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Effects of exercise on electroencephalography-recorded neural oscillations: a systematic review

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ABSTRACT

Research on the effects of exercise on cortical activity has grown significantly, with a predominant focus on the technique of electroencephalography (EEG). Technological advancements in EEG render this technique suitable for studies that explore human movement. There is a noticeable gap in the literature concerning how EEG-recorded cortical oscillatory activity is affected by exercise. Accordingly, the aim of this review was to summarise studies that investigated the effects of exercise on brain activity using EEG. This was a systematic review of 47 studies, predicated on PRISMA guidelines. The results were, on the whole, equivocal in nature, with the exception that activity in the alpha and beta frequency bands increased both during and post-exercise across the frontal, central, and limbic regions. The reported increases could be attributed to a variety of neural processes, such as neuro-connectivity, cortical inhibition, and sensory feedback loops. Future researchers need to give careful consideration to exercise parameters (e.g. mode of exercise, intensity, duration) to facilitate their interpretation of experimental data. The present findings support the notion that exercise alters alpha and beta neural oscillations but more work is needed to provide a fuller picture of the brain processes that manifest during exercise.

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KEYWORDS

Brain waves; cerebral activity; neuroimaging; neurosciences; physical activity

Introduction

Electroencephalography (EEG) has provided the research community with a vista into the electrical activity of the brain. It has also served to further understanding of the dynamic nature in which this most complex of organs functions. Given the high temporal sensitivity of this method, EEG has been widely used in the assessment of brain function and human behaviour (Babiloni et al., 2002; Bevilacqua et al., 2019). In the field of sport and exercise sciences in particular, the use of EEG has gained significant traction, as it

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affords easy access to an 'under-the-bonnet' view of human functioning (Cheval et al., 2018; Cooke et al., 2014). This review therefore aims to provide important insights into emerging trends regarding the recording of brain activity using EEG, as well as the strengths and limitations that characterise the extant literature, in order to stimulate future research.

The EEG signal is produced when multiple brain cells generate electrical activity that incorporates an array of frequencies. EEG is able to detect neural activity, which results from both excitatory and inhibitory postsynaptic potentials; thus, an EEG recording results from multiple frequencies created by the electrical activity of groups of neurons firing in synchronicity (Bigliassi et al., 2021). One of the data screening processes, conducted through frequency-domain analyses such as Fast Fourier transform (FFT), enables the brain frequencies to be distinguished in relation to different band waves.

The band waves include delta (0.5–4 Hz), theta (4.5–8 Hz), alpha (8.5–13 Hz), beta (13.5– 30 Hz), and gamma waves (30.5–100 Hz; Steriade et al., 1990). Alpha and beta ranges are sometimes subdivided to discriminate alpha-1 (8.5-10 Hz), alpha-2 (10-13 Hz), beta-1 (12-15 Hz), and beta-2 (15–20 Hz). Delta waves are slow-frequency waves normally associated with stages of deep sleep. Theta waves indicate that an individual is in a state of deep relaxation, such as sleep or meditation (Kochupillai, 2015). Theta waves also provide a basis for sensorimotor integration and coding of spatial information (Bland & Oddie, 2001; Buzsáki & Moser, 2013). Although alpha waves can be recorded during sleep, they are normally more prominent when an individual is in a relaxed mental state (Desai et al., 2015). In addition, alpha frequency plays a key role in top-down control of information processing and is thought to be a central timing mechanism for cognitive processes (Klimesch et al., 1996; Samaha et al., 2015). More specifically, alpha-1 waves (8.5-10 Hz) are often observed when an individual is in an alert, yet relaxed state, while alpha-2 waves (10-13 Hz) are observed during deep relaxation (e.g. meditative states; Srinivasan & Nunez, 2017).

Beta waves are present during normal waking consciousness, as they are generally observed throughout the completion of a task and during active concentration. Beta oscillatory activity can also be seen during slow movements and isotonic contractions (De & Mondal, 2020). More specifically, beta-1 waves (12-15 Hz) are usually associated with introverted, quiet concentration as well as motor planning and control (Kropotov, 2016), while beta-2 waves (15-20 Hz) are linked to increases in anxiety, performance, and energy levels (Abhang et al., 2016). Finally, gamma waves are indicative of increased attention and usually present during the execution of higher cognitive tasks (e.g. listening attentively to a lecture; Fitzgibbon et al., 2004).

