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EEG evidence for enhanced attentional performance during moderate-intensity exercise

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Abstract

Research on 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 behaviors such as engaging in physical activity, which is thought to modulate the availability of neurometabolic resources. Here, we used 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 moderate-intensity exercise, and during vigorous-intensity exercise. In addition to behavioral measures, attentional processing was assessed via lateralized ERPs referencing target selection (PCN) and distractor suppression (P_D) mechanisms. Whereas engaging in exercise resulted in speeded response times overall, moderate-intensity exercise was found to uniquely eliminate the expression of distractor interference 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 used overall.

KEYWORDS
aerobic exercise, attention, cognitive control, event-related potentials, executive function

1 | INTRODUCTION

The covert mechanisms subserving top-down attentional control are among the most actively investigated facets of visual cognition. Nevertheless, the functioning of these mechanisms during aerobic exercise—a physiological state far more common in daily life than in neurocognitive laboratory

settings—has remained largely underexplored. This is primarily because of the susceptibility of conventional neurocognitive measures to motion-based artifacts, leading most research regarding the exercise–cognition interaction to only monitor neural correlates before or after periods of physical activity, rather than immediately during exercise. However, modern advancements in the recording and processing of

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electroencephalography (EEG) signals have rendered the collection of robust event-related potentials (ERPs) possible even during full body motion (see de Sanctis et al., 2012; Gramann et al., 2010; Nathan & Contreras-Vidal, 2016; Reis et al., 2014). Therefore, the aim of this study was to record EEG during the exercise-concurrent performance of an attentional control task, to investigate how physiological state changes that occur during exercise might not only influence behavioral performance but also covert the aspects of the top-down mechanisms subserving attentional control.

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 prioritized 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 et al., 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 et al., 2012; Müller et al., 2003; Theeuwes, 2018); however, whether this should be clearly segregated from top-down mechanisms remains somewhat debated (Gaspelin & Luck, 2018; Liesefeld & Müller, 2021; Nobre & Stokes, 2019). These preliminary *priority signals* are conceptualized as being preattentively summated within a topographically organized attentional *priority map*, from which an ordinal hierarchy of attentional selection (i.e., *selection priority*) is then determined (Bisley & Goldberg, 2010; Fecteau & Munoz, 2006; Itti & Koch, 2001; Klink et al., 2014; Liesefeld & Müller, 2021; 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 to maintain control over attentional guidance (Liesefeld et al., 2019; Theeuwes, 2018). Efficient target selection, thus, depends on the performance of top-down mechanisms promoting the target objects' selection priority, even when 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 et al., 2012), whereas when they fail and a salient distractor gains the highest selection priority, *attentional capture* is said to occur (Hickey et al., 2006; Liesefeld et al., 2017; Rauschenberger, 2003; Ruz & Lupiáñez, 2002; Theeuwes, 2010; Theeuwes & Godijn, 2002).

The attentional capture phenomenon has been operationalized within various experimental frameworks (see Rauschenberger, 2003, for review), including the additional-singleton paradigm (ASP) (Theeuwes, 1992; Theeuwes & Godijn, 2002). In the ASP, observers covertly search for a predefined target singleton displayed among several homogenous nontargets. 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 randomized and noninformative 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 Figure 1 for example displays). Experiments using the ASP typically result in longer response times (RTs) 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).

1.2 | EEG indices of attentional control

ERPs of the 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 lateralized ERP (or, a so-called event-related lateralization, ERL), characterized by an enhanced negative deflection arising 175–300 ms poststimulus over posterior electrodes (typically PO7/PO8) contralateral to the attended hemifield (Eimer, 1996; Luck & Hillyard, 1994a; Töllner, Müller et al., 2012; Woodman & Luck, 1999, 2003). Although 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 index distractor suppression, predicting its amplitude to scale with target-proximal filtering requirements (Luck et al., 1997; Luck & Hillyard, 1994b; Töllner et al., 2015). However, others have elicited the PCN while only presenting distractors contralateral to the target, suggesting it may instead reference target-specific feature processing (Conci et al., 2006; Eimer, 1996; Hilimire et al., 2009; Mazza et al., 2009).

More recent studies suggest the PCN may represent the superposition of two subcomponents, each discretely indexing target-selective or distractor suppression mechanisms. Nonlateralized visual objects are equivalently processed in both cortical hemispheres, therefore being unlikely to evoke ERLs. This allows the processing of a lateralized stimulus to be electrophysiologically isolated by locating attentionally competitive stimuli along the vertical midline (90°/270°), a technique known as *systematic lateralization* (Woodman & Luck, 2003). Applying this technique, Hickey et al. (2009) found search arrays including a lateralized target and midline
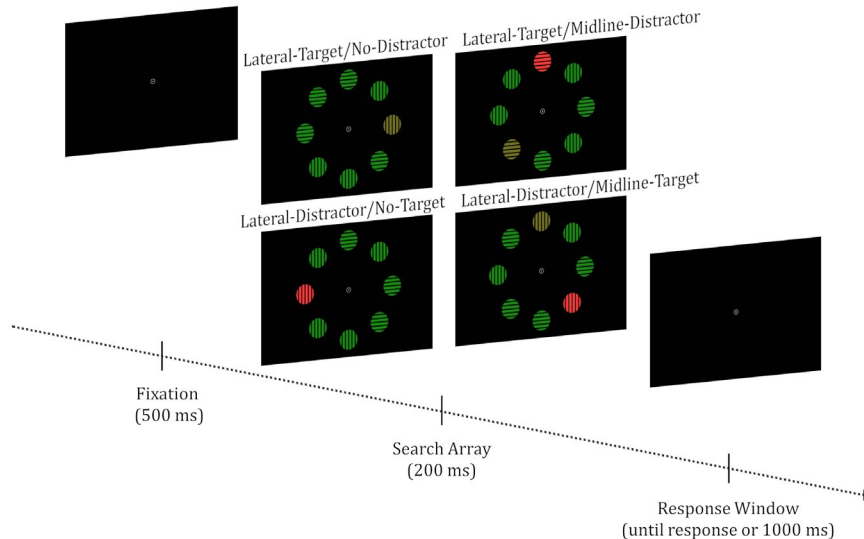
FIGURE 1 Sequence of events in the experiment. Each trial began with a fixation cross (500 ms), followed by a search array (200 ms) containing one of the four equally probable singleton configurations. The search array was then immediately followed by a response window containing only the fixation point, which remained on screen until a response was given (or, in the case of target-absent trials, for 1,000 ms). Participants were instructed to respond according to the orientation of the grating as depicted in the target singleton (yellow circle), while ignoring the distractor singleton (red circle)

