.7 (68-92) | 58.3 ± 12.5 (45-82) | 66.3 ± 12.8 (45-92) |
| BMI (kg/m$^2$) | 23.4 ± 2.1 (22-28) | 21.8 ± 3.8 (19-30) | 22.7 ± 3.1 (19-30) |

### 2.2.2 Equipment

Exercise equipment included a treadmill and recumbent stationary bike (LifeFitness Club Series, Brunswick Corporation, Rosemont, IL USA). A heart rate monitor chest strap and smart watch (Models H7, M400, Polar Electro, Kempele, Finland) were used to monitor cardiovascular activity continuously at a 1 Hz sampling rate. The EEG system included 64 Ag/AgCl active electrodes connected to a wireless amplifier (Brain Products ActiCAP, MOVE, Munich, Germany). Data was sampled continuously at 1 kHz and electrode positions matched the international 10-20 system (American Electroencephalographic Society, 1994). One electrode was placed on the inferior orbit of the left eye to control for blinks. All electrodes were referenced online to FCz, and impedances were kept below 5 Ω.

### 2.2.3 Study design, hemodynamic controls, and task

The study utilized a 2x2 within-participants factorial design, with factors of activity state ("active" exercise vs. "passive" rest) and modality (seated vs. standing), rendering 4 conditions – bike active (Ba), bike passive (Bp), treadmill active (Ta), and treadmill passive (Tp). Each condition included 4 blocks of 96 trials each, totalling 384 trials per condition. The experiment took place in the basement of a large university building (LMU Department of Psychology), where temperatures are maintained between 20-22° C. All conditions were completed within a single session, with the order of conditions counterbalanced across participants, and adequate time given between active and passive conditions for participants to return to their RHR. On both the bike and treadmill, participants were positioned ~140 cm (55.12 in) away from a 69-cm (27 in) computer screen (1024 × 768 resolution, 85-Hz refresh rate).

In the active conditions, participants either walked on the treadmill (Ta) or pedalled the bicycle (Ba). In Ta, participants maintained a walking pace of 6.0 km/h, selected according to the maximum comfortable walking speeds determined by R.W. Bohannon (Bohannon, 1997). In Ba, participants maintained a pedalling cadence of 70-80 rpm, selected as a balance between minimizing movement without requiring a substantial increase in pedal resistance that might cause muscle fatigue. A target heart rate of 65% HRR and acceptable range of 60-70% HRR was employed based on the study of Kashihara et al. (2009), which suggests the cognitive benefits of aerobic exercise are likely to occur at or near the aerobic threshold (VT1), approximate to 60 % - 70 % of vO2max (equivalent to % HRR). Individual target HR ranged from 142–153 bpm.

Active conditions began following 5–10 minutes of warm-up within the same postural modality as the proceeding condition. During warm-up and throughout the experimental condition, exercise intensity was gradually modulated to achieve and maintain individual target HR. This was done via stepwise changes to the slope of the treadmill (increments of 0.5° ranging from 0°-12°), or the pedal resistance of the stationary bike (increments of 10 watts ranging from 0-250 watts), depending on active HR. Passive conditions began following 5–10 minutes of rest within the same postural modality as the proceeding condition, either standing on the treadmill (Tp) or sitting on the bicycle (Bp). HR was monitored throughout to ensure it did not exceed a resting threshold of 30% HRR as defined in table 3 (Karvonen & Vuorimaa, 1988; Garber et al., 2011; Allen & Coggan 2012). An increase in HR equal to 10% of RHR was anticipated moving from seated (Bp) to standing (Tp) postures, based on findings regarding typical changes in HR following postural shift (Smith et al., 1994).

Each trial started with a central white fixation cross (500 ms), followed by a memory array (200 ms) containing 8 colored shape stimuli, including 2 target singleton items and 6 homogenous distractors in a circular arrangement of positions equidistant from screen centre (radius: 4.6° of visual angle). The target singletons could differ from distractors independently along the same or separate dimensions (shape, colour), but were never identical and always appeared in opposite hemifields with their exact lateral location and dimensional relation randomized trial by trial. Colour variant targets included circles in cyan (CIE: 0.208, 0.305, 4), purple (CIE: 0.294, 0.158, 4), yellow (CIE: 0.422, 0.496, 4), or green (CIE: 0.298, 0.598, 4), while shape variant targets included blue (CIE: 0.143, 0.068, 4) squares, triangles, diamonds, or crosses. The homogenous distractors were always blue circles (CIE: 0.143, 0.068, 4) (see Töllner et al., 2014). At this stage, the participant was naïve regarding the identity of the target to which they would respond, needing to maintain both potential targets in VWM. Following a retention interval (1000±100 ms, jittered randomly by 20 ms), a retro-cue was displayed (200 ms), containing a single, centrally presented, coloured shape stimulus. In 2/3rds of trials, the retro-cue matched one of the target stimuli (valid-cue trials), while in the other 1/3rd of trials it did not (invalid-cue trials). For valid-cue trials, participants were instructed to respond corresponding to the hemifield location of the matching target, by clicking a mouse button with their left or right thumb, respectively. A time-out was registered if no response was given within 1200 ms of retro-cue onset. For invalid-cued trials, participants were instructed to give no response. Errors and time-outs were indicated to the participant by an immediate red minus symbol at screen centre (1000 ms). A jittered inter-trial interval followed the response window (950-1050 ms) (see figure 2 for a visualization of the trial sequence).

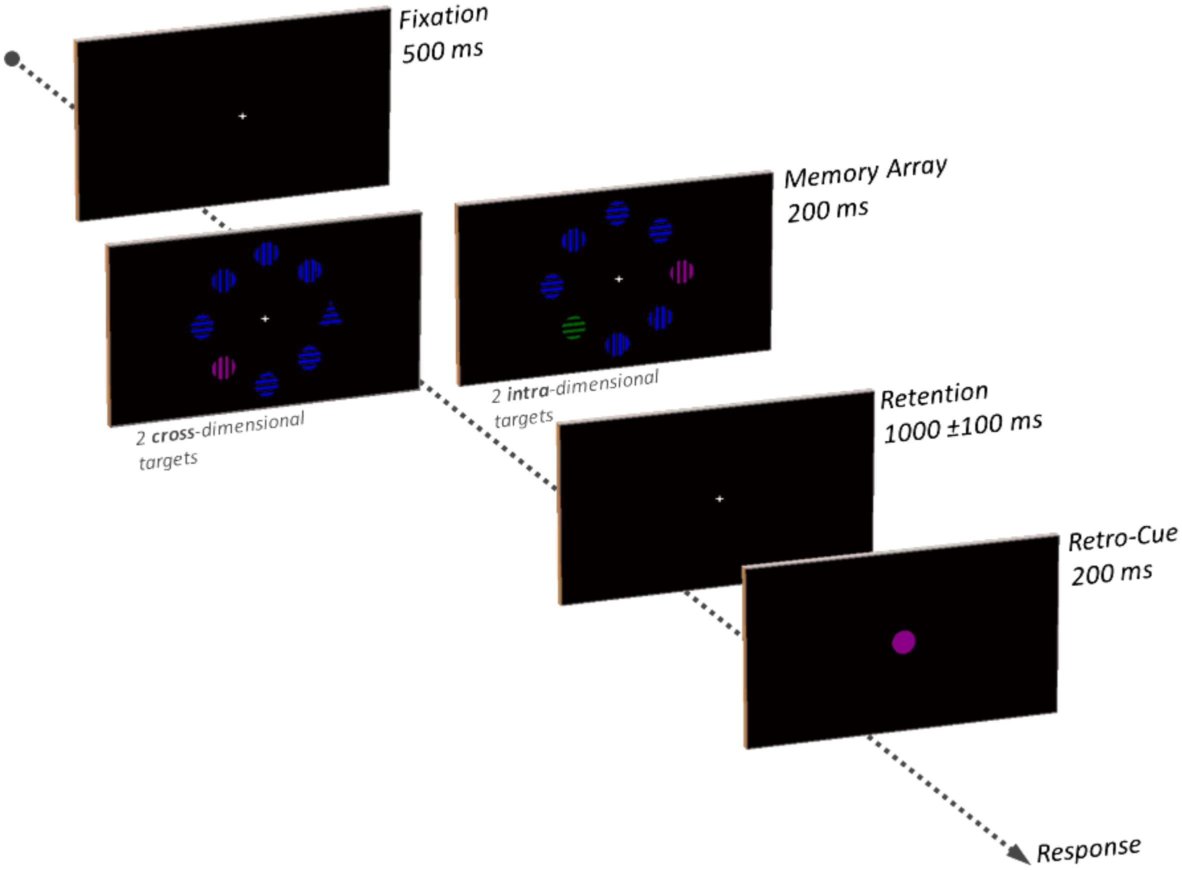

**Figure 2.** Sequence of events of the retro-cue paradigm. Each trial started with a fixation cross (500 ms), followed by a memory array (200 ms). Bilateral memory arrays contained two lateralized WM targets, randomly defined in the same or different feature dimensions. After a variable retention interval (1,000 ± 100 ms), a retro-cue was presented centrally (200 ms), requiring participants to indicate the position (left vs. right hemifield) of the retro-cued WM target.

### 2.2.4 Behavioural data processing and analysis

Behavioural data was pre-processed using Microsoft Excel (version 15.30, Microsoft Corp., Redmond, WA), then analysed using IBM SPSS (version 24.0, IBM Corp., Armonk, NY). In pre-processing, the average HR and error rate (ER) per block and condition was calculated for each participant. Those with an average ER above 20% or HR outside of their target range were rejected from further analysis. Trials with erroneous responses, target-absent trials, and trials with anticipations or delayed responses (<200 ms or >999 ms after retro-cue onset respectively) were removed. Reaction times (RTs) for the remaining trials were averaged per condition for each participant. The pre-processed data was then analysed using a 2x2 repeated measures ANOVA, with the factors "activity" (active, passive) and "modality" (bike, treadmill).

### 2.2.5 EEG data pre-processing and analysis

Brain Vision Analyser II (Brain Products GmbH, Munich, Germany) was used for processing EEG data. The continuous EEG data was first manually inspected to remove apparent noise such as electromyographic (EMG) bursts or wireless signal interference. Subsequently, a Butterworth infinite impulse response (IIR) high-pass filter at 1 Hz (24 dB/Oct) was applied (to further account for potential movement- and/or sweating-related signal distortions). Next, an infomax independent component analysis (ICA) was performed to identify components representing blinks and saccades, as well components related to movement showing clearly identifiable patterns (e.g., step frequencies). The identified ICA components were subsequently removed prior to back-projection of the residual components. After ICA processing, a Butterworth IIR low-pass filter at 30 Hz (24 dB/Oct) was applied. The continuous EEG was then re-referenced to the average of the whole-brain 63-channel electrode set and segmented into the 4 experimental conditions.

Each condition was segmented into 1200 ms epochs, ranging from 200 ms before to 1000 ms after the retro-cue display. The 200 ms interval prior to the retro-cue was used for baseline correction. Signals exceeding ±60 µV, voltage steps over 50 µV/ms, and activity changes lower than 0.1 µV over 100 ms were discarded via artefact rejection on an individual-channel basis. Epoched data was then re-segmented into left versus right hemifield VWM targets (relative to the retro-cued item). Data sets where the number of remaining trials fell below n=50 were rejected from further analysis. The respective segments for left and right target locations were then averaged accordingly (average segments per target hemifield: Left targets, 109.7; Right targets, 110.5; and averaged per condition: BP, 108.5; TP, 108.6; BA, 110.9; TA, 112.3). Following this, ERPs recorded ipsilateral to the location of the VWM target or side of the motor-response were subtracted from contralateral ERPs to produce lateralized difference waves. To compute the CDA, we used the standard formula: (PO8[left] – PO7[left] + PO7[right] – PO8[right])/2; for LRP computations, we used: (C4[left] – C3[left] + C3[right] – C4[right])/2. Segment sizes were kept as is for the CDA and sLRP waves, while for the rLRP wave, segments were trimmed to only include data from 600 ms before to 200 ms after response onset.

To investigate the ERL temporal dynamics, we first calculated the on- and offsets of the CDA (at channels PO7/8) and of the sLRP and rLRP (at channels C3/4) separately for each condition, using the jackknife-based method (Miller et al., 1998). In line with the suggestion of Ulrich and Miller (2001), threshold amplitudes of 50% for CDA and sLRP, and 90% for rLRP we utilized for ERL onsets. Following the jack-knife method, F-values were corrected using the formula: FCorrected = F/(n-1)2 (Miller et al., 1998). It should be noted that differences observed in the onset and offset timing of averaged ERL waveforms can potentially be due to differences in trial-to-trial variance within the respective conditions (e.g., Töllner et al., 2015). To control for this, we further calculated the CDA and LRP width (offsets-minus-onsets) for each condition. To analyze CDA, sLRP, and rLRP amplitudes, we averaged the 50 data points (i.e., milliseconds) before and after the component's maximum negative deflection of the grand-average ERLs based on visual inspection, respectively. In particular, we used 240 – 340 ms for CDA amplitudes, 290 – 390 ms for sLRP amplitudes, and -102 – -2 ms for rLRP amplitudes. The resulting mean amplitudes values as well as the calculated onset latencies and widths were then submitted to a 2 x 2 repeated measures ANOVA with factors of activity (passive vs. active) and modality (bike vs. treadmill).