EEG in the exercise and physical activity domain

This review refers to 'physical activity' and 'exercise' in terms of the World Health Organization (2010) definitions. Physical activity is defined as '... any bodily movement produced by skeletal muscles that requires energy expenditure.' (p. 53) and exercise as 'A subcategory of physical activity that is planned, structured, repetitive, and purposeful in the sense that the improvement or maintenance of one or more components of physical fitness is the objective.' (p. 52). The definition considered for sport relates to 'An

activity involving physical exertion and skill (...) one regulated by set rules or customs in which an individual competes against another or others.' (Oxford English Dictionary, 2021). The present review is more strongly predicated on exercise than either physical activity or sport.

For many years, EEG was deemed unsuitable for the analysis of brain activity during exercise. The reason for this is that study participants were generally required to sit relatively still in a quiet environment, in order to minimise movement artefacts (Enders & Nigg, 2016a). Recent technological advances have rendered EEG far more suitable to the collection of recordings during dynamic brain activities (Bigliassi et al., 2021). For example, EEG sensors allow for the signal to be amplified at source, they are more noise robust (vis-à-vis noise in the electrical signal) and smaller in size. Moreover, the number of EEG sensors applied has been increased from 32 to high-density grids comprised of up to 264 electrodes (Castermans et al., 2014), allowing for higher sensitivity and improved source localisation.

An important advancement for the field of sport and exercise science was the adoption of dry EEG in the early 1990s (Di Flumeri et al., 2019). The advantages of this method include improved signal-to-noise ratio as well as no requirements for skin preparation (e.g. shaving of the scalp) or the application of conductive paste (Taheri et al., 1994). This upstaging feature of dry EEG meant that experiments took less set-up time, as the cleaning of electrodes was made much easier. Moreover, dry EEG has proven to be less sensitive to electromagnetic intrusion from outside noise (Hinrichs et al., 2020), which has facilitated a stream of studies in real-world environments (e.g. cityscapes, Tilley et al., 2017; roads, Protzak & Gramann, 2018; running tracks, Bigliassi et al., 2019).

EEG has been used extensively to further understanding of the underlying effects of exercise on cognitive processing and most studies adopted a pre- vs. post-exercise design (e.g. Devilbiss et al., 2019; Hicks et al., 2018). Accordingly, this is one of the points of comparison in the present systematic review. The comparision of neural oscillations pre- vs. post-exercise will provide valuable insights in regard to the immediate effects of acute exercise, defined as a single bout of exercise (Sellami et al., 2018) on brain functioning. Nonetheless, the cognitive processes that occur during exercise have also been suggested to be of particular relevance in predicting exercise-related behaviours (e.g. regular engagement; Buckley et al., 2014). Similarly, the effects of long-duration exercise explored in the present review have also been a topic of interest in this field of study (e.g. Chaire et al., 2020; Sousa et al., 2019). Given that EEG recordings are prone to the vagaries of movement artefacts (Enders & Nigg, 2016a), studies investigating cortical activity during exercise were placed in a specific category in this review. The way by which exercise appears to modulate cortical oscillations is dependent on its intensity (see Ekkekakis, 2009), which constitutes a further focus of the present review. Moreover, the review addresses the effects of exercise per se on cortical activity through comparing exercise vs. no exercise conditions (e.g. Kao et al., 2020).

Although several EEG-related reviews have appeared in the exercise science literature (e.g. Crabbe & Dishman, 2004; Gramkow et al., 2020; Rahman et al., 2019), there has been no systematic review into the effects of exercise on cortical oscillatory activity, with a sole focus on healthy populations. Given that exercise has been shown to have an effect on brain plasticity and, in particular, cortical oscillatory activity, there is a need to summarise studies that report effects of this nature. With the intention to identify common patterns

in brain activation, the main purpose of this systematic review was to further knowledge pertaining to the modulation of cortical oscillatory activity due to exercise. Effect sizes (Cohen's d or partial eta squared $[n_n^2]$) pertaining to each statistical test were computed and are reported herein.

Method

The systematic review was performed following the recommended Preferred Reporting Items in Systematic Reviews (PRISMA) guidelines (Moher et al., 2010). Note that this study was not pre-registered.