distractor to elicit a PCN-like negativity contralateral to the target, whereas the inverse configuration (a lateralized distractor and midline target) resulted in a temporospatially similar positivity contralateral to the distractor. These systematically lateralized ERLs were coined the target negativity (N_T), reflecting target-selective enhancement, and the distractor positivity (P_D), indexing location-based distractor suppression (Hickey et al., 2009; Sawaki & Luck, 2010). Furthermore, linear summation of the isolated N_T and P_D has been found to predict the equivalent PCN in a spatially dependent manner (Gaspar & McDonald, 2014; Liesefeld et al., 2017).

The P_D is reliably observed in tasks where fixed or predictable singleton features are used, whereby reduced uncertainty allows attentional capture to be more effectively avoided (Allenmark et al., 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 et al., 2015; Gaspar & McDonald, 2014; Liesefeld et al., 2017; Sawaki & Luck, 2010; Töllner, Müller 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 et al., 2013; Töllner, Müller et al., 2012). Although these modulations can be considered an electrophysiological manifestation of the distractor interference effect, the driving force behind them remains

uncertain. Like 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 processing resources (Liu et al., 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 et al., 2011; Töllner et al., 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 et al., 2012; Jannati et al., 2013; Wiegand et al., 2015). More recent evidence suggests the Ppc may alternatively reference a preattentive 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 et al., 2017). However, direct investigations of this component are as of yet relatively sparse,

and thus interpretations of its functional role remain largely inconclusive.

1.3 | Neurometabolic resources during exercise

As for all executive functions, the neural mechanisms of top-down attentional control are both resource-limited and competitive, with performance becoming strained when task-demands exceed resource availability (Broadbent, 1958; Franconeri et al., 2013; Miller & Cohen, 2001). As such, the simultaneous engagement of distractor suppression and target-selective mechanisms could instigate resource competition, effectively impairing one or both. Similarly, the reticular-activating hypofrontality (RAH) model (Dietrich, 2006; Dietrich & Audiffren, 2011) suggests that cognitive performance may deteriorate during aerobic exercise, as the necessity to bring motor control processes online could instigate a competitive reallocation of neurometabolic resources away from cognitive control processes. Critically, this notion was derived from contemporaneous evidence that global cerebral blood flow, metabolism, and oxygen uptake remained relatively constant between states of rest and exercise (Ide & Secher, 2000), suggesting the brain did not receive additional metabolic resources during physical activity. However, more recent evidence has revealed both the local *and* global availability of cerebral hemodynamic, metabolic, and endocrinological factors to be dynamically modulated depending on the aerobic workload performed (Hellstrom et al., 2017; Rooks et al., 2010; Secher et al., 2008). As such, the cognitive impact of neurometabolic supply and demand during exercise may be more complex than the RAH originally proposed.

To compensate for the energetic requirements of aerobic exercise, additional hemodynamic, and metabolic resources become available within the systemic circulation almost immediately (Secher et al., 2008). Beyond merely counteracting increased demands, these modulations may provide a surplus of neurometabolic resources under certain workloads. At exercise intensities near the aerobic threshold (the first ventilatory threshold or VT_1), oxygen intake begins to exceed systemic requirements, cerebral blood flow increases by up to 30%, and cerebrovascular resistance is reduced (Ide et al., 1998; Secher et al., 2008). However, these effects rapidly diminish at higher workloads; between the anaerobic threshold (the second ventilatory threshold or VT_2) and maximal oxygen consumption (or VO_2 max), systemic demands begin to exceed oxygen intake, resulting in exercise-induced hypocapnia and cerebral vasoconstriction (Bain & Ainslie, 2014; González-Alonso et al., 2004; Querido & Sheel, 2007; Willie et al., 2012). Following a similar pattern, oxygen saturation 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 onward (Rooks et al., 2010). Although some evidence suggests modulations in the cerebral blood flow and oxygen saturation may not directly influence cognitive performance (Ando et al., 2011; Lucas et al., 2012; Ogoh et al., 2014), both the oxygen extraction fraction and metabolic rate of oxygen for cerebral tissue increase during exercise, implying an enhanced neurometabolic utilization capacity (Smith & Ainslie, 2017).

Besides these hemodynamic and metabolic 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 et al., 2001). Cognitive performance has long been hypothesized to follow an "inverted-U" pattern in response to increasing arousal (Hebb, 1955), and efficient functioning of the dorsolateral prefrontal 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 et al., 2014; MacDonald et al., 2000; Paneri & Gregoriou, 2017; Vanderhasselt et al., 2006) and particularly for distractor avoidance (de Fockert & Theeuwes, 2012; Leber, 2010; Lega et al., 2019; Liesefeld et al., 2014). 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.

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 workloads within the ITA, where an enhanced speed of processing is most often reported (Chang et al., 2012; Lambourne & Tomporowski, 2010; Ludyga et al., 2016; McMorris & Hale, 2012). The neurometabolic resource modulations brought on by exercise are generally considered a substantial driving force behind these effects; however, various moderator variables are also potentially involved, 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 reported expedited goal-driven attentional orienting (Pesce et al., 2007, 2011), improved feature selection in the lateral periphery (Hüttermann et al., 2014), and speeded responding in a sustained attention

task (González-Fernández et al., 2017), each alluding to a facilitation of top-down attentional control. Conversely, Davranche and colleagues found that although Simon's task performance was faster yet 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 et al., 2005; Rubichi et al., 1997; Stoffer & Yakin, 1994; van der Lubbe et al., 2012), an exercise-concurrent supplementation of stimulus-driven attentional control could also have enhanced the task-irrelevant response activation. Such bottom-up facilitation is similarly implied by the findings of Sanabria and colleagues, who found a diminished inhibition of return during exercise (Sanabria et al., 2011).