## 2.3 Results

### 2.3.1 Heart rate data

The average HRs achieved in both Bp and Tp conditions were successfully kept equal to or below the mean resting limit of 30% HRR (*M* = 98.9, *SD* = 6.02). The mean HR in the Bp condition was shown to be significantly below the mean resting limit (*M* = 80.14, *SD* = 10.64; t (17) = -9.66, p < 0.001), while the mean HR in the Tp condition did not significantly differ from the mean resting limit (*M* = 95.45, SD = 12.78; *t* (17) = -1.36, *p* = 0.190). Due to changes in HR following postural shift (Smith et al., 1994), HRs in the Bp condition were lower than in the Tp condition, substantiated by a significant difference in mean HRs in these conditions (Bp: *M* = 80.14, *SD* = 10.64; Tp: *M* = 95.45, *SD* = 12.78; *t* (17) = -4.90, *p* < 0.001).

The average HR in the Ta condition was comparable with the mean targeted “active” HR of 65% HRR (*M* = 147.20, *SD* = 3.67), as there was no significant difference between the mean HR in the Ta condition and the targeted “active” HR (*M* = 148.92, *SD* = 2.68; *t* (17) = 1.458, *p* = 0.163). The average HR in the Ba condition (*M* = 144.93, *SD* = 3.20) was slightly lower than in the Ta condition and the targeted “active” HR. There were significant differences between the mean HR in the Ba and Ta conditions (*t* (17)= -4.811, *p* < 0.001), and between the mean HR in the Ba condition and the targeted “active” HR (*t* (17) = -2.384, p = 0.029). Importantly, however, the mean HR in Ba condition was still above the 60% HRR lower limit of the acceptable range (M = 140.30, SD = 3.97), as there was a significant difference between the mean HR in the Ba condition and the 60% lower limit (t(17) = 4.603, p < 0.001).

### 2.3.2 Behavioural data

As shown in figure 3, RTs exhibited a decrease in active relative to passive conditions (476 ms, 447 ms (Bp, Tp) vs. 440 ms, 429 ms (Ba, Ta)), and were also considerably lower in upright relative to seated conditions (429 ms, 447 ms (Ta, Tp) vs. 440 ms, 476 ms (Ba, Bp)). These patterns were substantiated by significant main effects of activity state (*F* (1,17) = 26.320, P < 0.001) and modality (*F* (1,17) = 5.387, *p* = 0.033). There was no reliable interaction between activity and modality (*F* (1,17) = 2.312, *p* = 0.147).

ERs also showed a tendency to be lower in upright relative to seated conditions (6.55, 7.20% (Ta, Tp) vs. 8.41, 9.14% (Ba, Bp)), which was substantiated by a significant main effect of modality (*F* (1,17) = 28.694, *p* < 0.001). While ERs also seemed to be reduced during exercise (8.41, 6.55% (Ba, Ta) vs. 9.14, 7.20% (Bp, Tp)), the effect of activity failed to reach significance (*F* (1,17) = 1.695, *p* = 0.091). No significant interaction between activity and modality was observed regarding error rates (*F* (1,17) = 0.004, *p* > 0.948).

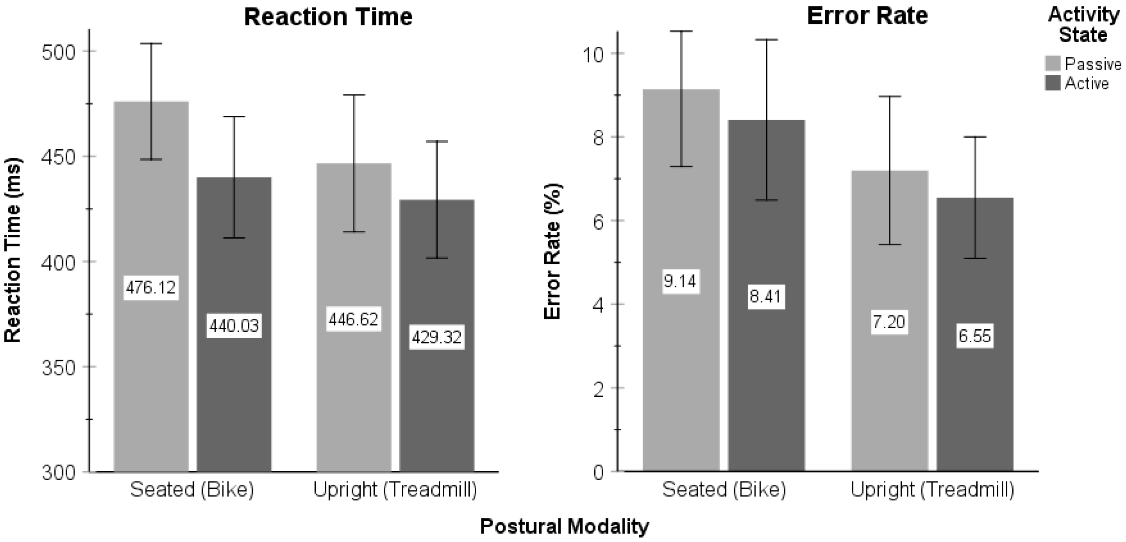

**Figure 3.** Left Panel – displays the mean reaction times for both active and passive conditions in each modality (bike and treadmill). There was a significant main effect of both activity state and modality, such that response times were significantly faster in active vs passive conditions, and in upright vs seated conditions. No interaction was observed. Right Panel – displays the mean error rates for both active and passive conditions in each modality (seated and upright). There was a significant main effect of modality, such that error rates were significantly lower in upright vs. seated conditions. While there was no main effect of activity state, a trend is apparent for decreased error rates from passive to active conditions. No interaction was observed.

### 2.3.3 Electrophysiological data

As indicated by figure 4, CDA onsets appeared to be delayed in treadmill conditions as compared to bike conditions (244, 245 ms (Ta, Tp) vs. 196, 230 ms (Ba, Bp)). This temporal modulation was substantiated by a significant main effect of modality (*F* (1,17) = 4.80, *p* = 0.040). No other effects or interactions involving CDA onset were revealed (all other *p* values > 0.119). The analysis of the CDA widths (all *p* values > 0.129) and CDA mean amplitudes (all *p* values > 0.638) did not yield any significant main effects or interactions.

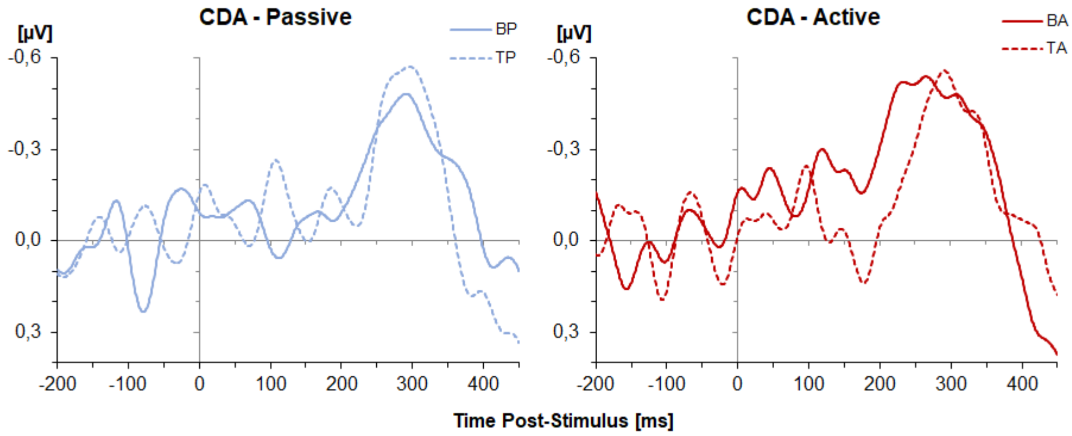

**Figure 4.** Left Panel – CDA waveforms for passive conditions (Bp, Tp) at electrodes PO7/8. Right Panel – CDA waveforms for active conditions (Ba, Ta) at electrodes PO7/8. Both panels – an increase in the CDA onset timing was observed from seated to upright conditions (Bp, Ba vs. Tp, Ta) and was substantiated by a significant main effect of modality. No main effect of activity state or interaction was observed.

sLRP onset, as illustrated in figure 5, was found to occur earlier in active relative to passive conditions (259, 235 ms (Ba, Ta) vs. 267, 255 ms (Bp, Tp)), and were also expedited in upright relative to seated conditions (259, 267 ms (Ba, Bp) vs. 235, 255 ms (Ta, Tp)). These effects were substantiated by significant main effects of activity ($F$ (1,17) = 5.58, $p$ = 0.030) and modality ($F$ (1,17) = 6.24, $p$ = 0.023). No significant interaction was observed between these factors ($p$ = 0.489). While there were no significant effects evident for rLRP onsets (all $p$ values > 0.279), we observed significant main effects of activity for both sLRP ($p$ = 0.019) and rLRP amplitudes ($p$ = 0.046).

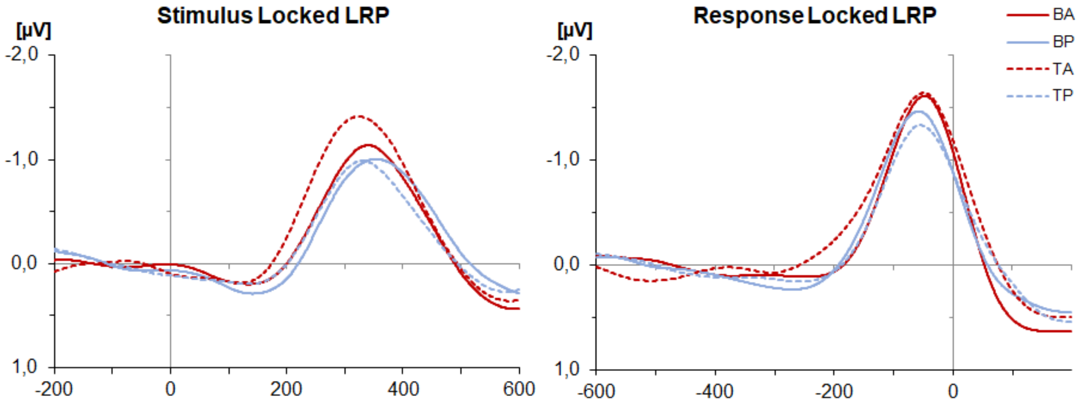

**Figure 5.** Left Panel – sLRP waveforms (time-locked to the retro-cue onset for all conditions) at electrodes C3/4. A decrease in the onset timing of the sLRP component was observed from passive to active conditions (Bp, Tp vs. Ba, Ta), as well as from bike to treadmill conditions (Ba, Bp vs. Ta, Tp), substantiated by a significant main effect of both activity state and modality. No interaction was observed. Right Panel – rLRP waveforms (time-locked to response input for each condition) at electrodes C3/4. No main effects of activity state or modality were observed.

It is worth noting that there is no consistent picture as to whether enhanced (relative to reduced) LRP amplitudes can be taken to indicate facilitated (relative to impaired) processing dynamics in the respective processing stage. While enhanced LRP amplitudes were found to be associated with a RT cost for cross-trial changes (relative to repetitions) of the motor-response in visual search (Töllner et al., 2008), the opposite pattern has been reported in another visual search study in which enhanced LRP amplitudes owing to localization task demands (relative to, e.g., detection task demands) were associated with a RT benefit (Töllner et al., 2012). Given this mixed RT-LRP amplitude relation in the literature, in the following, we will concentrate our discussion solely on the temporal differences found in the LRP waves.

## 2.4 Discussion

The present study was designed to examine the influence of moderate acute aerobic exercise and upright posture on the temporal dynamics of concurrent VWM performance. Our behavioural results indicate that both acute aerobic exercise and upright posture expedited the overall speed of processing as compared to passive and seated conditions, while upright posture additionally served to reduce error rates. Our electrophysiological results demonstrated these effects to be temporospatially dynamic, having differential influences depending on the stage of processing being observed. In the following sections, we will review these results and then discuss the insight this study can provide regarding the seemingly transient nature of interactions between cognition and aerobic exercise.

Engagement in acute, moderate aerobic exercise produced a significant decrease in RTs as compared to resting conditions. This is in general agreement with the various findings of prior research (Bullock et al., 2015, Cereatti et al., 2009; Lichtman & Poser, 1983; Martins et al., 2013; Hillman et al., 2003; Hogervorst et al., 1996; Olson et al., 2016; Pesce & Audifferen, 2011; Tomporowski 2003; Tomporowski et al., 2005), providing further evidence that moderate aerobic exercise can enhance concurrent executive functions such as, in the present case, working-memory performance. Although a trend towards lower ERs in active versus passive conditions did not prove to be significant, this finding allows us to rule out the possibility of a speed accuracy trade-off in our results. Reduced accuracy has been observed during exercise in prior research (e.g., Olsen et al., 2016; Pontifex & Hillman, 2007). However, these studies employed exercise protocols where the targeted exercise intensity fell below VT1 (40–60% VO2 max and 60% MHR, respectively), whereas the present study aimed to maintain intensity at or above VT1, which may have contributed to our contrasting findings. A substantial influence of body posture on VWM performance was however revealed, where both RTs and ERs were found to be significantly lower in upright as compared to seated conditions. This implies that VWM performance may be modulated by postural factors independent of activity.

### 2.4.1 Delayed WM access in upright posture

No effects of exercise were observed in relation to the CDA timing, suggesting that temporal aspects of target access in VWM are not likely to be substantially influenced by exercise per se. However, a main effect of body posture was indicated, where CDA onset occurred significantly later in upright postures—in direct contrast with our behavioural findings. Importantly, subsequent analysis of CDA width revealed no significant influence of differential variance across conditions, allowing us to rule out that the observed differences in CDA onset are attributable to differences in trial-by-trial variance. These results partially support our second hypothesis, but also indicate that body posture has a dynamic influence on overall VWM performance.