Search strategy and study selection

Articles were searched using Google Scholar, Medline, PsycINFO, PubMed, and SPORTDiscus for the period of 1 January 1986–31 March 2022 using Boolean logic and the following search terms: 'EEG OR Electroencephalogram OR Electroencephalography' AND 'exercise OR physical activity' AND 'oscillation'. A manual search of the references sections of the initially retrieved articles (n = 50) was also conducted, which resulted in an additional 31 studies (n = 81). Of the 81 studies, five were duplicates, leading to the screening of titles and abstracts of 76 studies, of which 29 were removed for not meeting the inclusion criteria. The remaining 47 studies were included in the review. The searches were conducted by the first author in consultation with the last author.

Data extraction

A MicrosoftTM Excel spreadsheet was used to extract basic information in relation to the retrieved studies (n = 81). For each study, the following informational elements were extracted: published year, number of participants, sex of participants, mean age, study design, intervention type (physical exercise type, intensity, duration), EEG paradigm (data processing and analysis method, number of electrodes used, artefact correction method), and main results. These elements are presented in Tables 1-5. Informational elements that were unavailable are clearly indicated within each revelant table to acknowledge risk of bias in a transparent manner. Duplicates and studies that did not meet the criteria were highlighted in red with the reason for removal identified and written next to the study title. The remaining 47 studies were then categorised as follows: (a) pre- vs. post-exercise condition (n = 37); (b) pre-/post- vs. during-exercise condition (n = 15); (c) comparisons among different exercise intensities (n = 43); (d) exercise vs. control group (n = 6). A MicrosoftTM Excel spreadsheet was used to ascertain which studies were eligible for each synthesis category; specifically by colour coding each study according to the intervention characteristics.

Quality assessment

Study quality was assessed by the first and last authors. A modified version of the Quality Assessment Tool for Quantitative Studies (QATQS; National Collaborating Center for Methods and Tools, 2008) was used, with additional quality assessment criteria pertaining

Table 1. Characteristics of Studies.

Authors	Year	N (% female)	M_{age} (SD) in years	Study design	Experimental task	Intervention	Participants	Number of electrodes	Method of analysis
Bailey et al.	2008	20 (0)	24 (1.5)	Single group	Recumbent cycle ergometer	Started at 50 W and 50-W increase every 2 min until volitional exhaustion. EEG was recorded before exercise, during the last minute of each 2-min stage of exercise, immediately postexercise, and 10 min post-exercise.	Healthy adults	Initially 21, but only 8 electrodes (F3, F4, F7, F8, C3, C4, P3, P4) used in the final analysis	Frequency analysis and alpha/beta ratio
Bixby et al.	2001	27 (51.8)	23.3 (3.5)	Single group	Cycle ergometer	2 × 30-min exercise at low (75% of ventilatory breakpoint) and high intensity (ventilatory aerobic breakpoint). EEG was recorded for 2 min at 0, 5 and 10 min during pre-exercise stage, then again during exercise at 10, 20, and 30 min, and again at 10, 20, and 30 min post-stage.	Healthy adults	F8, F7, F4, F3, P4, P3	Frequency analysis and alpha asymmetry score
Boutcher & Landers	1988	30 (0)	Runners: 29.9 (9) Non-runners: 26.7 (4.6)	Cross-over	Treadmill	20 min at 80–95% HR _{max} . EEG was recorded every 2 min for 5 s during pre- and post-exercise stages.	Healthy runners	T3, T4	Frequency analysis
Brümmer et al.	2011	1: 33.3,		Experiment 1: Quasi- randomised cross-over; Experiment 2: Single-arm	Experiment 1: Treadmill, bicycle, arm crank, and isokinetic dynamometer; Experiment 2: Incremental arm crank test	Experiment 1: 30-min treadmill, 30-min bicycle, 3 × 10-min arm crank, and 3 × 20 consecutive wrist flexions at 50 and 80% of VO _{2max} and target intensity; Experiment 2: Start at 20 W and 20-W increase every 5 min until volitional exhaustion.	Experiment 1: Healthy recreational runners; Experiment 2: Semi-professional hand-cycling athletes with spinal cord injuries	Experiment 1: Fp1, Fp2, F3, F4, F7, F8, Fz, C3, C4, Cz, P3, P4, P7, P8, Pz, T7, T8, O1, O2 Experiment 2: Fp1, Fp2, F7, F3, Fz, F4, F8, FC5, FC1, FC2, FC6, T7, C3, Cz, C4, T8, TP9, CP5, CP1, CP2, CP6, TP10, P7,	sLORETA