Although these results illuminate behavioral aspects of the exercise-cognition interaction, the covert neurocognitive mechanisms thereof have been substantially less explored, with only a select few employing EEG to monitor individual processing events during exercise (e.g., Bullock et al., 2015; de Sanctis et al., 2014; Dodwell et al., 2019; Grego et al., 2004; Olson et al., 2016; Pontifex & Hillman, 2007; Yagi et al., 1999). Those examining the attentional performance have mainly focused on nonlateralized ERP components like the P3, the magnitude and onset of which are considered to reflect resource allocation and object classification speed, respectively (Polich, 2007). However, electrocortical effects have proven inconsistent across various workloads and cognitive tasks. For example, in the performance of a visual oddball task, Yagi et al. (1999) found an expedited but diminished P3 during efforts near the ITA-median—denoting an exercise-induced attenuation of allocable resources—to be behaviorally paralleled by a speed-accuracy trade-off. Conversely, performing a flanker task during efforts near VT$_1$ was shown by Pontifex and Hillman (2007) to elicit an enhanced (although delayed) P3, indicating an increased allocation of 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" exercise near VT$_1$, and "high-intensity" exercise near the ITA-median. In both exercise conditions, an earlier P3a onset was observed relative to infrequent distractors, whereas 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 nontargets exclusively during the "low-intensity" exercise condition. The later of these object-selective sensory effects was suggested to represent a workload-specific facilitation of sensory gain control (see Hillyard et al., 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.

1.5 | Study rationale

The present study was designed to examine how top-down mechanisms of attentional control might be influenced during acute aerobic exercise. To accomplish this, EEG was recorded as participants performed a unidimensional variant of the ASP task[1] across three workloads of aerobic activity: at rest, during moderate exercise near VT$_1$, and during more vigorous exercise near the ITA-median. To maximize the effective level of top-down attentional control, our variant of the ASP included fixed target and distractor identities. Furthermore, systemic lateralization was used, 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. First, in congruence with the wider range of behavioral findings, we can anticipate speeded responding during exercise (see Chang et al., 2012; Ludyga et al., 2016)—however, whether such an effect will scale with increasing workloads remains uncertain. Second, considering the resource-limited and competitive nature of top-down attentional mechanisms, we can predict that a supplementation of neurometabolic resources during ITA workloads may be reflected by the PCN, the P$_D$, or both components. More specifically, an increased availability of neurometabolic resources during exercise may allow for a greater allocation thereof toward the networks governing 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 exercise near VT$_1$, 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.

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[1]In the present experiment, both the target and distractor "singletons" are defined within the same dimension (colour), as in Gaspar et al. (2016). However, in the original format of the ASP, each singleton would be defined in separate dimensions (e.g., a colour target and shape distractor).

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2 | METHOD

2.1 | Participants

The predefined sample size reported in the subsequent analyses was 24 participants (12 females, age = 23.5 ± 2.5, 3 left-handed). The sample size estimate was calculated using $\alpha = .05$ and $1 - \beta = .80$ relative to the RT effect observed in our previous study ($d_z = .60$; Dodwell et al., 2019).[2] A total of 32 volunteers took part in the experiment; however, four were removed because of excessively high error rates (ERs) (>20%), whereas another four were excluded because of physical performance issues (e.g., being unable to maintain the required effort). 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 hr as well as any tobacco or caffeine for at least 2 hr prior to testing. The experimental procedure was approved by the ethics committee of the Department of Psychology, Ludwig-Maximilians University of Munich, in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

2.2 | Task and stimuli

The behavioral task was presented on a 68.58 cm (27″) desktop monitor (Acer XF270H: 1,920 × 1,080 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 center (0.51° ⌀, 500 ms). This was followed by a search array (200 ms) containing eight circles (2.04° ⌀), distributed across two midlines (90°, 270°) and six lateralized positions (45°, 0°, 315°, 225°, 180°, and 135°), all radially equidistant (radius: 5.08°) from the central fixation point. Each stimulus contained a randomized vertical or horizontal grating composed of five black bars (0.13 × 2.04° ⌀) separated by four gaps (0.38 × 2.04° ⌀). In each trial, all stimuli within the search array were approximately isoluminant and included one or both of two color 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 among green nontargets (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 and midline distractor (lateral-target/midline-distractor), a lateral target and no distractor (lateral-target/no-distractor), a lateral distractor and midline target (lateral-distractor/midline-target), or a lateral distractor and no target (lateral-distractor/no-target).

The search array was followed by a response window displaying only the fixation point, which remained until observers provided a response on target-present trials (lateral-target/midline-distractor, lateral-target/no-distractor, lateral-distractor/midline-target), or for 1,000 ms on target-absent trials (lateral-distractor/no-target). On target-present trials, participants were instructed to indicate the orientation of the target grating 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 lateralized; 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 center (500 ms). An intertrial interval (950–1,050 ms, randomized) occurred prior to the next trial (See Figure 1). The search task included 576 trials evenly split across eight blocks, with the trial types presented in random order but with equal proportions. The task was repeated once for each exercise condition (see below), resulting in 144 presentations of each trial type per condition.

2.3 | Hemodynamic controls and exercise conditions

At the beginning of each experimental session, participants rested in a supine position for 5 min, during which a heart rate (HR) monitoring chest strap and smart watch (Models H7, M400, Polar Electro, Kempele, Finland) continuously sampled their HR (measured in beats per minute or *bpm*) at 1,000 Hz. The lowest recorded value provided an approximation of their resting heart rate (RHR), whereas their maximum heart rate (MHR) was estimated using a standardized formula [MHR = 208 − (0.7 × age)] (Tanaka et al., 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 normalized across participants by adding a standardized percentage of HRR to RHR (% HRR), resulting in individually targeted HR values that account for variability in cardiovascular capacity and aerobic fitness between subjects (Swain & Leutholtz, 1997).