Prior research has indicated a partial overlap between (visuo)spatial (but not non-spatial) working-memory and sensorimotor networks involved in balance, particularly in the DLPFC and inferior parietal lobules (Anguera et al., 2010; Chen et al., 2018; Kerr et al., 1985). As such, the processing of spatial information necessary for maintaining standing balance may interfere with the performance of VWM tasks also requiring spatial information processing (Fuhrmann et al., 2015). The delayed CDA onset observed during upright postures in the present study could therefore be an indication of such interference, given the present VWM retro-cue task requires participants to identify the spatial location of a target held in VWM. Nevertheless, this early processing cost for upright conditions did not result in correspondingly delayed RTs, suggesting the speeded RTs in active conditions are likely to arise from a substantial acceleration of cognitive processing during subsequent, post-selective processing stages.

### 2.4.2 Speeded motor-response decisions during exercise

Analysis of the sLRP timing showed a comparable pattern to RTs, characterized by a significantly earlier onset in active and upright conditions. These findings demonstrate that both acute aerobic exercise and upright posture expedite the onset of response selection, which may be the critical source of the observed decreases in RT. The onset of rLRP, by contrast, did not demonstrate any differences between conditions. Importantly, this finding indicates that differential motor facilitation between conditions is not likely to be responsible for the speeded responses found in relation to exercise and posture. In other words, the observed effects must originate from pre-motor stages of the processing pipeline. The congruence between the RT and sLRP-timing effects provide support for our primary hypothesis, namely, that the temporal facilitation observed in the behavioural data can be attributed to specific processing stages.

The pattern of effects observed across the CDA and sLRP waves indicate that both acute aerobic exercise and upright posture serve to facilitate and expedite information processing, likely during an intermediary stage between the onsets of these ERLs, in parallel with a substantial facilitation of RT performance in the present retro-cue task. In terms of processing levels, this intermediary would fall in a range starting from the process of accessing and analysing target representations stored in VWM and ending with selecting an appropriate motor response based on this information, both of which can be considered explicit, executive functions. Figure 6 provides a visualization of the observed ERP onset modulations relative to the conditions under which they were found to occur.

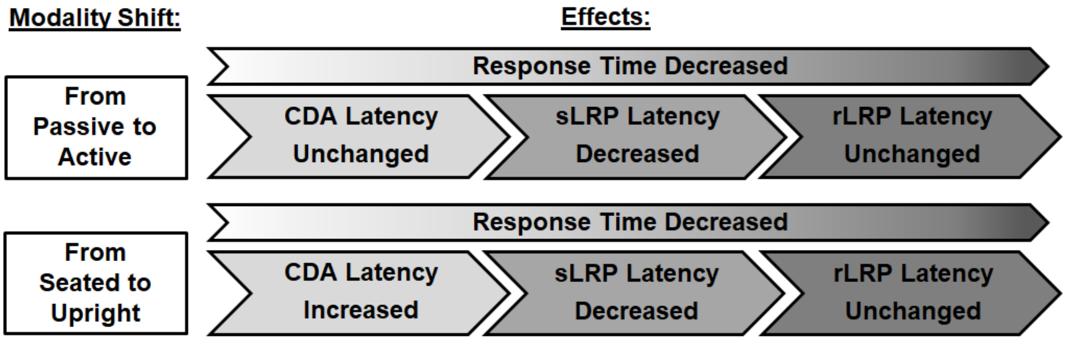

**Figure 6**. A visualization of the modulations in ERL component onset latencies relative to the modality shift in which they were observed. sLRP latency was found to decrease from passive to active conditions as well as from seated to upright conditions. CDA latency was found to increase from seated to upright conditions. No changes were observed in rLRP latency.

### 2.4.3 Relation to theoretical perspectives

Regarding neural-resource modulations, the present study provides a challenge to Dietrich's RAH model. While increased activity in motor-control networks propagates a parallel increase in neural resource demands (Gusnard & Raichle, 2001), our findings indicate that under the targeted cardiovascular workload, the availability and distribution of neural resources did not become a limiting factor to VWM performance. Moreover, our results suggest that facilitation occurred temporally between the stages of target access in WM and motor-response selection. These processes are thought to involve regions of the FPN and DLPFC (Rowe et al., 2000; Sauseng et al., 2005), both of which the RAH would predict to be inhibited. The present results therefore suggest that the net pool of neural resources may have been supplemented or expanded sufficiently enough during exercise to not only prevent resource competition between executive and motor-control systems, but to drive facilitation of the executive processes involved in VWM performance.

While such a theoretical increase in metabolic resources during the targeted intensity of aerobic exercise may prevent cognitive interference due to resource limitations, there may be a more direct path by which an increased supply of oxygen could facilitate VWM performance. Improved performance in the Stroop task, for example, has been correlated with increased oxygenation of the DLPFC following moderate aerobic exercise as compared to rest (Byun et al., 2014; Yanagisawa et al., 2010). The DLPFC plays a critical role in WM performance and is particularly active when computations such as response selection must be performed on the contents thereof (Smith & Jonides, 1997), as well as during the retention interval of delayed-response tasks (Curtis & D'Esposito, 2003). The DLPFC itself does not maintain VWM representations, but rather acts as a mediator of their top-down control – enhancing representations of task-relevant stimuli as well as motor plans associated with these representations in the premotor cortex (Curtis & D'Esposito, 2003; Kastner & Ungerleider, 2001). In effect, increased oxygenation of the DLPFC during moderate aerobic exercise as indicated by Rooks and colleagues (2010) could facilitate executive performance in similar fashion, and therefore may serve as a mechanistic underpinning of the accelerated response selection observed in the present study.

The benefits observed here demonstrate that VWM processing is expedited from resting levels of arousal to a state corresponding to cardiovascular workloads between VT1 and below VT2. Providing an endocrinological basis for this, the arousal induced by moderate exercise has been shown, in animal studies, to be driven by an increase in the cortical plasma concentration and metabolic processing of several catecholamines (Gerin and Privat, 1998; McMorris et al., 2009). In turn, prior research has also demonstrated improvements in human information processing speed with relation to increased cerebral concentrations of endocrinological factors such as adrenaline (McMorris & Graydon, 2000), corticotrophin (McMorris et al., 2009), and norepinephrine (Chmura et al., 1994). Further, WM tasks with a greater involvement of the central executive (such as the VWM retro-cue task) are thought to rely heavily on noradrenergic and dopaminergic pathways (Lacey & Lacey, 1970), as various sub-components of the central executive, particularly the DLPFC, are dependently activated by norepinephrine and dopamine (Cereatti et al., 2009). This dependency may play a role in the effects on the sLRP timing observed in this study.

There may equally be a relationship between endocrinological factors and the observed effects of postural change. Given the marked increase in plasma catecholamine concentrations when moving from seated to upright posture (Jacob et al., 1998; Smith et al., 1994), it is reasonable to suspect that standing might produce RT facilitation like that found during active aerobic exercise. Increased arousal due to physical stressors such as upright posture has also been related to moderate increases in activation of the limbic system (which is subserved by norepinephrine and dopamine), promoting memory consolidation (Nielson & Powless, 2007). While the present results regarding RTs, error rates, and sLRP onset all lend support to the of idea posture-induced arousal, the effects observed regarding CDA onset in upright postures lend support to the view that overlap between the neural mechanisms governing posture regulation and spatial VWM can impede spatial processing when activated concurrently.

### 2.4.4 Potential limitations

The present study faced some limitations regarding the precision of our hemodynamic controls. Maximal exercise testing is not feasible in many settings, and this study was no exception. In such scenarios, MHR is often estimated using the standard formula [MHR = 220 – age] (Tanaka et al., 2001), which is generally accepted for healthy adults (Garber et al., 2011). However, as this formula is only an estimate based on large-scale statistics, it has been shown to have a large inherent error of ~7-11 bpm (Robergs & Landwehr, 2002). It should thus be understood that individual variability in MHR is common and is modulated by a variety of factors including age, dietary habits, smoking, sex, body composition, and physical fitness (Nes et al., 2013). As such, our estimates of MHR, and thus estimates of HRR which we used to determine individual target heart rates, are potentially skewed. Several revisions of the formula for estimating MHR have been proposed to accommodate this (Nes et al., 2013; Tanaka et al., 2001), where that of Tanaka and colleagues would have provided a more accurate estimate. However, precise options for monitoring and standardizing cardiovascular workload such as direct spirometry may be advisable in future studies.

A second potential limitation was a limited control of participants' metabolic conditions. While participants were asked to refrain from consuming alcohol, caffeine, or tobacco prior to the study, the reality of this being the case was taken on good faith. Stimulants such as caffeine and nicotine, or depressants such as alcohol hold the potential to alter the performance of cognitive tasks and pose additional potential influences regarding hemodynamic functions. Further, while participants were asked to be well nourished and rested prior to the experiment, the study was conducted at various times throughout the day across participants, with start times ranging from 9:00–17:00, potentially introducing variation in the time span between study participation and the participants' last meal and last period of rest. This in turn could influence blood glucose levels as well as other endocrinological factors associated to digestion, and/or introduce fatigue. In future research, it may thus be advisable to attempt controlling for the time span between meals, rest, and participation, or to perhaps monitor blood sugar as an added control metric.

## 2.5 Conclusion

Acute aerobic exercise and upright body posture can have faciliatory effects on VWM performance. Within an optimal range of cardiovascular load, aerobic exercise can significantly improve processing speed, while upright posture can enhance both processing speed and response accuracy. Of note, VWM performance was found to be lowest in resting, seated conditions—the physiological and postural state in which nearly all other psychological/neuro-cognitive research is conducted. Theoretically, the observed benefits of both aerobic exercise and upright posture could be driven by state-dependent increases in the availability of metabolic and/or endocrinological resources, particularly in frontal sub-components of the VWM system.

Analysis of ERL waves isolated speed of processing facilitation to a finite temporospatial stage of the cognitive processing pipeline, providing a clear indication of when, and some suggestion as to where the neural origins of the observed effects took place. The present study is unique in these findings, as to the best of our knowledge no prior research has attempted to disentangle the temporal dynamics of exercise-concurrent VWM performance using a staged ERL approach. As such, this study provides an ample theoretical and methodological basis to inform future investigations of visual cognition during exercise.

# 3

# EEG EVIDENCE FOR ENHANCED ATTENTIONAL PROCESSING DURING LOW INTENSITY EXERCISE

Gordon Dodwell, Heinrich R. Liesefeld, Markus Conci,
Hermann J. Müller, and Thomas Töllner

## 3.0 Abstract

Researching executive functions such as attentional control within real-world contexts has become substantially more feasible and thus frequent over the past decade. However, relatively little is known regarding how these processes may be influenced by common naturalistic behaviours such as engaging in physical activity, which is thought to modulate the availability of cognitive resources. Here, we employed an event-related potential (ERP) approach to determine whether various intensities of aerobic exercise might affect the concurrent performance of attentional control mechanisms. Participants performed an additional-singleton visual search task across three levels of aerobic activity while seated on a stationary bicycle: at rest, during low-intensity exercise, and during moderate-intensity exercise. In addition to behavioural measures, attentional performance was assessed via lateralised ERPs referencing target selection (PCN) and distractor suppression (PD) mechanisms. Whereas engaging in exercise resulted in speeded response times overall, low-intensity exercise was found to uniquely eliminate distractor-induced delays in attentional allocation as expressed by the PCN, while also giving rise to an unanticipated distractor-elicited Ppc. These findings demonstrate workload-specific and object-selective influences of aerobic exercise on attentional processing, providing insights not only for approaching attention in real-world contexts, but also for understanding how attentional resources are utilised overall.

## 3.1 Introduction

### 3.1.1 Cognitive Control of Attentional Selection

The temporospatial deployment of visual attention (i.e., attentional selection) is conventionally regarded as being guided by interactions between distinct bottom-up and top-down mechanisms. That is to say, selection is prioritised depending on the interplay between stimulus-driven signals evoked by the novelty or salience of stimulus features, and modulatory goal-driven signals relative to current task objectives (Corbetta, Patel, & Shulman, 2008; Corbetta & Shulman, 2002; Egeth & Yantis, 1997; Fecteau & Munoz, 2006; Itti & Koch, 2001). Implicit learning based on prior attentional deployments (e.g., selection history) has also been proposed as a contributing signal (Awh, Belopolsky, & Theeuwes, 2012; Müller, Reimann, & Krummenacher, 2003; Theeuwes, 2018), however whether this should be clearly segregated from top-down mechanisms remains somewhat debated (Gaspelin & Luck, 2018; Nobre & Stokes, 2019). These preliminary priority signals are conceptualised as being pre-attentively summated within a topographically organised attentional *priority map*, from which an ordinal hierarchy of attentional selection (i.e., *selection priority*) is then determined (Bisley & Goldberg, 2010; Klink, Jentgens, & Lorteije, 2014; Fecteau & Munoz, 2006; Itti & Koch, 2001; Liesefeld & Müller 2020, Wolfe, 2012). Goal- and experience-modulated priority signals can be independently facilitative or suppressive of any given object or location within the priority map, thereby enhancing or attenuating stimulus-driven priority signals in order to maintain control over attentional guidance (Liesefeld, Liesefeld, Pollmann, & Müller, 2018; Theeuwes, 2018). Efficient target selection thus depends on the performance of top-down mechanisms promoting the target objects' selection priority, even when hierarchically contested by bottom-up interference from highly salient distractors (Liesefeld & Müller, 2019). When top-down mechanisms succeed, salient distractors can be attentionally avoided (e.g., Töllner, Müller, & Zehetleitner, 2012), whereas when they fail and a salient distractor gains the highest selection priority, *attentional capture* is said to occur (Hickey, McDonald, & Theeuwes, 2006; Liesefeld, Liesefeld, Töllner, & Müller, 2017; Rauschenberger, 2003; Ruz & Lupiáñez, 2002; Theeuwes, 2010; Theeuwes & Godijn, 2002).