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						Experiment 1: EEG was recorded before exercise and 17.6 ± 2.9 min post-exercise. Experiment 2: EEG was recorded for 5 min pre- and immediately post-exercise.		P3, Pz, P4, P8, P09, O1, Oz, O2, PO10	
Büchel et al.		16 (0)	24.56 (3.3)	Within-subjects	Treadmill	Incremental treadmill exercise at 50% (10 min), 70% (10 min), and 90% speed VO _{2 peak} (all-out) followed by cool-down running (8 min) and active recovery (10 min). EEG was recorded preexercise, during break just before every intensity change, during cool down, and during active recovery.	Healthy, physically active adults	65 electrodes	Frequency analysis
*Chaire et al.	2020	43 (53.5)	25.33 (3.62)	Single group	Treadmill	Exercise group: Run for 45– 75 min at 70–90% HR _{maw} 3 times/week for 16 weeks. Control group: Walk for 10–12 min at 50–60% HR _{max} for 2 times/week. EEG was recorded a day before and 2–3 days after the end of the 4– month intervention, while participants performed 120 trials of a DMS WM task and 60 trials of a VAS task.	young adults	F3, Fz, F4, P3, Pz, P4	Frequency analysis
Ciria et al.	2018	20 (0)	23.8	Cross-over	Cycle ergometer	30 min flanked by 10-min 20% VO _{2max} warm- up and cool down, two conditions;	Healthy adults	30 electrodes (10–20 positioning)	Frequency analysis, current source density

			M _{age} (SD)					Number of	
Authors	Year	N (% female)	in years	Study design	Experimental task	Intervention	Participants	electrodes	Method of analysis
						Low intensity: 20% VO _{2max} . Moderate intensity: 80% VO _{2max} . EEG was recorded in all experimental conditions (both rest periods, warm- up, exercise, cool down, both flanker tasks).			
Ciria et al.	2019	20(0)	23.9	Cross-over	Cycle ergometer	100 min (approx.): 10-min 30% VO _{2max} warm-up and cool down (after completion of cycling and oddball task); Low intensity: 30% VO _{2max} ; High intensity: 80% VO _{2max} . EEG was recorded during the high-intensity cycling and oddball task, and again during the low-intensity cycling task.	Adults with high level of aerobic fitness	30 electrodes (10–20 positioning)	Frequency analysis and event-related spectral perturbation analysis
Contreras- Jordán et al.	2022	6 (33.33)	25.67 (3.61)	Within-subjects	Non-specified aerobic	Exercise group: Moderate- to-vigorous noncognitively engaging or aerobic (calisthenic- type) exercise for 10 min. Control group: Sitting for 10 min. EEG was recorded pre- and post-exercise.	Healthy adults	32 electrodes	Frequency analysis
Devilbiss et al.	2019	16 (50)	Men: 19.9 Women: 19.6	Single group	Grass track running	1 mile all-out run (~5–10 min). EEG was recorded pre- and 1–2 min post-exercise	Healthy soccer players	Fp1	Frequency analysis
*Dishman et al.	2010	36 (Intensity: Moderate: 66	Moderate intensity: 23 (4.2)	Two-arm, randomised, controlled	Cycle ergometer	20 min, 3 times/week for 6 weeks, low (40% VO _{2max}) or high intensity (75%	Healthy adults	256 electrodes	Frequency analysis