The experiment was performed while seated on a recumbent stationary cycling ergometer (LifeFitness Club Series, Brunswick Corporation, Rosemont, IL USA). Thresholds for the three

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[2]Although a power analysis based on the electrophysiological effects of attentional control during exercise would have been more ideal for the present experiment, no such source material was available at the time of writing.

exercise workloads—rest (target < 30% HRR; tested $M = 84.55$ bpm), moderate (target = 40%–50% HRR [≈VT1]; tested $M = 122.55$ bpm), and vigorous (target = 60%–70% HRR [≈ITA-median]; tested $M = 147.35$ bpm), were based on the limits defined in Garber et al. (2011). Each of the three exercise conditions lasted approx. 20–25 min, and all were completed within a single experimental session. The order in which the exercise conditions were performed was counterbalanced across participants, with all the tested observers being pseudo-randomly assigned to one of the six possible sequences, ensuring the final sample would include four participants within each group.[3] The rest condition took place while seated on the cycling ergometer without pedaling. The moderate and vigorous conditions began with a 5-min warmup period, wherein participants pedaled a fixed cadence of 70–80 rpm as measured by the cadence sensor of the ergometer. Pedaling resistance was then gradually modulated by 10-watt increments until achieving a stabilized effort within the individually targeted HR range for each workload. Thereafter, participants maintained a 70–80 rpm cadence throughout the task, with their HR being regulated via stepwise adjustments to pedal resistance as necessary. Participants whose mean HR fell outside their targeted range for more than one block per workload were rejected from further analysis. 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).

2.4 | Behavioural data processing and analysis

Behavioural data were processed using Microsoft Excel (version 16.0, Microsoft Corp., Redmond, WA) and Pandas (McKinney, 2010). Because the only behaviorally relevant trial type manipulation was whether a distractor would be presented along with the target (thus inducing the distractor interference effect), our behavioral analysis focused purely on distractor absence versus presence. The behavioral results from the lateral-target/midline-distractor and lateral-distractor/midline-target trial types were, therefore, combined to simply represent "distractor-present" trials, whereas the lateral-target/no-distractor trial type served as the "distractor-absent" trials. Prior to calculating both RT and ER, trials where the button

press could be considered anticipatory or delayed were removed (<200 or >1,000 ms after extinction of the search array). The ER was then calculated per workload for each participant, with those having a mean ER greater than 20% across all workloads being rejected from further analysis. The RTs from the distractor-absent and distractor-present trials were then averaged separately per workload for each participant. Lastly, the resulting mean RTs and ERs from each participant were statistically analyzed with Pingouin (Vallat, 2018) using a 2×3 repeated-measures ANOVA with factors of distractor presence (distractor-absent, distractor-present) and workload (rest, moderate, vigorous). The Šidák method was applied as necessary to correct for multiple comparisons, whereas Bayes factors (BF_{10}) were also calculated where necessary to elucidate any theoretically relevant nonsignificant findings.

2.5 | EEG recording and data processing

The EEG data were 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 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 extended Infomax independent component analysis (ICA) was performed across all 64 channels of the continuous data (512 steps, convergence bound = 1×10^{-7}) to remove ICA components representing blinks and saccades, which were identified based on a visual inspection of their individual time courses and topologies. Those components identified as artefacts were then removed prior to a back-projection of the residuals. 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 (rest, moderate, vigorous) and segmented into 1,000 ms epochs (−200 to +800 ms from search array onset) per trial type. These segments were baseline corrected to their 200 ms pre-stimulus intervals, then passed through an artefact rejection to exclude those containing signals over ±60 μV, voltage steps exceeding 50 μV/ms, and activity changes below 0.1 μV over 100 ms. Across participants, this resulted in an average of 132, 117, and 104 (with a minimum of 66, 50, and 50) useable segments per trial type within the rest, moderate, and

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[3]Given the often-reported cognitive aftereffects of aerobic exercise (for review, see Ludyga et al., 2016), it is possible that performance during the rest condition could differ between counterbalancing groups depending on whether it was directly preceded by an exercise condition. To ensure that no such order effects were present in the current experiment, we conducted a series of exploratory pairwise *t*-tests across each dependent measure (RT, ER, PCN amplitude & latency, P_D amplitude & latency, Ppc amplitude) to assess whether performance in the rest condition differed as a function of its ordinal position (rest 1st, 2nd, or 3rd). The results did not indicate any significant order effects (all *p*s > .077).

vigorous workload, respectively, thus providing enough trials to avoid any substantial differences between conditions because of trial count. The surviving segments were separated into left and right hemifield trials relative to the lateralized 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 lateralized singleton), then averaging the resulting ERLs across both left and right hemifield trials (formula: [(PO8 − PO7 [left-singleton]) + (PO7 − PO8 [right-singleton])/2]).

2.6 | EEG analysis

As expected, the PCN was observed in the grand-averaged waveform of lateralized target trials (lateral-target/midline-distractor, lateral-target/no-distractor), whereas both the P_D and a Ppc were observed in the grand-averaged waveform of lateralized distractor trials (lateral-distractor/midline-target, lateral-distractor/no-target). Our analysis, therefore, primarily focused on the mean amplitude and onset latency of the PCN and P_D, with an additional post hoc exploratory analysis of the distractor-elicited Ppc component.

Time windows for calculating the mean amplitudes of the PCN (230–290 ms) and P_D (250–290 ms) were adopted from prior well-established research examining these components within a highly comparable version of the ASP (see Gaspar et al., 2016; Gaspar & McDonald, 2014; Hickey et al., 2006, 2009).[4] To identify single-participant onset latencies for each component, we first calculated the 70% peak amplitude latencies for each workload and relative trial type (also adopted from Gaspar & McDonald, 2014), using the jackknife-based approach (Ulrich & Miller, 2001). Single-participant onset latency estimates were then retrieved from these subaverage scores using the transformation provided by Smulders (2010),[5] which allows statistical analysis of the resulting data set 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: lateral-target/midline-distractor, lateral-target/no-distractor; P_D: lateral-distractor/midline-target, lateral-distractor/no-target) and workload (rest, moderate, vigorous). The Šidák method was applied as

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[4]To confirm the veracity of our findings within the PCN, various other analytic approaches were also tested, including a 200–300 ms mean amplitude window, a 235–295 ms mean amplitude window (based on the 50% onset/offset latencies), and an analysis of the ±10 ms peak amplitudes. The pattern of results remained consistent across all tested approaches.