The attentional capture phenomenon has been operationalised within the additional-singleton paradigm (ASP) (Theeuwes, 1992; Theeuwes & Godijn, 2002). In this task, observers covertly search for a pre-defined target singleton displayed amongst several homogenous non-targets. However, on some proportion of trials, an additional task-irrelevant distractor singleton is also displayed, interfering with target selection by competing for selection priority. All presented stimuli contain a randomised and non-informative binary feature (e.g., line or grating), and observers are instructed to provide a discriminative response regarding this feature as contained by the target (see Fig. 1 for example displays). Experiments utilising the ASP typically result in longer response times when the target and distractor are concurrently presented, often referred to as the *distractor interference effect* (Folk & Remington, 1998; Sawaki & Luck, 2010; Theeuwes, 1992; Theeuwes & Godijn, 2002, 2004).

### 3.1.2 EEG Indices of Attentional Control

Event-related potentials (ERPs) of the electroencephalogram (EEG) have proven instrumental in developing our understanding of attentional selection, particularly the *posterior-contralateral negativity,* or *PCN* (also referred to as the *N2pc*). The PCN is a lateralised ERP (ERL), characterised by an enhanced negative deflection arising 175-300 ms post-stimulus over posterior electrodes (typically PO7/PO8) contralateral to the attended hemifield (Eimer, 1996; Luck & Hillyard, 1994a; Töllner et al., 2012; Woodman & Luck, 1999, 2003). While the PCN is widely considered to reflect the spatial deployment of attentional selection, its mechanistic origins are less certain. The PCN has been proposed to exclusively index distractor suppression, predicting its amplitude to scale with target-proximal filtering requirements (Luck, Girelli, McDermott, & Ford, 1997; Luck & Hillyard, 1994b). However, others have elicited the PCN while only presenting distractors contralateral to the target, suggesting it may instead reference target-specific feature processing (Eimer, 1996; Hilimire, Mounts, Parks, & Corballis, 2009; Mazza, Turatto, & Caramazza, 2009).

More recent studies suggest the PCN may represent the superposition of two sub-components, each discretely indexing target-selective or distractor suppression mechanisms. Non-lateralised visual objects are equivalently processed in both cortical hemispheres, therefore being unlikely to evoke ERLs. This allows the processing of a lateralised stimulus to be electrophysiologically isolated by locating attentionally competitive stimuli along the vertical midline (90°/270°), a technique known as *systematic lateralisation* (Woodman & Luck, 2003). Applying this technique, Hickey et al. (2009) found search arrays including a lateralised target and midline distractor to elicit an PCN-like negativity contralateral to the target, while the inverse configuration (a lateralised distractor and midline target) resulted in a temporospatially similar positivity contralateral to the distractor. These systematically lateralised ERLs were coined the target negativity ($N_T$), reflecting target-selective enhancement, and the distractor positivity ($P_D$), indexing location-based distractor suppression (Hickey, di Lollo, & McDonald, 2009 Sawaki & Luck, 2010). Further, linear summation of the isolated $N_T$ and $P_D$ have been found to predict the equivalent PCN in a spatially dependent manner (Gaspar & McDonald, 2014; Liesefeld, Liesefeld, Töllner, & Müller, 2017).

The $P_D$ is reliably observed in tasks where fixed or predictable singleton features are employed, whereby reduced uncertainty allows attentional capture to be more effectively avoided (Allenmark, Zhang, Liesefeld, Shi, & Müller, 2019). By contrast, tasks including variable or unpredictable singleton features more often result in attention capture by the distractor singleton, rendering a distractor-elicited PCN (or $N_D$ – distractor negativity) rather than or prior to a $P_D$ (Burra & Kerzel, 2013; Feldmann-Wüstefeld, Uengoer, & Schubö, 2015; Gaspar & McDonald, 2014; Liesefeld et al., 2017; Sawaki & Luck, 2010; Töllner et al., 2012). Within variants of the ASP, both the amplitude and latency of the $P_D$ have been found to increase with greater demand for distractor suppression, whereas distractor presence (or increased distractor interference) has conversely decreased the amplitude and/or delayed the onset of the PCN (see Burra & Kerzel, 2013, 2014; Gaspar & McDonald, 2014; Jannati, Gaspar, & McDonald, 2013; Töllner et al., 2012). Although these modulations can be considered an electrophysiological manifestation of the distractor interference effect, the driving force behind them remains uncertain. Similar to the $P_D$ in relation to suppression demands, the magnitude of the PCN has been positively correlated with the difficulty of target feature discrimination, indicating higher amplitudes to reflect an increased allocation of attentional resources (Liu, Lin, Zhao, & Robertson, 2016). However, increasing target-distractor similarity in visual search is shown to reduce the amplitude and delay the onset of the PCN, suggesting early feature-contrast computations might moderate the subsequent allocation of available resources across attentionally competitive items (Conci, Töllner, Leszczynski, & Müller, 2011; Töllner, Zehetleitner, Gramann, & Müller, 2011; Zhao et al., 2011). As such, the presence of a salient distractor in the ASP may reduce or delay the PCN by lowering target conspicuity, thereby requiring a wider distribution of resources and/or more processing time for the target to be pre-attentively isolated.

Occasionally, an earlier positivity has also been observed accompanying the PCN and $P_D$ prior to attentional deployment (100 – 200 ms after stimulus onset), commonly referred to as the "positivity posterior contralateral" or *Ppc*. Elicited by either targets or distractors, the Ppc has been proposed to represent an automatic spatial index for the most salient item within the salience map, potentially guiding later attentional processes (Corriveau et al., 2012; Fortier-Gauthier, Moffat, Dell'Acqua, McDonald, & Jolicœur, 2012; Jannati et al., 2013). More recent evidence suggests the Ppc may alternatively reference a pre-attentive suppression mechanism (sometimes referred to as an "early $P_D$"), selectively dampening early salience signals according to attentional demands (Barras & Kerzel, 2017; Feldmann-Wüstefeld & Vogel, 2019; Gaspelin & Luck, 2018; Weaver, van Zoest, & Hickey, 2017). However, direct investigations of this component are relatively sparse, and thus interpretations of its functional role remain largely inconclusive.

### 3.1.3 Attentional Resources during Exercise

As for all executive functions, the neural mechanisms of top-down attentional control are both resource-limited and competitive, becoming performatively strained when task-demands exceed resource availability (Broadbent, 1958; Franconeri, Alvarez, & Cavanagh, 2013; Miller & Cohen, 2001). The simultaneous engagement of both distractor suppression and target-selective mechanisms could therefore instigate resource competition, effectively impairing one or both. Aerobic exercise has been suggested to similarly impede concurrent cognitive performance, inducing resource competition between networks governing more implicitly driven motor control and/or more explicitly driven cognitive control processes. Critically, this reticular-activating hypofrontality (RAH) model (Dietrich, 2006; Dietrich & Audiffren, 2011) was derived from the contemporaneous notion of a rather static pool of neuronal resources (Ide & Secher, 2000), thus necessitating competitive reallocation as motor control networks come online. However, while neuronal populations generally remain acutely fixed, more recent evidence indicates the local and global availability of haemodynamic, metabolic, and endocrinological factors to be dynamically modulated during aerobic exercise, depending on the aerobic workload (Hellstrom, Fischer-Colbrie, Wahlgren, & Jogestrand, 2017; Rooks, Thom, McCully, & Dishman, 2010; Secher, Seifert, & van Lieshout, 2008).

To compensate for the energetic requirements of aerobic exercise, additional haemometabolic resources become systemically available almost immediately (Secher et al., 2008). Beyond merely counteracting increased demands, these modulations may increase the utilisation or even provide a surplus of neurometabolic resources under certain workloads. At exercise intensities near the aerobic threshold ($VT_1$), cerebral blood flow (CBF) increases by up to 30%, coupled with a reduction in cerebrovascular resistance (Ide, Pott, van Lieshout, & Secher, 1998; Secher et al., 2008). These effects rapidly diminish for workloads ranging between the anaerobic threshold ($VT_2$) and maximal aerobic capacity ($VO_2$ max), as exercise-induced hypocapnia (a reduction in the concentration of carbon dioxide in the blood) instigates cerebral vasoconstriction (Bain & Ainslie, 2014; González-Alonso et al., 2004; Querido & Sheel, 2007; Willie et al., 2012). Following a similar pattern, oxygen saturation ($sO_2$) in the prefrontal cortex (PFC) rises substantially between $VT_1$ and $VT_2$ (referred to as the inter-threshold area, or *ITA*), before regressing from $VT_2$ onwards (Rooks et al., 2010). Although some evidence suggests modulations in CBF and $sO_2$ may not directly influence cognitive performance (Ando, Kokubu, Yamada, & Kimura, 2011; Lucas et al., 2012; Ogoh et al., 2014), both the oxygen extraction fraction (OEF) and metabolic rate of oxygen ($CMRO_2$) for cerebral tissue increase during exercise, implying the presence of an enhanced neurometabolic utilisation capacity (Smith & Ainslie, 2017).

Beyond these haemometabolic effects, aerobic exercise is also widely regarded as an “arousal-inducing” activity, acutely promoting the endocrine production and cerebral concentration of several hormonal neurotransmitters, particularly norepinephrine and dopamine (McGaugh, 1983; McMorris, 2009; Meeusen, Piacentini, & de Meirleir, 2001). Cognitive performance has long been hypothesised to follow an “inverted-U” pattern in response to increasing arousal (Hebb, 1955), and efficient functioning of the dorsolateral pre-frontal cortex

(DLPFC) correspondingly shows an inverted-U relation to the cerebral concentrations of these catecholamines (Arnsten, 2011). Several lines of evidence convincingly suggest an involvement of the PFC and DLPFC in top-down attentional control (Liesefeld, Liesefeld, & Zimmer, 2014;MacDonald, Cohen, Stenger, & Carter, 2000; Paneri & Gregoriou, 2017; Vanderhasselt, de Raedt, Baeken, Leyman, & D'haenen, 2006) and particularly for distractor avoidance (de Fockert & Theeuwes, 2012; Leber, 2010; Lega et. al., 2019). Given these findings, it would not be unreasonable to expect the performative aspects of top-down attentional mechanisms to follow a similar inverted-U pattern in response to aerobic exercise.

### 3.1.4 Attentional Performance during Exercise

Several meta-analyses have revealed a small positive effect of aerobic exercise on concurrent cognitive performance, with benefits being most prevalent during ITA workloads, and enhanced speed of processing being most often reported (Chang, Labban, Gapin, & Etnier, 2012; Lambourne & Tomporowski, 2010; Ludyga, Gerber, Brand, Holsboer-Trachsler, & Pühse, 2016; McMorris & Hale, 2012). The aforementioned resource modulations are generally considered a substantial driving force behind these effects; however, various moderator variables are also indicated, including the duration and modality of exercise, individual cardiorespiratory fitness, and the aspect of cognition being assessed. As such, findings between individual studies have proven somewhat inconsistent.

Attentional benefits have included expediated goal-driven attentional directing (Pesce, Cereatti, Forte, Crova, & Casella, 2011; Pesce, Tessitore, Casella, Pirritano, & Capranica, 2007), enhanced feature selection in the lateral periphery (Hüttermann, Memmert, & Simons, 2014), and speeded responding in a sustained attention task (González-Fernández, Etnier, Zabala, & Sanabria, 2017), each alluding to a facilitation of top-down attentional control. Conversely, Davranche and colleagues found that while Simon task performance was faster and no less accurate during exercise, the magnitude of the Simon effect increased; suggesting that although top-down cognitive control was predominantly maintained, response inhibition may have become impaired (Davranche & McMorris, 2009). As the premotor theory of attention predicts strong associations between response preparation and attentional orienting (Eimer, Forster, van Velzen, & Prabhu, 2005;

Rubichi, Iani, Nicoletti, & Umiltà, 1997; Stoffer & Yakin, 1994; van der Lubbe, Abrahamse, & de Kleine, 2012), an exercise-concurrent supplementation of stimulus-driven attentional control could have enhanced the task-irrelevant response activation. Such bottom-up facilitation is similarly implied by the findings of Sanabaria and colleagues, who found a diminished inhibition of return during exercise (Sanabria et al., 2011).

While these results illuminate behavioural aspects of the exercise-cognition interaction, the covert neurocognitive features thereof have been substantially less explored, with only a select few employing EEG to monitor individual processing events during exercise (e.g., Bullock, Cecotti, & Giesbrecht, 2015; de Sanctis, Butler, Malcolm, & Foxe, 2014; Dodwell, Müller, & Töllner, 2019; Grego et al., 2004; Olson et al., 2016; Pontifex & Hillman, 2007; Yagi, Coburn, Estes, & Arruda, 1999). Those examining attentional performance have mainly focused on non-lateralised ERP components like the P3, the magnitude and onset of which are considered to reflect attentional resource allocation and object classification speed, respectively (Polich, 2007). However, electrocortical effects have proven inconsistent across various ITA workloads and cognitive tasks. For example, in the performance of a visual oddball task, Yagi and colleagues (1999) found an expedited but diminished P3 during high-intensity exercise (≈ VT2) – denoting an exercise-induced attenuation of allocable attentional resources – behaviourally paralleled by a speed-accuracy trade-off. Conversely, performing a flanker task during moderate-intensity exercise (≈ ITA-median) was shown by Pontifex & Hillman (2007) to elicit an enhanced (although delayed) P3, indicating an increased allocation of attentional resources. Electrocortical effects within individual experiments have also been found to differ across various ITA workloads. For instance, Bullock and colleagues (2015) recorded ERPs as an oddball task was performed during conditions of rest, low-intensity (≤ VT1), and moderate-intensity (≈ ITA-median) exercise. In both exercise conditions, an earlier P3a onset was observed relative to infrequent distractors, while the P3b demonstrated a similar trend relative to targets. However, the P1 component (serving as an index of sensory processing [Woldorff et al., 1997]) exhibited faster onset for targets and increased amplitude for frequent non-targets exclusively during "low-intensity" exercise. The later of these object-selective sensory effects was suggested to represent a workload-specific facilitation of sensory gain control (see Hillyard, Vogel, & Luck, 1998), which may in turn have benefited more latent attentional selection processes. However, whether aerobic exercise similarly influences top-down mechanisms of attentional selection has yet to be elucidated.