		Low: 75 Controls: 83)	Low intensity: 24 (4.7) Controls: 21 (2.4)			VO _{2max}). EEG was recorded for 4 min pre- and post-exercise, or pre- and post-rest.			
Enders et al.	2016b	10 (0)	27.5 (5.6)	Single group	Cycle ergometer	Time-to-exhaustion test at 85% MAP. EEG was recorded during exercise.	Healthy, experienced cyclists	64 channel (10–20 positioning)	Frequency analysis
Fumoto et al.	2010	10 (10)	32 (2.2)	Single group	Cycle ergometer	15 min at an intensity of Borg scale = 12–13. EEG was recorded 1 min pre- and post-exercise, as well as during Minute 1, 5, 10, and 15 of exercise.	Healthy, light exercisers	Cz, Pz	Frequency analysis
Guimarães et al.	2015	10 (0)	20–27 (age range)	Randomised cross-over	Cycle ergometer	Submaximal protocol with 30–62 min at ± 9% VO _{2max} . Maximal protocol with a start at an unspecified intensity (warm up) and increased each minute by 10% of VO _{2max} until VO ₂ plateau ≤ 150 mL/min or 2 kg mL/min, HR ≥ 90%, Borg scale ≥ 18 or ≥ 1.15 respiratory exchange ratio, and voluntary failure to maintain the cadence. Supramaximal protocol with a 30-s sprint against a workload of 0.075 kp body mass (1/kg). EEG was recorded for 5 min pre- and 15 min post-exercise.	exercisers	Fz, Cz, Pz, Oz, Fp1, Fp2, F3, F4, F7, F8, C3, C4, T3, T4, T5, T6, P3, P4, O1, O2	sLORETA
*Gutmann et al.	2015	10 (0)	22.7 (2)	Single group	Cycle ergometer (one-legged cycling)	12 sessions of 30 min over the course of 4 weeks at 50% of peak power output (~65–75%		Fp1, Fp2, F3, Fz, F4, T7, C3, Cz, C4, T8, P3, Pz, P4, O1, O2	Individual alpha peak frequency

Table 1. Continued.

			M _{age} (SD)					Number of	
Authors	Year	N (% female)	in years	Study design	Experimental task	Intervention	Participants	electrodes	Method of analysis
						HR _{max}); intensity increased by 5% each week. EEG was recorded for 2 min pre-exercise, immediately post-exercise, and 10 min post-exercise.			
*Gutmann et al.	2018a	10 (0)	22.7 (2)	Single group	Cycle ergometer (one-legged cycling)	12 sessions of 30 min over the course of 4 weeks, 50% of peak power output ~65–75% HR _{max} , intensity increased by 5% each week. EEG was recorded preexercise, immediately post-exercise, and 10 min post-exercise.	Healthy adults	Fp1, Fp2, F3, Fz, F4, T7, C3, Cz, C4, T8, P3, Pz, P4, O1, O2	Individual alpha peak frequency
Gutmann et al.	2018b	Rest groups: 97 (1 = 21, 2 = 26, 3 = 40, 4 = 33), Exercise groups: 95 (1 = 28, 2 = 28, 3 = 38, 4 = 33)	1 = 23.4 (3.6) 2 = 23.8 (3.5) 3 = 24.3 (3.8) 4 = 24.3 (3.8)	Parallel group	Cycle ergometer	Graded exercise test until volitional exhaustion followed by rest (four groups: No rest, 30-min, 60-min, and 90-min rest), and 30-min exercise at low (45–50% HR _{max}), moderate (65–70% HR _{max}), high intensity (85–90% HR _{max}), or control. EEG was recorded preexercise and immediately postexercise to exhaustion, and after group-specific rest (no rest, 30-min, 60-min, and 90-min rest). It was then recorded preexercise, immediately	Healthy adults	Fp1, Fp2, F3, Fz, F4, T7, C3, Cz, C4, T8, P3, Pz, P4, O1, O2	Individual alpha peak frequency

						post-exercise, and 20 min post-exercise.			
Gwin & Ferris	2012	8 (12.5)	21–31 (age range)	Single group	Isometric muscle activations and isotonic movements of the right knee and right ankle joints	20 × ~3 s (5-s rest in between). EEG was recorded during exercise.	Healthy adults	264 channels	Frequency analysis
Hicks et al.	2018	12 (58)	22.3 (3.1)	Randomised cross-over	Recumbent cycle- ergometer	Pedalling without resistance for 30 min at 60–70% HR _{max} . EEG was recorded for 8 min preexercise and for 32 min post-exercise, which was divided into four 8-min periods.	Healthy adults	32 channels, but only F3 and F4 used in the final analysis	Frequency analysis and frontal alpha asymmetry
Hilty et al.	2011	17 (0)	25.9 (3.5)	Single group	Cycle trainer	60% VO ₂ peak (245.6 ± 28.6 W) until volitional exhaustion. EEG was recorded for 1 min every 5 min.	Healthy, regular endurance exercisers	128 channels	sLORETA and mean lagged synchronisation in alpha band
Hottenrott et al.	2013	16 (0)	25.9 (3.8)	Single group	Cycle ergometer	60 min at 90% lactate threshold. EEG was recorded at rest, after warm-up, just before every cadence change during exercise, after cool down, and at rest (exact times not specified).	Healthy, endurance cydists	32 electrodes (10–20 positioning)	Frequency analysis
Kao et al.	2020	23 (52.2)	19.2 (0.6)	Within-subjects	Treadmill walk	20 min at 60–70% HR _{max} or sitting quietly for 20 min followed by 30-min n- back task. EEG was recorded during the n-back task.	Healthy adults	P3, Fz, FCz, Cz, CPz, Pz	Frequency analysis
Kao et al.	2021	36 (50)	21.5 (0.5)	Single group	Treadmill	20-min bout of HIIT (90% HR _{max}), MICE (70% HR _{max}), or rest on three different days.	Healthy adults	Fz, FCz	Frequency analysis