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

necessary to correct for multiple comparisons, whereas Bayes factors (BF_{10}) were also calculated where necessary to elucidate any theoretically relevant nonsignificant findings.

Although a Ppc was observed accompanying the P_D in the grand-averaged waveform of lateralized distractor trials collapsed across all participants, its presence was somewhat erratic between workloads, only being predominantly apparent during moderate exercise. Furthermore, because of 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 (lateral-distractor/midline-target, lateral-distractor/no-target). For this reason, it was deemed necessary to determine whether a Ppc could be statistically differentiated from baseline activity when collapsed across the lateralized distractor trials of each workload. To accomplish this, we first defined time windows within the grand-averaged waveform collapsed across 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 paired-sample t tests.

3 | RESULTS

3.1 | Behavioral performance

RTs demonstrated a general trend to become faster as workload increased, and slower with distractor presence (see Figure 2). These observations were supported by the ANOVA results, which indicated the main effects of both workload and distractor presence ($F(2,46) = 6.17$, $p = .004$, $\eta_p^2 = .21$; $F(1,23) = 27.21$, $p < .001$, $\eta_p^2 = .54$), without an interaction detected between the two factors ($p = .22$). Follow-up pairwise comparisons between workloads confirmed RTs to be faster during vigorous exercise than rest (567 vs. 596 ms; $t(23) = −4.23$, $p = .001$, $d = −.55$), although no differences were indicated between vigorous and moderate exercise (567 vs. 579 ms; $p = .35$), or moderate exercise and rest (579 vs. 596 ms; $p = .28$). Moreover, the significant main effect of distractor presence confirmed the presence of the anticipated distractor-interference effect. However, although the interaction term was not significant, we, nevertheless, also performed a further set of exploratory comparisons between trials types as a function of workload—revealing that although the distractor-interference effect could be confirmed both at rest (592 vs. 599 ms; $t(23) = −3.17$, $p = .004$, $d = −.14$) and during moderate exercise (574 vs. 585 ms; $t(23) = −4.94$,
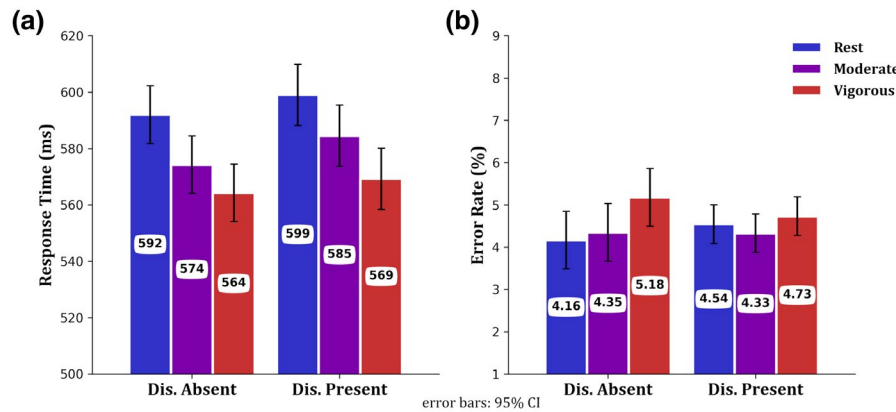
(a)

(b)

error bars: 95% CI

FIGURE 2 (a) Mean response times for the distractor-absent and distractor-present (lateral-target/midline-distractor + midline-target/lateral-distractor) trials within each workload (rest, moderate, vigorous). (b) Mean error rates for the distractor-absent and distractor-present (lateral-target/midline-distractor + midline-target/lateral-distractor) trials within each workload (rest, moderate, vigorous)
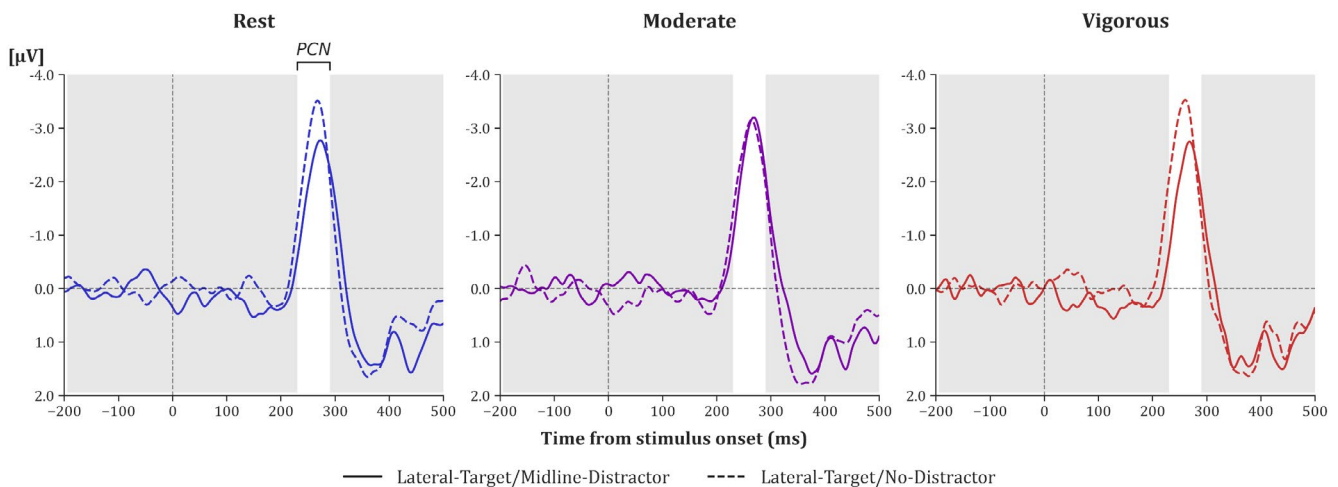

— Lateral-Target/Midline-Distractor   ---- Lateral-Target/No-Distractor

FIGURE 3 PCN waveforms at PO7/8 for the target-lateral trial types (distractor-absent, dashed-line; lateral-target/midline-distractor, solid-line) within each workload (left to right: rest, moderate, vigorous)

$p < .001$, $d = -.16$), only a marginal difference was detected between trial types during vigorous exercise (564 vs. 569 ms; $t(23) = -2.00$, $p = .058$, $d = -.09$).