### 3.1.5 Study Rationale

The present study was thus designed to examine how top-down mechanisms of attentional control might be influenced during acute aerobic exercise. To accomplish this, the EEG signal was recorded as participants performed an ASP task across three workloads of aerobic activity: at rest, during low-intensity exercise (≈ VT1), and during moderate-intensity exercise (≈ ITA-median). To maximise the effective level of top-down attentional control, our variant of the ASP included fixed target and distractor identities. Further, systemic lateralisation was employed, allowing the selective processing of both target and distractor objects to be electrophysiologically isolated via the PCN and $P_D$ components, respectively.

Developing hypotheses concerning how top-down attentional performance might be influenced during aerobic exercise is less than straightforward, although specific effects can be predicted given previous trends. Firstly, in congruence with the wider range of behavioural findings, we can anticipate speeded responding during exercise – however, whether such an effect will scale with increasing workloads remains uncertain. Secondly, considering the resource-limited and competitive nature of top-down attentional mechanisms, we can predict that a supplementation of resources during ITA workloads may be reflected by the PCN, the $P_{D,}$ or both components. More specifically, an increased availability of attentional resources during exercise may allow for a greater allocation thereof towards target selection and/or distractor suppression mechanisms, resulting in an enhanced amplitude and/or faster onset of the PCN or $P_D$. Lastly, considering the findings of Bullock and colleagues (2015) regarding improved sensory gain control specifically during low-intensity exercise, we can suspect that similarly workload-specific effects may also arise in more latent attentional processes. That is, a workload-specific enhancement of sensory processing might be paralleled by or even influence a comparable modulation within the top-down mechanisms of attentional control, or potentially within the Ppc if present.

## 3.2 Methods

### 3.2.1 Participants

A total of 32 volunteers completed the experiment, however, four were removed due to excessively high error rates (>20%), while another four either could not complete the study, or their data was later excluded due to physical performance issues (e.g., being unable to maintain the required effort). The final analysed sample therefore included our target of 24 participants (12 females, age = 23.5 ± 2.5, 3 left-handed) which was calculated using $\alpha = .05$ and the response time (RT) effect ($1 - \beta = .80$, $d_z = 0.60$) observed in our previous study (Dodwell et. al., 2019). All participants provided written informed consent, reported normal or corrected-to-normal vision, and indicated no history or diagnosis of neurological, cardiorespiratory, or neuromuscular illnesses. Participants were requested to refrain from consuming alcohol for at least 24 hours as well as any tobacco or caffeine for at least two hours prior to testing. The experimental procedure was approved by the ethics committee of the Department of Psychology, University of Munich, in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

### 3.2.2 Task & Stimuli

The behavioural task was presented on a 68.58 cm (27”) desktop monitor (Acer XF270H: 1920 × 1080 resolution, 144-Hz refresh rate) positioned ~140 cm away from the participant. Each trial began with the presentation of a white fixation point at screen centre (0.51° ⌀, 500 ms). This was followed by a search array (200 ms) containing eight circles (2.04° ⌀), distributed across two midline (90°, 270°) and six lateralised positions (45°, 0°, 315°, 225°, 180°, 135°), all radially equidistant (radius: 5.08°) from the central fixation point. Each stimulus contained a randomised vertical or horizontal grating composed of five black bars (0.13 × 2.04° ⌀) separated by four gaps (0.38 × 2.04° ⌀). In each trial, the search array could include one or both of two isoluminant (45.5 cd/m$^2$) singletons - a yellow target singleton (CIELUV: 45.79, 3.32, 46.08) and red distractor singleton (CIELUV: 55.95, 155.96, 33.63), otherwise displayed amongst less luminant (28.0 cd/m$^2$) green non-targets (CIELUV: 48.90, -44.20, 57.83). A target or distractor singleton presented alone would always appear at one of the six lateral positions, while simultaneously presented target and distractor singletons never appeared in the same position set;

that is, a lateral target would always appear with a midline distractor, or vice versa. This rendered four equally probable singleton configurations per trial (trial types): a lateral target with no distractor (TL), a lateral target and midline distractor (TLDM), a lateral distractor and no target (DL), or a midline target and lateral distractor (TMDL).

The search array was followed by a response window displaying only the fixation point, which remained until response on target-present trials (TL, TLDM, TMDL), or for 1000 ms on target-absent trials (DL). On target-present trials, participants were instructed to indicate the target's grating orientation by pressing a pre-defined key on a standard two-button mouse (response assignments counterbalanced across participants), whereas no response was required for target-absent trials. Response generation was lateralised; the left button always being pressed with the left thumb, and the right button with the right thumb. Incorrect responses immediately triggered a white minus symbol at screen centre (500 ms). An inter-trial interval (950-1050 ms, randomised) occurred prior to the next trial (See Fig. 1 for a depiction of the stimuli, trial types, and overall trial sequence). Each exercise condition included 576 trials evenly split across eight blocks in which trial types were presented in random order but equal proportions, resulting in 144 presentations of each trial type per condition.

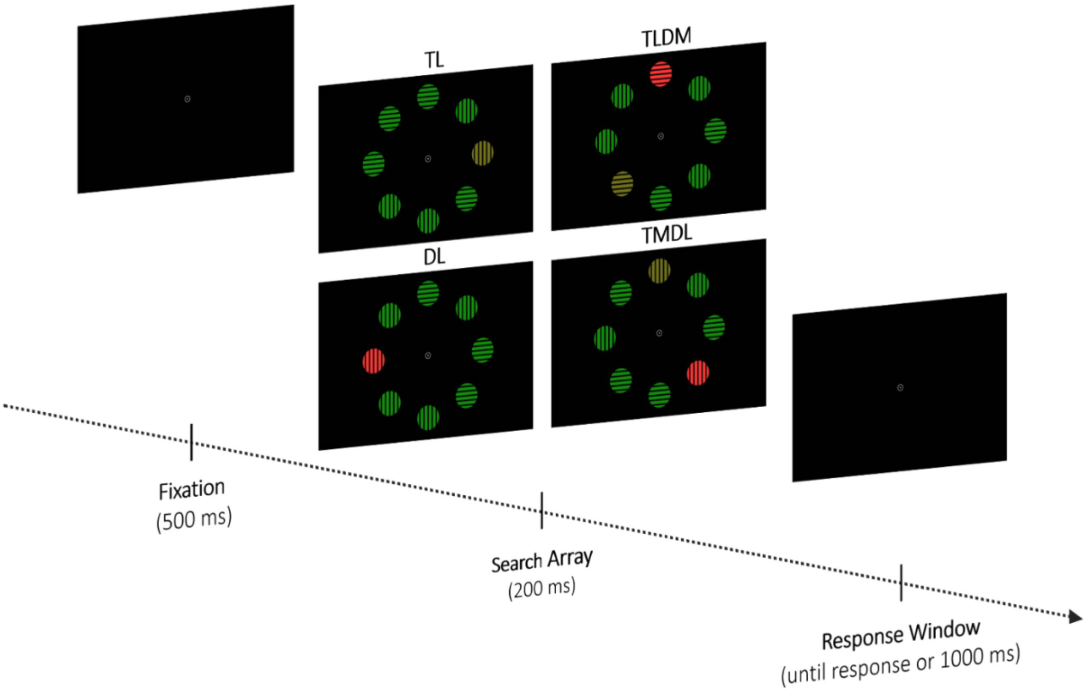

**Figure 1.** Sequence of events in the additional-singleton paradigm. Each trial began with a fixation cross (500 ms), followed by a search array (200 ms) containing one of four equally probable singleton configurations; a lateral target and no distractor (TL), lateral target and midline distractor (TLDM), lateral distractor and no target (DL), or midline target and lateral distractor (TMDL). The search array was then immediately followed by a response window containing only the fixation point, which remained on screen until a response was given (or, in the case of the DL trial type, for 1000 ms). Participants were instructed to respond according to the orientation of the grating contained by the target singleton (yellow circle), while ignoring the distractor singleton (red circle). A randomized inter-trial interval (950-1050 ms) including only a blank screen occurred between each trial.

### 3.2.3 Haemodynamic Controls & Exercise Conditions

At the beginning of each experimental session, participants rested in a supine position for five minutes, during which a heart rate monitoring chest strap and smart watch (Models H7, M400, Polar Electro, Kempele, Finland) continuously sampled their heart rate (HR) at 1 Hz. The lowest recorded value provided an approximation of their resting heart rate (RHR), while their maximum heart rate (MHR) was estimated using a standardised formula [MHR = 208 – (0.7 x age)] (Tanaka, Monahan, & Seals, 2001). Their heart rate reserve (HRR) was then calculated (equal to MHR – RHR), providing a metric of individual cardiovascular capacity (Karvonen & Vuorimaa, 1988). Importantly, the intensity of physical efforts can be normalised across participants by adding a standardised percentage of HRR to RHR (% HRR) on an individual basis, resulting in a uniquely targeted heart rate accounting for variability in cardiovascular capacity and aerobic fitness (Swain & Leutholtz, 1997).

The experiment was performed while seated on a recumbent stationary bicycle (LifeFitness Club Series, Brunswick Corporation, Rosemont, IL USA). Thresholds for the three workloads – passive rest (PR; >30% HRR), low-intensity exercise (LE; 40-50% HRR, ≈ VT1), and moderate-intensity exercise (ME; 60-70% HRR, ≈ ITA-median), were based on the limits defined in Table 1 (Dodwell et al., 2019; adapted from Garber et al., 2011; Karvonen & Vuorimaa, 1988). All three conditions were performed within a single experimental session in counterbalanced order across participants. The PR condition took place while seated on the stationary bicycle without pedalling. The LE and ME conditions began with a five-minute warmup period, wherein participants pedalled a fixed cadence of 70-80 rpm as pedal resistance was gradually modulated by 10-watt increments until achieving a stabilised workload within their individually targeted HR range. Thereafter, participants maintained a 70-80 rpm cadence throughout the task, with their HR being regulated via stepwise adjustments to pedal resistance, as necessary. The opportunity to hydrate was available between blocks (although exercise was continuous), and adequate time was given between conditions for recovery to a resting state (>30% HRR).

**Table 1.** Classification scale of exercise workloads relative to various cardiorespiratory metrics, including percent max heart rate (%MHR), percent maximal aerobic capacity (%$VO_2$ max), percent heart rate reserve (%HRR), and perceived effort. Each workload "zone" can be generally defined by the relative intensity of exercise (e.g., "low-intensity" for zone 2, "moderate-intensity" for zone 3) or the ventilatory threshold typically occurring therein (e.g., VT2 for zone 4).

| *Workload* | *% MHR* | *% $vO_2$ max* | *% HRR* | *Perceived Effort (1 – 10)* |
|---|---|---|---|---|
| Zone 0<br>Rest ($vO_2$ rest) | < 57 | < 37 | < 30 | ≤ 2 |
| Zone 1<br>Minimal (sub-VT1) | 57 – 63 | 37 – 45 | 30 – 39 | 2 – 3 |
| Zone 2<br>Low (≥ VT1) | 64 – 76 | 46 – 63 | 40 – 59 | 4 – 5 |
| Zone 3<br>Moderate (ITA) | 77 – 95 | 64 – 90 | 60 – 89 | 6 – 7 |
| Zone 4<br>High (≥ VT2) | ≥ 96 | ≥ 91 | ≥ 90 | 8 – 9 |
| Zone 5<br>Maximal ($vO_2$ max) | ≥ 99 | ≥ 99 | ≥ 99 | ≥ 9 |

### 3.2.4 Behavioural data processing and analysis

Behavioural data was processed using Microsoft Excel (version 16.0, Microsoft Corp., Redmond, WA) and pandas (McKinney, 2010). First, we calculated each participant's mean HR and error rate (ER) per block and workload (PR, LE, ME). Participants whose mean HR fell outside their targeted range for more than one block, or those with a mean ER above 20% across all blocks were rejected from further analysis. Because the only behaviourally relevant trial type manipulation was whether a distractor was presented along with the target (thus inducing the distractor interference effect), our behavioural analysis focused purely on distractor absence vs presence. The behavioural results from the TL condition therefore served as "distractor-absent" trials, while results from the TLDM and TMDL trials were combined to represent "distractor-present" trials. The mean ER of the distractor-absent and distractor-present trials were then calculated per workload for each participant. To calculate RT, trials where the button press could be considered anticipatory or delayed were first removed (<200 or >999 ms after extinction of the search array); the remaining trials (distractor-absent vs distractor-present) were then averaged per workload for each participant. Lastly, the RT and ER results from each participant were statistically analysed in IBM SPSS (version 25.0, IBM Corp., Armonk, NY) using a 2×3 repeated-measures ANOVA with factors of distractor presence (distractor-absent [TL], distractor-present [TLDM + TMDL]) and workload (PR, LE, ME), with the Šidák method applied to correct for multiple comparisons.