			$M_{\rm age}$ (SD)					Number of	
Authors	Year	N (% female)	in years	Study design	Experimental task	Intervention	Participants	electrodes	Method of analysis
*Kubitz & Landers	1993	30 (60)	23.04 (3.62)	Randomised, controlled	Cycle ergometer	EEG was recorded during working memory task. 40 min at 60%–85% HR _{maw} three times per week, for 8 weeks. EEG was recorded for Minutes 1–2 of the baseline, stressor task, and Minutes 1–2 of recovery periods.	Healthy, non- regular exercisers	F3, F4	Frequency analysis, and alpha and beta asymmetry
Kubitz & Mott	1996	34 (41)	23.4 (3.7)	Non-randomised, controlled	Cycle ergometer	15 min, starting at 50 W and every 5 min there was a Watt increment set in accord with participant HR (see Pollack et al., 1978). EEG was recorded during Minutes 8–10 of adaptation period, Minutes 3–5, 8–10, and 13–15 of the exercise period, and Minutes 8–10 of the recovery period.	Healthy adults	F3, F4, T3, T4	Frequency analysis
Lattari et al.	2016	20	26.5 (3.8)	Cross-over	Cycle ergometer	Prescribed exercise: 20 min at 50% VO _{2max} . Self-selected exercise: 20 min at individually selected tempo. EEG was recorded for 8 min pre- and post-exercise.	Healthy, physically active (exercised aerobically 3 times/week)	Fp1, Fp2, Fz, F3, F4, F7, F8, Cz, C3, C4, T3, T4, T5, T6, Pz, P3, P4, Oz, O1, O2; only F3 and F4 analysed	Frontal alpha asymmetry
Ludyga et al.	2016	29 (37.93)	18–35 (age range)	Cross-sectional	Cycle ergometer (indoors)	Session 1: 5 min warm-up at 80 W (f)/100 W (m), intensity increased by 25 W every 3 min until volitional exhaustion; Session 2: 5 min warm up at 80 W (f)/100 W (m),	Healthy cyclists and triathletes with minimum cycling training of 4 h per week	F3, F4, Fz, F7, F8, C3, C4, Cz, P3, P4, Pz, P7, P8	Frequency analysis and alpha/beta ratio

						then 30 min at 100% of the individual anaerobic threshold, 5-min cool down at 80 W (f)/100 W (m). EEG was recorded in Session 2 only, pre- exercise for 2 min and during exercise for 1 min at 10, 20, and 30 min.			
*Ludyga et al.	2017	22 (Low cadence training = 27, High cadence training = 36)	27 (4)	Two-arm, randomised	Cycle ergometer (indoors and outdoors)	4 hr/week for 4 weeks, individual heart rate targets (70%–80% of anaerobic threshold). High cadence (120–140 rpm) and low cadence (60 rpm) groups also engaged in four 60-min sessions per week of supervised cadence-specific exercise. EEG was recorded pre- and during exercise, at Minutes 10, 20, and 30.	Healthy cyclists	Fz, F3, F4, F7, F8	Frequency analysis and alpha/beta ratio
Mechau et al.	1998	19 (10.5)	42.4 (8.3)	Single group	Track running		Healthy, leisure- time athletes	17 electrodes (10–20 positioning)	Frequency analysis
Mierau et al.	2009	30 (0)	26 (4)	Three-arm, randomised	Treadmill		Healthy runners	Fp1, Fp2, Fz, F3, F4, C3, C4, Cz, P3, P4, Pz, F7, F8, T7, T8, P7, P8, O1, O2	Frequency analysis

Table 1. Continued.