ERs showed a slight tendency to increase during vigorous exercise, appearing particularly elevated in distractor-absent trials. However, this was shown to be negligible by the ANOVA results, which indicated an absence of main effects for workload and distractor presence ($p = .19$, $p = .92$), as well as a lack of interaction between these factors ($p = .25$). Within distractor-absent trials, Bayesian analysis provided moderate evidence for the lack of an effect between rest and moderate exercise ($BF_{10} = 0.23$), although only anecdotal support was present between rest and vigorous exercise ($BF_{10} = 0.84$). However, within distractor present trials, there was moderate evidence for the lack of an effect when comparing rest and moderate exercise ($BF_{10} = 0.26$) as well as rest and vigorous exercise ($BF_{10} = 0.24$). Our RT effects, therefore, could

not be attributed to differential speed-accuracy trade-offs between workloads.

3.2 | Target selection: PCN

Distractor presence (lateral-target/midline-distractor vs. lateral-target/no-distractor trials) appeared to reduce PCN mean amplitudes both at rest and during vigorous exercise—however, this effect was not observable during moderate exercise (see Figure 3). This was supported by the ANOVA results, which revealed both a main effect of trial type (reducing PCN amplitudes by 0.5 µV overall; $F(1,23) = 25.36$, $p < .001$, $\eta_p^2 = .52$), as well as an interaction between trial type and workload ($F(2,46) = 3.95$, $p = .026$, $\eta_p^2 = .15$), whereas no main effect of workload was detected ($p = .66$). To disentangle the interaction effect, we performed pairwise

comparisons between trial types within each workload, revealing amplitudes in lateral-target/midline-distractor trials to be significantly reduced compared to lateral-target/no-distractor trials during both rest (−2.07 vs. −2.74 µV; $t(23) = 3.47$, $p = .006$, $d = .49$) and vigorous exercise (−2.07 vs. −2.82 µV; $t(23) = 3.61$, $p = .004$, $d = .61$). However, no significant difference was revealed between trial types during moderate exercise (−2.49 vs. −2.57 µV; $p = .89$), which was supported by moderate Bayesian evidence for the lack of an effect ($BF_{10} = 0.26$). Importantly, pairwise comparisons were also performed between workloads within each trial type, to test whether this lack of an effect during moderate exercise was due to an amplitude shift in lateral-target/midline-distractor trials, lateral-target/no-distractor trials, or both. This revealed amplitudes in lateral-target/midline-distractor trials to be significantly greater during moderate exercise (−2.49 µV) than both rest (−2.07 µV; $t(23) = −2.74$, $p = .012$, $d = −.36$) and vigorous exercise (−2.07 µV; $t(23) = −2.28$, $p = .032$, $d = −.37$), whereas the rest and vigorous amplitudes did not differ ($p = .99$, $BF_{10} = 0.22$). By contrast, no amplitude differences were detected between workloads in the lateral-target/no-distractor trials (all $p > .15$, all $BF_{10} < 0.55$). As such, the presence of a distractor was found to specifically reduce PCN amplitudes during both rest and vigorous exercise, but this effect was extinguished during moderate exercise.

Distractor presence also appeared to somewhat delay the PCN onset latencies during both vigorous exercise and rest, although no such effect was apparent during moderate exercise (see Figure 3). However, this could not be verified by the ANOVA results, which only indicated a main effect of trial type (delaying PCN onsets by 7.17 ms overall; $F(2,46) = 10.96$, $p = .003$, $\eta_p^2 = .32$), although no main effect of workload ($p = .13$) or interaction ($p = .29$) were indicated. Nevertheless, exploratory comparisons between trial types within each workload did demonstrate a significant delay during vigorous exercise (247 vs. 236 ms; $t(23) = 3.07$, $p = .005$, $d = .68$), although this effect was only marginal at rest (246 vs. 250 ms; $t(23) = 1.99$, $p = .058$, $d = .31$) and was no longer detected during moderate exercise ($p = .15$, $BF_{10} = 0.56$).

3.3 | Distractor suppression: P_D

Target presence (lateral-distractor/midline-target vs. lateral-distractor/no-target) appeared to increase P_D mean amplitudes across workloads (see Figure 4). This observation was substantiated by the ANOVA results, which indicated a main effect of trial type ($F(1,23) = 7.28$, $p = .013$, $\eta_p^2 = .24$), whereas no main effect of workload or interaction was detected ($p = .39$; $p = .70$). That is, the presence of a target was found to increase the amplitude of the P_D, and this effect occurred independently of the workload condition (rest 0.84 vs. 0.65 µV; moderate 0.71 vs. 0.41 µV; vigorous 0.75 vs. 0.32 µV).

Target presence did not seem to reliably influence P_D onset latencies in any workload. This was supported by the ANOVA results, which did not indicate main effects of workload, trial type, or an interaction between these factors (all $p > .72$, all $BF_{10} < 0.26$). The present results, therefore, do not indicate that P_D timing was influenced by either target presence or exercise.