### 3.2.5 EEG recording and data processing

The EEG data was continuously sampled at 1 kHz from 64 active Ag/AgCl electrodes connected to a wireless amplifier (250-Hz low-pass filter, 10-s time constant; Brain Products ActiCAP, MOVE, Munich, Germany). Electrode positions matched the international 10-10 system, with the exception of one additional electrode being located on the inferior orbit of the left eye to record the vertical electrooculogram (VEOG), and electrode FCz serving as the online reference. Impedances were adjusted to 5 kΩ or less, being maintained as necessary between conditions.

The EEG data were processed using Brain Vision Analyser II (Brain Products GmbH, Munich, Germany). The continuous EEG was first visually inspected to exclude apparent noise (e.g., electromyographic bursts). A 1 Hz high-pass and 50 Hz notch IIR filter were then applied, limiting low-frequency artefacts related to sweat and line noise. Following this, an infomax independent component analysis (ICA) was performed to remove components representing blinks and saccades. A 30 Hz low-pass IIR filter was then applied before re-referencing all EEG signals to the 64-channel common average. The resulting data were separated by workload (PR, LE, ME) and segmented into 1000 ms epochs (-200 to +800 ms from search array onset) per trial type (TL, TLDM, DL, TMDL). These segments were baseline corrected to their 200 ms pre-stimulus intervals, then passed through an artefact rejection, excluding those segments containing signals over ±60 µV, voltage steps exceeding 50 µV/ms, and activity changes below 0.1 µV per 100 ms. The surviving segments were separated into left and right hemifield trials relative to the lateralised singleton in the given trial (excluding errors) and averaged accordingly. Finally, difference waves were calculated for each condition over electrodes PO7/PO8 by subtracting the ipsilateral from contralateral waveform (relative to the lateralised singleton), then averaging the resulting ERLs across both left and right hemifield trials (formula: [(PO8 – PO7 [left-singleton]) + (PO7 – PO8 [right-singleton])/2]).

### 3.2.6 EEG analysis

As expected, the PCN was observed in the grand-averaged waveform of lateralised target trials (TL, TLDM), while both the $P_D$ and an unanticipated Ppc were present in the grand-averaged waveform of lateralised distractor trials (DL, DLTM). Our analysis therefore primarily focused on the mean amplitude and onset latency of the PCN and $P_D$, with an additional post-hoc exploration of the distractor-elicited Ppc component.

Time windows for calculating the mean amplitudes of the PCN and $P_D$ were first defined by the onset and offset latencies (50% peak amplitude) of their respective grand-averaged waveforms (PCN: 235-295 ms; $P_D$: 240-290 ms), then applied to the single-participant data for each workload and relative trial type (PCN: TL, TLDM; $P_D$: DL, TMDL). To identify single-participant onset latencies for each component, we first calculated subaverage scores (70% peak amplitude) per workload and relative trial type using the jackknife-based approach (Ulrich & Miller, 2001). Single-participant onset latency estimates were then retrieved from the subaverage scores using the transformation provided by Smulders (2010)[2], which allows statistical analysis of the resulting dataset without the need for variance adjustments. The compiled mean amplitude and latency measurements for the PCN and $P_D$ were then each submitted to a 2×3 repeated-measures ANOVA with factors of trial type (PCN: TL, TLDM; $P_D$: DL, TMDL) and workload (PR, LE, ME), with the Šidák method applied to correct for multiple comparisons.

Although a Ppc was observed accompanying the $P_D$ in the grand-averaged waveform of lateralised distractor trials, its presence was somewhat erratic between workloads, only being predominantly apparent during LE. Further, due to a relatively low signal-to-noise ratio and high variability between participants, the Ppc was not consistently discernible from baseline within each of the relative trial types (DL, TMDL). For this reason, it was deemed necessary to determine whether a Ppc could be statistically differentiated from baseline activity when collapsed across the lateralised distractor trials of each workload. To accomplish this, we first defined time windows within the grand-averaged waveform over all participants and workloads, ranging +/- 50 ms from the latency of the most positive peak detected between 100 to 200 ms for the Ppc (peak: 145 ms, window: 95 to 195 ms), and -150 to -50 for the baseline (peak: -131 ms, window: -179 to -79 ms). The mean positive amplitude within these windows was then calculated from the single-participant waveform of each workload. The resulting single-participant Ppc and baseline means were then compared per-workload in a series of exploratory paired samples t-tests.

## 3.3 Results

### 3.3.1 Behavioural Performance

Response time demonstrated a general trend to become faster as workload increased, and slower with distractor interference (see Fig 2). These observations were statistically supported by main effects of both workload and distractor presence ($F$ (2,46) = 6.17, $p$ = .004, $\eta_p^2$ = 0.21; $F$ (1,23) = 27.43, $p$ < .001, $\eta_p^2$ = 0.54), although no interaction between factors was indicated ($p$ = .22). In pairwise

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[2] $\boldsymbol{o_i} = \boldsymbol{n\bar{J}} - (\boldsymbol{n} - \mathbf{1})\boldsymbol{j_i}$, where $\boldsymbol{\bar{J}}$ represents the mean of all subaverage scores, $\boldsymbol{n}$ the number of participants, $\boldsymbol{j_i}$ the individual subaverage, and $\boldsymbol{o_i}$ the "retrieved" individual latency (Smulders, 2010).

comparisons between workloads, RTs were confirmed to be faster during ME than PR (567 vs 596 ms; *t* (23) = -4.23, *p* = .001, *d* = -0.55), although no differences were indicated between ME and LE (567 vs 579 ms; *p* = .35), or LE and PR (579 vs 596 ms; *p* = .28). Responding was therefore shown to become progressively speeded as workload increased. This pattern (ME<PR) persisted within distractor-absent trials (564 vs 591 ms; *t* (23) = -4.00, *p* = .002, *d* = -0.54) and distractor-present trials (569 vs 599 ms; *t* (23) = -4.24, *p* = .001, *d* = -0.56). Response times were also shown to be generally faster in distractor-absent as compared to distractor-present trials (577 vs 584 ms; *t* (23) = -5.24, *p* < .001, *d* = -0.15), demonstrating a presence of the anticipated distractor-interference effect. As a function of workload, this pattern (distractor-absent < distractor-present) was confirmed during PR (592 vs 599 ms; *t* (23) = -3.18, *p* = .004, *d* = -0.14) and LE (574 vs 585 ms; *t* (23) = -4.96, *p* < .001, *d* = -0.16), however, the effect was only marginal during ME (564 vs 569 ms; *t* (23) = -2.00, *p* = .057, *d* = -0.09). As such, the distractor-interference effect was seemingly diminished during moderate-intensity exercise.

Error rates showed a slight tendency to increase with exercise and distractor interference, however these patterns were indicated to be negligible by an absence of main effects for workload (*p* = .14) and distractor presence (*p* = .85), as well as a lack of interaction between these factors (*p* = .14). Although the ER in distractor-absent trials appeared particularly elevated during ME, pairwise comparisons between workloads within the distractor-absent condition did not indicate a significant difference between ME and PR (5.44 vs 4.25 %; *p* = .12) or ME and LE (5.44 vs 4.49 %; *p* = .16). Similarly, no differences were indicated between workloads within the distractor-present condition (all *p* > .86). This indicates that our RT effects cannot be explained by differential speed-accuracy trade-offs between workloads. Further, no significant differences were detected between distractor-absent and distractor-present trials within each workload (all *p* > .27). Any workload-specific influence of distractor presence on response accuracy could therefore also be disregarded.

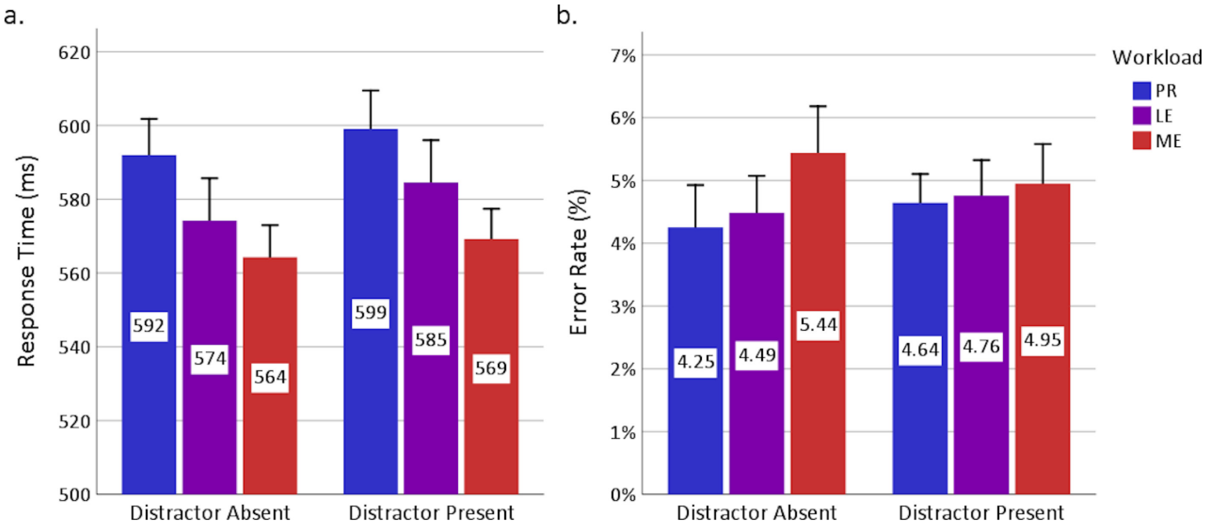

**Figure 2.** (a) Mean response times for the distractor-absent (TL) and distractor-present (TLDM + TMDL) trials within each workload (PR, LE, ME). Responses became generally more rapid as workload increased and were also delayed by distractor presence, demonstrating speeded responding during exercise as well as the typical distractor interference effect. (b) Mean error rates for the distractor-absent (TL) and distractor-present (TLDM + TMDL) trials within each workload (PR, LE, ME). ANOVA results did not reveal main effects of workload, distractor presence, or interaction between these factors, allowing us to rule out the possibility of differential speed-accuracy trade-offs between workloads.

### 3.3.2 Target Selection: PCN

Distractor presence (TLDM vs TL trials) appeared to reduce PCN mean amplitudes during both PR and ME – however, this effect was not visibly present during LE (see Fig. 3). Both a main effect of trial type and a relatively weak interaction between factors were indicated ($F$ (1,23) = 15.70, $p$ = .001, $\eta_p^2$ = 0.41; $F$ (2,46) = 3.19, $p$ = .050, $\eta_p^2$ = 0.12), whereas no main effect of workload was detected ($p$ = .61). The observed pattern was confirmed in pairwise comparisons between trial types within each workload; amplitudes in TLDM trials were significantly reduced compared to TL trials during both PR (-2.20 vs -2.78 µV; $t$ (23) = 2.91, $p$ = .008, $d$ = 0.43) and ME (-2.14 vs -2.73 µV; $t$ (23) = 2.88, $p$ = .008, $d$ = 0.49), whereas no significant difference was indicated during LE (-2.57 vs -2.59 µV; $p$ = .85). Further, amplitudes were only shown to differ between workloads in TLDM trials, proving significantly greater during LE (-2.57 µV) than both PR (-2.20 µV; $t$ (23) = -2.31, $p$ = .030, $d$ = -0.31) and ME (-2.14 µV; $t$ (22) = -2.34, $p$ = .029, $d$ = -0.38), whereas no differences were detected in TL trials (all $p$ > .36). As such, PCN amplitudes were reduced by distractor presence during both PR and ME, but this effect was extinguished during LE.

Distractor presence also seemed to delay PCN onset latencies during both PR and ME, while no such effect was apparent during LE. This observation was partially supported by a main effect of trial type ($F$ (2,46) = 10.96, $p < .003$, $\eta_p^2 = 0.32$), whereas no main effect of workload ($p$ = .13) or interaction ($p$ = .29) was revealed. Comparisons between trial types (TLDM vs TL) within each workload indicated the observed delay to be highly significant during ME (247 vs 236 ms; $t$ (22) = 3.07, $p$ = .005, $d$ = 0.68), but only marginal during PR (246 vs 250 ms; $t$ (22) = 1.99, $p$ = .058, $d$ = 0.31), while no difference was detected during LE ($p$ = .15). As such, while distractor presence tended to delay target selection during PR and ME, this effect was also extinguished during LE. Further, onset latencies within TL trials tended to decrease with increasing workload, occurring marginally earlier during ME as compared to PR (236 vs 246 ms; $t$ (22) = -2.52, $p$ = .056, $d$ = -0.60), although no differences were indicated between ME and LE (236 vs 241 ms; $p$ = .71), or LE and PR (241 vs 246 ms; $p$ = .35). By contrast, no such differences were detected between workloads within TLDM trials (all $p > .58$). Moderate-intensity exercise therefore tended to expedite target selection as compared to rest in distractor-absent trials, although having no detectable effect in distractor-present trials.