3.4 | Preattentive processing: Ppc

The Ppc appeared in the various workload conditions, but it was only clearly discernible from baseline activity during moderate exercise (see Figure 5). A series of paired-sample
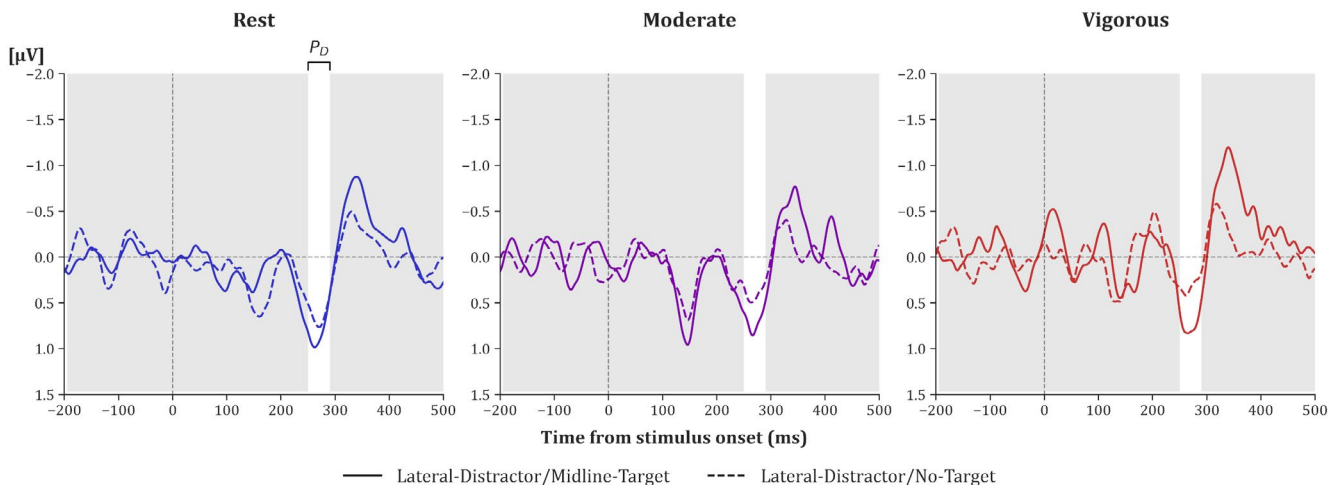

FIGURE 4 PD waveforms at PO7/8 for the distractor-lateral trial types (lateral-distractor/midline-target, lateral-distractor/no-target) within each workload (left to right: rest, moderate, vigorous)
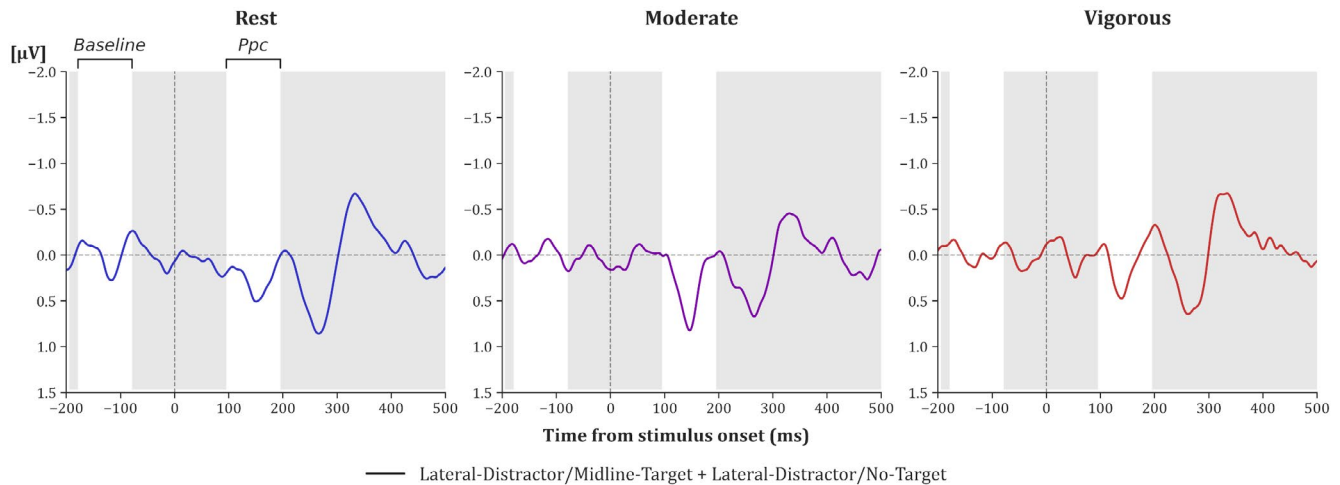
FIGURE 5 Ppc waveforms at PO7/8 for the distractor-lateral trials (lateral-distractor/midline-target + lateral-distractor/no-target) within each workload (left to right: rest, moderate, vigorous)

t tests confirmed this observation, indicating that mean positive activity within the Ppc window ($M = 0.65$ μV, $SD = 0.37$) only significantly exceeded that of the baseline window during moderate exercise ($M = 0.47$ μV, $SD = 0.34$; $t(23) = 2.35$, $p = .028$, $d = -.53$), whereas no differences were detected during rest or vigorous exercise ($p = .18$; $p = .54$). The Ppc, thus, appears to have been uniquely activated during the moderate workload.

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 a unidimensional variant of the ASP across conditions of rest, moderate exercise, and vigorous exercise. Behaviorally, responses were slowed overall by the presence of the salient distractor, and responses became faster as workload increased (without revealing a corresponding accuracy effect). Furthermore, moderate exercise was found to have induced specific electrophysiological effects, both eliminating distractor interference as indexed by the PCN, and enhancing preattentive processing as revealed by the presence of a Ppc. Each of these findings are discussed below in further detail.

4.1 | Task performance: More rapid responding as the intensity of exercise increases

RTs became significantly faster as workload increased without a substantial parallel reduction in response accuracy, denoting a facilitation of cognitive performance during ITA workloads. That is, were accuracy to have markedly

decreased during exercise, it could be argued that a more lenient decision criterion had been adopted or that cognitive control had indeed deteriorated as predicted by the RAH (Dietrich, 2006; Dietrich & Audiffren, 2011). For the present task, however, a substantial loss of cognitive control was not detected, at least during workloads between VT$_1$ and the ITA-median. Regardless, although the slight increase in ERs observed during vigorous exercise proved to be insignificant, it should not be entirely discounted. Firstly, ERs 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. Secondly, it is entirely plausible that workloads beyond the ITA-median may elicit more substantial effects, with errors increasing as exercise becomes even more demanding. 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 et al., 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 et al., 2011). Similarly, a previous working memory study (Dodwell et al., 2019) provided novel evidence from the lateralized readiness potential (LRP) tracing speeded responding during exercise near the ITA-median to the facilitation of higher cognitive processes. The LRP is an ERL indicative of lateralized motor preparation (Coles, 1989) and can be calculated relative either to the stimulus (sLRP) or response (rLRP) (Wiegand et al., 2013). The sLRP latency represents the time required for response selection (Eimer, 1998; Töllner, Rangelov et al., 2012),

whereas the rLRP latency indicates the time needed for motor production of the selected response (Miller et al., 1998). Whereas latencies for accessing working memory and the rLRP did not differ between conditions of rest and exercise, RT 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 may have been somewhat mitigated during vigorous workloads. This could be partially explained by the findings of Hüttermann and colleagues, who demonstrated enhanced attentional processing in the lateral periphery (or *attentional breadth*) during vigorous cycling (Hüttermann et al., 2014). In the present study, a similar lateral facilitation during vigorous exercise may have promoted better avoidance of midline distractors by enhancing the processing of lateralized targets, thereby reducing the overall distractor interference effect.

4.2 | ERP pattern: Moderate-intensity exercise enhances attentional resource allocation

Our EEG results offer compelling evidence that attentional control networks receive an increased allocation of neurometabolic resources specifically during moderate exercise, demonstrating an inverted-U function of electrophysiological effects in conjunction with increasing workload. The PCN was attenuated by distractor presence during both the rest and vigorous exercise conditions, showing a reduced amplitude (and in the case of vigorous exercise, a significantly delayed onset) in distractor-present trials. By contrast, this effect was eliminated during moderate exercise, with the PCN amplitude remaining similar 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 moderate exercise, target-selective mechanisms used 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. This finding aligns well with prior notions of an inverted-U pattern of facilitation during exercise, suggesting the peak of this performative curve (at least, for the mechanisms governing attentional control) to occur within the lower half of the ITA. Whether this facilitation is driven by increased cerebral blood flow (Secher et al., 2008), greater oxygen saturation in the PFC (Rooks et al., 2010), a more optimal concentration of catecholamines within the DLPFC (Arnsten, 2011), or a

combination of these factors remains uncertain. In any case, our results are in line with the idea that a moderate level of exercise is ideal for promoting efficient cognitive processing and provide the first evidence of this kind with regard to the efficiency of attentional allocations.

Beyond providing evidence for an exercise-induced supplementation of neurometabolic resources in EEG measures, the contextual specificity of their utilization further alludes to a mechanistic hierarchy of resource distribution. Were the distribution of neurometabolic resources 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 neurometabolic resources equally across workloads, whereas target-selective mechanisms only maintained full functionality during moderate exercise, where additional resources presumably became available. As such, distractor suppression mechanisms may have been given distributional priority, their performance being preserved at the expense of target-selective mechanisms when neurometabolic demands exceeded the available supply. Although mainly speculative, this might be corroborated through additional manipulations to the attentional demands of both distractor and target processing—for instance, by assessing whether this hierarchy is maintained when the levels of target or distractor saliency are modified (see Constant & Liesefeld, 2021; Liesefeld et al., 2016; Töllner et al., 2011).

Of note, the presence of the distractor-elicited Ppc was substantiated exclusively during moderate 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 object-selective enhancement of the P1 during exercise near VT_1, 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.[6] However, a direct neurometabolic supplementation of the mechanism(s) underlying the Ppc could be equally likely, resulting in a more robust or less transient signal. Regardless, the enhancement of the P1 and Ppc during proximal workloads 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

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[6]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 et al., 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.

role (e.g., Feldmann-Wüstefeld & Vogel, 2019; Gaspelin & Luck, 2018; Weaver et al., 2017). It should be noted, however, that the present experiment used a unidimensional variant of the ASP, wherein the target and distractor singletons were defined by fixed features and were approximately equal in salience. As such, this suppression account may be further supported were a similar pattern to be confirmed in an ASP variant where the target is most salient (e.g., exp. 2 in Jannati et al., 2013), or where the most salient item varies between trials.

Furthermore, the concurrent emergence of a pronounced Ppc and preservation of the PCN during moderate 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 preattentive processing reflected by the Ppc, rather than an independent supplementation of target-selective mechanisms. Were this pre-attentive processing to provide a suppression effect that ubiquitously benefited attentional control, one might also suspect the resource demands exhibited by the P_D to be similarly reduced or eliminated—however, 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, nor preclude the supplementation of neurometabolic 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 behavioral results. Nevertheless, this should not be taken to suggest the observed effects could not have influenced behavioral performance whatsoever. For instance, the concurrent preservation of the PCN amplitude and emergence of the Ppc during moderate exercise were not coupled with improvements in response accuracy. However as was previously mentioned, the error sensitivity of the present task may have simply been too low for any performative changes elicited by these modulations to be detected. Likewise, during both rest and moderate exercise, the distractor-interference effect delayed responses regardless of the PCN latency being unaffected, while conversely during vigorous exercise, the distractor-interference effect may have been somewhat mitigated despite a significantly delayed PCN. However, this pattern may only serve as evidence that the temporal origins of the distractor interference effect were not traced by or are otherwise unrelated to PCN latency, even at rest. Equally, this does not exclude the possibility that any temporal effects during attentional selection may have simply been overshadowed by more substantial modulations during postattentional processing (e.g., Dodwell et al., 2019).

4.3 | Conclusion

Our findings provide several key insights regarding both the behavioral 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, RTs became faster with increasing workloads within the ITA without a corresponding loss of accuracy being detected, denoting a facilitation of cognitive performance that coincides with various predicted supplementations of neural resources. Secondly, and most importantly, our EEG findings not only demonstrate a facilitation of top-down attentional processing during moderate exercise but also suggest that neural resources may be hierarchically distributed between target-selective and distractor suppression mechanisms. Lastly, the preattentive processing of lateralized distractors was also shown to have been selectively enhanced during moderate 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 neurometabolic resource availability and utilization might dynamically influence attentional performance.

CONFLICT OF INTEREST
The authors report no conflicts of interest.

AUTHOR CONTRIBUTIONS
Gordon Dodwell: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Project administration; Validation; Visualization; Writing-original draft; Writing-review & editing. **Heinrich René Liesefeld:** Methodology; Supervision; Writing-review & editing. **Markus Conci:** Software; Writing-review & editing. **Hermann J Mueller:** Funding acquisition; Resources; Supervision; Writing-review & editing. **Thomas Toellner:** Conceptualization; Funding acquisition; Methodology; Project administration; Resources; Supervision.

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