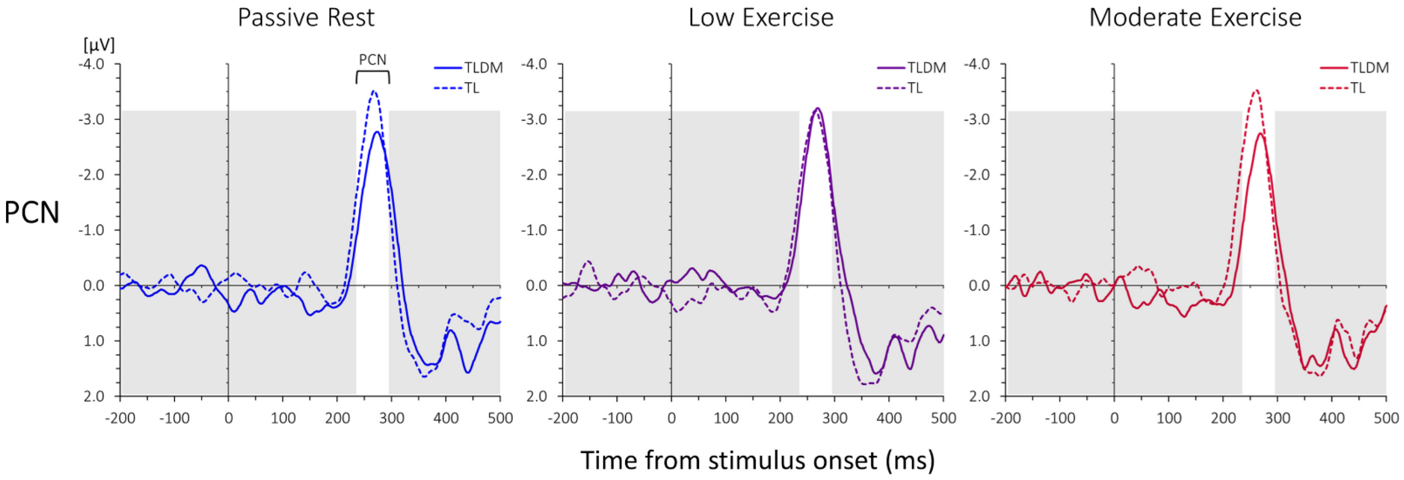

**Figure 3.** PCN waveforms at PO7/8 for the target-lateral trial types (TL, TLDM) within each workload (left to right: PR, LE, ME). *Amplitude* – During PR and ME, the PCN amplitude was reduced in TLDM trials (solid line) as compared to TL trials (dashed line), demonstrating the typical distractor interference effect. However, this reduction was not present during LE (middle panel). Between workloads, differences were only detected in TLDM trials, whereas amplitudes did not significantly differ in TL trials. *Latency* – During ME, distractor presence (TLDM vs TL trials) significantly delayed the onset of the PCN, with a similar (although only marginal) trend during PR. By contrast, no onset differences were indicated between trial types during LE.

### 3.3.3 Distractor Suppression: $P_D$

Across workloads, the $P_D$ mean amplitude was noticeably greater in TMDL trials than in DL trials, denoting an increased demand for distractor suppression when a target was present (see Fig. 4). This pattern was supported by a main effect of trial type ($F$ (1,23) = 8.58, $p$ = .008, $\eta_p^2$ = 0.27), whereas no main effect of workload or interaction was indicated ($p$ = .33; $p$ = .85). However, the observed effect was not detected in comparisons between trials types within each workload (all $p$ > .13), therefore only being confirmed as a global attribute. Further, while $P_D$ amplitudes in DL trials appeared reduced during both LE and ME as compared to PR, neither these comparisons nor those within TMDL trials proved significant (all $p$ > .15). The presence of a distractor was therefore only shown to globally increase the magnitude of the $P_D$ across workloads.

Analysis of $P_D$ onset latencies did not indicate main effects of workload, trial type, or an interaction between these factors (all $p$ > .72). Further, no significant effects were detected in comparisons between workloads as a function of trial type, or between trial types as a function of workload (all $p$ > .52). As such, the present results do not indicate that $P_D$ timing was influenced by target presence or exercise.

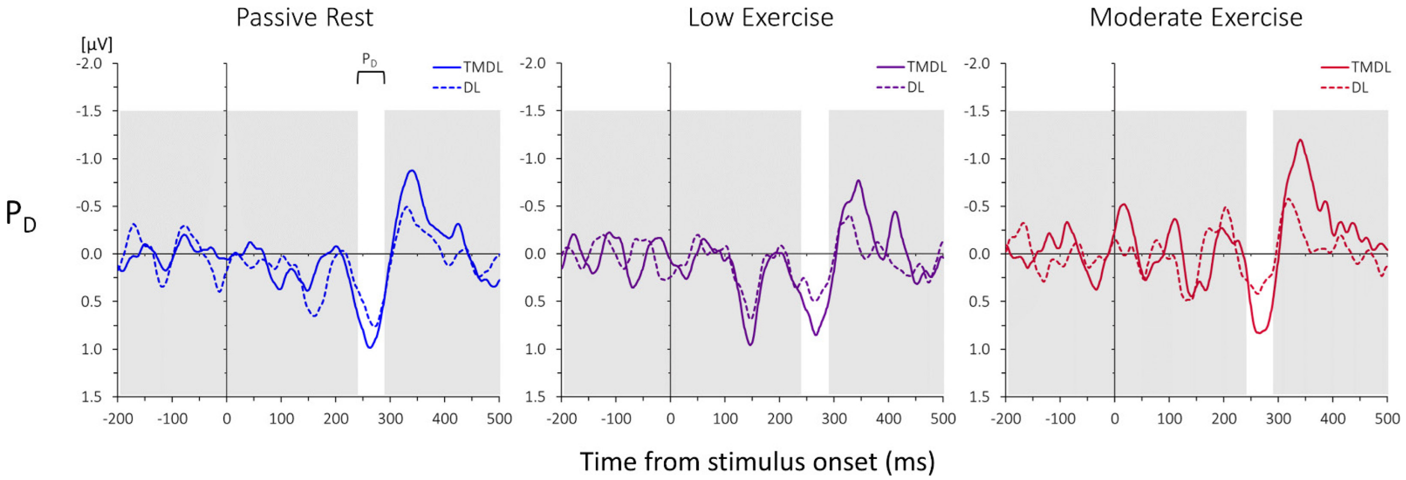

**Figure 4.** $P_D$ waveforms at PO7/8 for the distractor-lateral trial types (DL, TMDL) within each workload (left to right: PR, LE, ME). *Amplitude* – Across workloads, the $P_D$ amplitude was increased in TLDM trials (solid line) as compared to TL trials (dashed line), demonstrating an increased demand for distractor suppression. However, this increase was not detected within the individual workloads, and no differences were detected between workloads. The effect therefore only occurred globally between trial types. *Latency* – No differences were detected between workloads or trials types regarding the onset of the $P_D$, suggesting that, at least within the present task, $P_D$ timing was not substantially influenced by target presence or exercise.

### 3.3.4 Pre-attentive Processing: Ppc

The Ppc appeared inconsistently across workloads, only being clearly discernible from baseline activity during LE (see Fig 5). Exploratory paired samples t-tests confirmed this observation, demonstrating that during LE, the mean positive activity within the Ppc window (*M* = 0.65 µV, *SD* = 0.37) significantly exceed that of the baseline window (*M* = 0.47 µV, *SD* = 0.34; *t* (23) = 2.35, *p* = .028, *d* = -0.53), whereas no differences were indicated during PR or ME (*p* = .17; *p* = .54). As such, positive activity within the Ppc window could only be statistically differentiated from baseline during LE, suggesting that the Ppc was uniquely facilitated during low-intensity exercise.

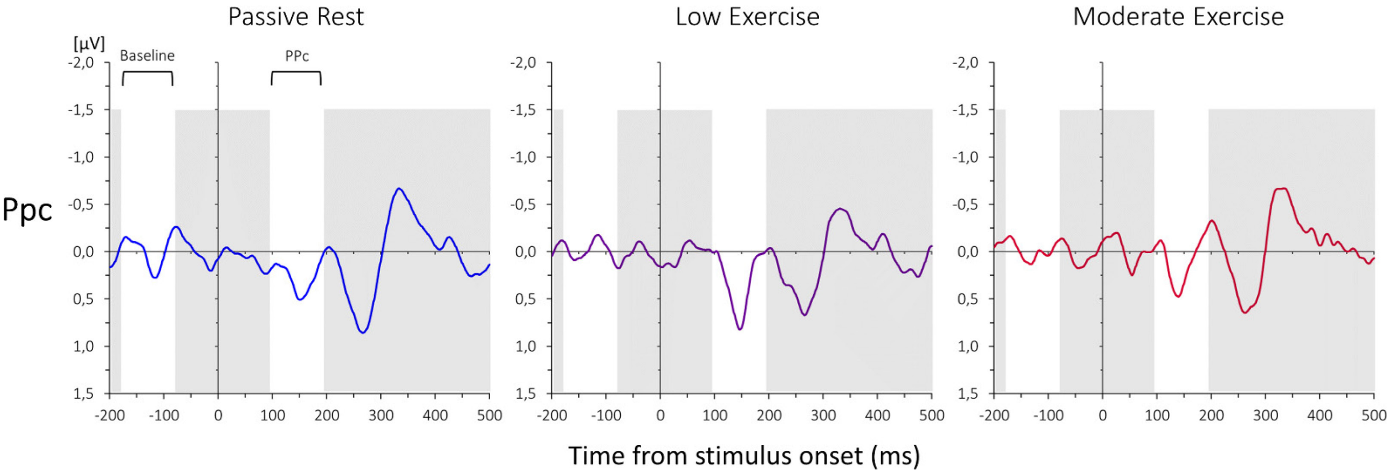

**Figure 5.** Ppc waveforms at PO7/8 for the distractor-lateral trials (DL + TMDL) within each workload (left to right: PR, LE, ME). The mean positive activity within the Ppc window was shown to significantly differ from that of the baseline window during LE, whereas no differences were indicated between the baseline and Ppc windows during PR or ME. As such, the Ppc component could only be substantially differentiated from baseline activity during LE, suggesting a workload-specific facilitation of early salience suppression mechanisms.

## 3.4 Discussion

The present study aimed to investigate the performance of top-down attentional control during acute bouts of aerobic exercise. ERPs reflecting attentional selection and distractor suppression were monitored as participants performed an additional-singleton task across conditions of rest, low-intensity exercise, and moderate-intensity exercise. Behaviourally, responses become more rapid as workload increased without a corresponding loss of accuracy, while the distractor-interference effect was also marginalised during moderate-intensity exercise. Further, low-intensity exercise was found to have induced novel electrophysiological effects, both eliminating the distractor interference exhibited by the PCN, and eliciting an enhanced Ppc. Each of these findings are discussed below in further detail.

### 3.4.1 Task performance: More rapid responding as the intensity of exercise increases

Response times became significantly more rapid as workload increased without a substantial parallel reduction in response accuracy, denoting a facilitation of cognitive performance during ITA workloads. That is to say, were differential speed-accuracy trade-offs indicated between workloads, it could be argued that during exercise, a more lenient decision criterion had been adopted, or cognitive control had deteriorated as predicted by the RAH (Dietrich, 2006; Dietrich & Audiffren, 2011). For the present task, however, no loss of cognitive control due to exercise was indicated, at least during workloads within the ITA. However, it must be noted that while the observable tendency for error rates to slightly increase along with workload proved to be insignificant, it should not be entirely discounted. Firstly, error rates across all conditions remained consistently near floor levels (circa 5%), which could suggest the present task may have simply been too low in demand, or too weak in error sensitivity, for accuracy effects to arise. Even so, workloads beyond the ITA may have elicited more substantial effects, were the trajectory of the observed trend to persist. Future investigations involving more challenging tasks demands and higher workloads would therefore be warranted.

Although considered here to reflect cognitive facilitation, some suggest that speeded responding during exercise may instead be primarily driven by more efficient motor processes (Davranche, Burle, Audiffren, & Hasbroucq, 2006; Davranche & McMorris, 2009). However, several studies have demonstrated this effect to coincide with reduced P3 latency, therefore being at least partially attributable to a more rapid classification of stimuli (McMorris & Hale, 2012; McMorris, Sproule, Turner, & Hale, 2011). Similarly, a previous working memory study (Dodwell et al., 2019) provided novel evidence from the lateralised readiness potential (LRP) tracing speeded responding during exercise to the facilitation of higher cognitive processes. The LRP is an ERL indicative of lateralised motor preparation (Coles, 1989), and can be calculated relative either to the stimulus (sLRP) or response (rLRP) (Wiegand, Finke, Müller, & Töllner, 2013). The sLRP latency represents the time required for response selection (Eimer, 1998; Töllner, Rangelov, & Müller, 2012), while the rLRP latency indicates the time needed for motor production of the selected response (Miller, Patterson, & Ulrich, 1998). Whereas latencies for accessing working memory and the rLRP did not differ between conditions of rest and moderate-intensity exercise, response time facilitations were mirrored by the sLRP latency (Dodwell et al., 2019). This indicated the facilitations observed during exercise to have originated during some intermediary stage between target analysis and response selection, rather than during response production.

The anticipated distractor interference effect was also observed, although it became somewhat marginalised during moderate workloads. This may be partially explained by the findings of Hüttermann and colleagues, who demonstrated enhanced attentional processing in the lateral periphery (or *attentional breadth*) during moderate-intensity cycling (Hüttermann et al., 2014). In the present study, a similar lateral facilitation during moderate-intensity exercise may have promoted better avoidance of midline distractors by enhancing the processing of lateralised targets, thereby reducing the overall distractor interference effect. However, as our design was by no means intended to examine attentional breadth, a further targeted investigation of this particular finding should also be considered.

### 3.4.2 ERP pattern: Low-intensity exercise enhances attentional resource allocation

Our EEG results offer compelling evidence for an increased allocation of attentional resources specifically during low-intensity exercise, demonstrating an inverted-U function of performative facilitation. The PCN was modulated by distractor presence during both resting and moderate-intensity exercise conditions, showing a reduced amplitude (and in the case of moderate-intensity exercise, a significantly delayed onset) in distractor-present trials. By contrast, these effects were seemingly eliminated during low-intensity exercise, with the PCN amplitude and onset remaining unchanged between distractor-absent and distractor-present trials. Importantly, no corresponding workload-specific amplitude modulations were shown by the PCN in distractor-absent trials, or by the $P_D$. Our findings therefore suggest that during low-intensity exercise, target-selective mechanisms utilised additional resources when an attentionally competitive distractor was present, and that this supplementation was not attributable to a redistribution of resources away from distractor suppression mechanisms.

Beyond merely providing neurocorrelative evidence for an exercise-induced supplementation of attentional resources, the contextual specificity of their utilisation alludes to a mechanistic hierarchy of resource distribution. That is to say, if the distribution of resources were mechanistically agnostic, their supplementation would be expected to drive an equivalent facilitation of both target-selective and distractor suppression mechanisms. In the present results, however, distractor suppression mechanisms seem to have drawn upon the available attentional resources equally across workloads, whereas target-selective mechanisms only maintained full functionality once additional resources became available during LE. As such, it would appear that for the present task, distractor suppression mechanisms may have been given distributional priority, their performance being preserved at the expense of target-selective mechanisms when resource demands exceeded the available supply. Although mainly speculative, this might be corroborated through additional manipulations to the resource demands of both distractor and target processing, for instance by modulating the feature contrast between the target and distractor as in Töllner and colleagues (2011).

Of note, the presence of the distractor-elicited Ppc was substantiated exclusively during low-intensity exercise, although the cause for its emergence remains somewhat unclear. One potential explanation can be derived from Bullock and colleagues (2015), who observed a comparably workload-specific and object-selective enhancement of the P1, which was proposed to reflect an exercise-induced facilitation of sensory gain. Such a facilitation may have similarly promoted pre-attentive salience processing, rendering the distractor-elicited Ppc observed here.[3] However, a direct metabolic supplementation of the mechanism(s) underlying the

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[3] This is not to suggest that selective facilitations of sensory gain are exclusively intended to promote attentional suppression; enhanced P1 waveforms have been similarly indicated contralateral to feature singletons possessing a reward-associated colour, regardless of whether the singleton was a target or distractor (e.g., Hickey, Chelazzi, & Theeuwes, 2010). How these enhanced sensory signals are treated (that is, whether they are attentionally selected or suppressed) may therefore depend upon previous experiences and top-down control settings for the given task.

Ppc could be equally likely, resulting in a more robust or less transient signal. Regardless, the congruent enhancement of the P1 and Ppc should not be disregarded. Perhaps just as interestingly, a corresponding target-elicited Ppc was not observed, lending intuitive support to more suppressive interpretations of its functional role (e.g., Feldmann-Wüstefeld & Vogel, 2019; Gaspelin & Luck, 2018; Weaver et al., 2017). It should be noted, however, that the present experiment employed fixed singleton features, with the distractor always being most salient. As such, this suppression account may be further supported were a similar pattern to be confirmed with either the target always being most salient (e.g., Jannati, Gaspar, & McDonald, 2013), or the most salient item being varied between trials.

Further, the concurrent emergence of the Ppc and elimination of distractor interference in the PCN during low-intensity exercise may be more than mere coincidence. Considering both are thought to interact with the pre-attentive salience map, distractor interference costs otherwise exhibited by the PCN could have been negated through the additional pre-attentive processing reflected by the Ppc, rather than an independent supplementation of target-selective mechanisms. Were this pre-attentive processing to be globally suppressive, one might also suspect the resource demands exhibited by the $P_D$ to be similarly reduced or eliminated, although such was not evident in the present results. Regardless, this does not necessarily dismiss the possibility that the presence of the Ppc may have selectively influenced the PCN, or preclude the supplementation of neural resources during exercise as a driving factor; instead, it would simply suggest a more finite supplementation of pre-attentive rather than more latent attentional mechanisms.

It is important to note that these electrophysiological effects do not necessarily reflect the observed behavioural results. For instance, during low-intensity exercise, the concurrent preservation of the PCN amplitude and emergence of the Ppc were not coupled with improvements in response accuracy or speed. Likewise, during low-intensity exercise, the distractor-interference effect delayed responses regardless of the PCN latency being unaffected, while conversely during moderate-intensity exercise, the distractor-interference effect was marginalised despite a delayed PCN. However, this should not be taken to suggest the observed electrophysiological effects could not have influenced behavioural performance. As previously mentioned, error sensitivity may have simply been too low to detect subtle changes arising while the speed of processing effects observed during attentional selection could likely be overshadowed by modulations during post-attentional processes such as response selection (e.g., Dodwell et al., 2019).

## 3.5 Conclusion

Our findings provide several key insights regarding both the behavioural and electrophysiological influence acute aerobic exercise can have on concurrent attentional performance, indicating workload-specific effects even within the finite range of the ventilatory thresholds. Firstly, response times became faster during moderate-intensity exercise without a corresponding loss of accuracy, denoting a facilitation of cognitive performance that coincides with various predicted supplementations of neural resources. Secondly, the distractor interference effect was found to be marginalised during moderate-intensity exercise, possibly supporting prior indications of an expanded attentional breadth during physical activity. Thirdly, and most importantly, our EEG findings not only demonstrate a facilitation of top-down attentional control during low-intensity exercise, but also suggest that neural resources may be hierarchically distributed between target-selective and distractor suppression mechanisms. Lastly, the pre-attentive processing of lateralised distractors was also shown to have been selectively enhanced during low-intensity exercise, alluding to a more suppressive role of the mechanism being indexed by the Ppc. In sum, these findings expand our understanding of attentional control both at rest and during exercise, illuminating previously untapped aspects of how resource availability and utilisation might influence attentional performance.

# 4 GENERAL DISCUSSION

## 4.0 Synopsis

In the present dissertation, both behavioural and electrophysiological measures of visual working memory and attentional control revealed performative benefits during acute aerobic exercise within ITA workloads. In each of experiments detailed above, moderate exercise was shown to expediate responses as compared to rest, without a substantial loss of response accuracy. These findings further support the general trend for speeded responding during excise that has been by several prior meta-analyses (Chang et al., 2012; Lambourne & Tomporowski, 2010; Ludyga et al., 2016; McMorris & Hale, 2012), and also offer a direct challenge to the assumptions of the RAH model (Dietrich, 2006; Dietrich & Audiffren, 2011). However, interpreting this result alone would leave open questions regarding how and when the speeded processing and simultaneous preservation of response accuracy may have occurred. For example, purely behavioural measures would be unable to distinguish whether the observed response time effects indicate a facilitation of cognitive processing, or alternatively, may only represent an exercise-induced facilitation of motor processes (Davranche et al., 2006; Davranche & McMorris, 2009). Similarly, it becomes difficult to convincingly suggest that the observed preservation (or in the case of standing upright, facilitation) of response accuracy may have been driven by an exercise-induced supplementation of neural resources, without having some neurocorrelative evidence to reflect such. Fortunately, monitoring lateralized ERPs referencing covert stages of processing as executive control tasks were performed during exercise provided the neural correlates necessary to address both of these questions, shedding new light on how aerobic exercise within the ITA might benefit cognitive performance. The following sections will address the primary findings of each experiment, as well as their implications for future studies.

## 4.1 Exercise benefits response selection, not execution

The VWM experiment in chapter 2 elucidated a critical aspect of the speeded responding observed during ITA workloads – exposing this effect to be driven by cognitive facilitation rather than motor facilitation. The onset latencies of the sLRP indicated facilitations during standing and exercise to have occurred within the cognitive processing pipeline prior to motor execution of the selected response, whereas the latencies of the rLRP did not differ between postural modalities or cardiovascular workloads. Further, the temporal pattern of the latency effects observed in the sLRP closely resembled those of the behavioural results, providing a convincing argument for a relation between these two findings. It's important to note that both the behavioural and electrophysiological effects were present regardless of whether exercise was performed in a seated or standing posture, and in fact, the effect seemingly overcame the delayed access to working memory representations observed during standing conditions.

The resilience of the effect in this regard allowed for it to be isolated to an intermediary processing stage ranging between analysis of the accessed VWM representation and selection of an appropriate motor response. This finding holds two major benefits: firstly, at least in similar contexts to the VWM retro-cue task utilized here, the speeded processing observed during exercise can be predicted to occur within a rather specific range of processing events. Secondly, those events are presumably governed or at the very least temporally overlapped by activity within frontal executive control networks, offering a potential contradiction to the inhibitory predictions of the RAH. In concert, these characteristics of the observed facilitation suggest that although resource supplementations should be generally available throughout the global cerebral blood flow, the utilisation of those additional resources may demonstrate a more regional and contextual specificity. In other words, while some networks or cognitive mechanisms may take advantage of the additional supply (in the present case, those governing executive control), others may not exploit the additional resources equally or at all.

## 4.2 Dynamic effects of postural shift

The influence of upright posture may be of no less interest. Specifically, both response time and accuracy benefits were observed simply due to postural shift from seated to standing positions. The response time effect was nearly as substantial as that brought on by exercise, while the response accuracy effect was entirely absent from exercise manipulations, serving as a testament to the potency of the arousal indued by postural shift (Jacob et al., 1998, Robertson et al., 1979, Smith et al., 1994). Further, as was the case for the exercise manipulation, the pattern of response time benefits due to postural shift was observable in the electrophysiological data as well. Conversely, standing upright was also shown to delay working memory access, demonstrating the performative influence of such postural shifts to be somewhat differential across cognitive dynamics.

As mentioned in the discussion of chapter 2, this delayed access to working memory might have been driven by interference between visuospatial working memory and sensorimotor networks involved in maintaining upright balance (Anguera et al., 2010; Chen et al., 2018; Fuhrmann et al., 2015; Kerr et al., 1985). It could therefore be argued that the observed effect offers some parallel to the basic principles of the RAH. However, the present findings would more accurately suggest exercise-related deficits to have arisen not because of resource-competition between distal unrelated processes, but rather due to functional overlaps between networks that would not have otherwise been simultaneously engaged (for a similar interpretation from meta-analysis, see Lambourne & Tomporowski, 2010). As such, the additional cognitive demands situationally present when engaging in specific modalities of exercise may pose a greater deficit to overall performance than the neural resource demands of performing exercise related movement in of itself. This is made evident as no such deficit was observed in the seated exercise condition, where the requirement to maintain balance would have been largely negated.

## 4.3 Exercise supplements cognitive resources in a workload-specific manner

The attentional control experiment detailed in chapter 3 provided the most compelling evidence for a supplementation of attentional resources during exercise, which was observed specifically within workloads towards the lower end of the ITA (nearer to VT1). While the presence of a distractor caused a marked drop in the amplitude of the PCN during both rest and moderate-intensity exercise, this effect was extinguished during low-intensity exercise, where the PCN no longer differed between distractor absent and distractor present workloads. Further, a distractor-elicited Ppc emerged during low-intensity exercise that was otherwise statistically insignificant in other workloads, providing an additional pre-attentive layer of distractor suppression. These findings suggest that there was a substantial enough supplementation of resources during low-intensity exercise to not only prevent the demands of distractor suppression from interfering with those of target detection, but to also allow an otherwise forfeit pre-attentive process to become activated.

As was discussed in the chapter, it remains unclear as to whether the mechanisms driving the PCN and Ppc were both directly supplemented, or whether the effect observed in the PCN amplitude and latency was a by-product of the activation of the mechanism reflected by the Ppc. Regardless, either scenario would still be explainable in terms of an exercise-induced resource supplementation. Beyond this, however, the accumulation of findings surrounding the PCN, $P_D$, an Ppc exposed a characteristic of the attentional mechanisms reflected by these components that has until now been entirely inaccessible – namely the proposed hierarchy of resource distribution between them. That is, given an insufficient supply of resources, it would appear (at least within the present context) the performance of the cognitive processes reflected by either the PCN, Ppc, or both (depending on which pattern of supplementation described above is considered) are sacrificed at the expense of maintaining the performance of those reflected by the $P_D$. In relation to the prevalent theories of attentional control, this interpretation provides a substantial insight regarding the long-standing dispute between those proposing a mechanistic dominance of either distractor-suppression of target-selection mechanisms. Furthermore, the finding also promotes the use of aerobic exercise not only to investigate the influence of its effects in of themselves, but also as a methodological tool for endogenously manipulating the availability of resources, potentially exposing similarly competitive hierarchies within other cognitive domains as well.

## 4.4 Implications for future research

The findings of these studies can help to inform not only future research concerning the influence of aerobic exercise on cognitive performance, but also that of the growing community looking to investigate cognitive functions within more dynamic and real-world environments. Particularly, it should be all the more apparent that purely physiological aspects of engaging in more realistic environments are highly relevant when comparing cognitive effects observed therein to equivalent processes observed in the laboratory at rest. As such, establishing within the laboratory not only a cognitive baseline, but also a physiological baseline to which performance within more dynamic environments might be compared would be highly warranted. Further, considering the finite range in which benefits were observed even within highly controlled ITA workloads, the transience of cognitive effects observed during exercise in past studies may be largely explained by a lack of control across, or individual differences between subjects. As such, monitoring performance over an incremental range of individually tailored workloads may be advisable to identify and standardize not only where benefits arise, but also where they begin to regress. Lastly, whether in the laboratory or more real-world contexts, these findings demonstrate a clear need to consider the compound effects of postural control, when approaching cognitive performance in scenarios where such demands are present.

## 4.5 Conclusion

The content of this dissertation has demonstrated that cognitive performance can be improved during aerobic exercise within ITA workloads, and that the physiological bases of these effects can be explored neurocognitive measures. Further, the methodological approach developed here may serve as a means by which to elucidate covert aspects of visual cognition that have otherwise remained largely inaccessible. Exploring cognitive performance during exercise therefore provides a viable means to expand our understanding of the human mind, both within the laboratory and more ecologically valid contexts.

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