A		A1 (0) (5	$M_{\rm age}$ (SD)	Contraction	E	to a constant	0	Number of	Mark at a Caral at
Authors	Year	N (% female)	in years	Study design	Experimental task	Intervention	Participants	electrodes	Method of analysis
Moraes et al.	2007	10 (60)	25.6 (4.1)	Single group	Cycle ergometer	by 0.5 m/s every 5 min. EEG was recorded pre- and post-exercise for 2 min. Started at 15W and	Healthy, cycle	Fp1, Fp2, Fz, F3, F4,	Frequency analysis
						increased by 15–30 W/min until volitional exhaustion, Borg scale ≥ 18, heart rate ≥ 90% HR _{max} or incapacity to continue the test. EEG was recorded for 8 min pre- and post-exercise.	ergometer exercisers	F7, F8, Cz, C3, C4, T3, T4, T5, T6, Pz, P3, P4, Oz, O1, O2	
Moraes et al.	2011	29	old age group: 70.4 (7) Young age group: 25 (1.5)	Parallel group	Cycle ergometer	20 min at 80% HR _{max} . EEG was recorded for 8 min pre- and post-exercise.	Healthy, moderately active	Fz, Cz, Pz,Oz, Fp1, Fp2, F3, F4, F7, F8, C3, C4, T3, T4, T5, T6, P3, P4, O1, O2	Frequency analysis and LORETA
Mott et al.	1995	33 (42)	23.4 (3.7)	Non-randomised, controlled	Cycle ergometer	15 min at 50% VO _{2max} . EEG was recorded for 2 min at rest, during last 2 min of exercise and during last 2 min of 10-min rest period post-exercise.	Healthy adults	F3, F4, T3, T4	Coherence analysis
Nielsen et al.	2001	7 (0)	26.3 (1.9)	Single subject	Cycle ergometer	Hot condition (42°C): 60% VO _{2max} until exhaustion; Cool condition (19°C): Until voluntary exhaustion. EEG was recorded for three 30-s periods pre-exercise and every 5 min during exercise.	Endurance-trained cyclists	F3, F4	Frequency analysis
Ohmatsu et al.	2014	16 (50)	Intervention 23.5 (1.9)	Non-randomised, controlled	Cycle ergometer	30 min at 50% of VO _{2max} . EEG was recorded pre- and	Healthy	32 electrodes (10–20 positioning)	Frontal asymmetry and sLORETA

			(1.9)			times not specified).			
Petruzzello & Landers	1994	20 (0)	22.7 (2.4)	Single group	Treadmill	30 min at 75% MAP. EEG was recorded pre- and post-exercise (exact times not specified).	Healthy, regular exercisers	F3, F4, T3, T4	Frequency analysis
Petruzzello & Tate	1997	20 (25)	22.6 (3.3)	Randomised, cross-over	Cycle ergometer	30 min at 55 and 70% VO _{2max} . EEG was recorded pre- and post-exercise for eight 1-min periods with a 2-min interval between fourth and fifth recordings.	Healthy, regular exercisers	F3, F4, P3, P4	Frequency analysis and frontal alpha asymmetry
Schneider et al.	2009a	24 (37.5)	30.1 (7.6)	Single group	Outdoor running	Low (50%–55% VO ₂ peak), high (80%–85% VO ₂ peak), and preferred, affect-based intensity. EEG was recorded pre- exercise, immediately post-exercise, and 15 min post-exercise for 5 min.	Healthy runners	Fp1, Fp2, F3, F4, F7, F8, Fz, C3, C4, Cz, P3, P4, P7, P8, Pz, T7, T8, O1, O2	Frequency analysis and frontal asymmetry
Schneider et al.	2009b	12 (33.3)	26.3 (3.8)	Cross-over	Treadmill, arm-crank, and cycle ergometer	Each activity was graded and continued until volitional exhaustion. The treadmill started at 2 m/s and increased by 0.5 m/s every 3 min. The arm-crank started at 20 W and increased by 20 W every 3 min. The cycling started at 50 W and increased by 50 W every 3 min. EEG was recorded for 5 min before exercise and again 2, 15, and 30 min post-exercise.		Fp1, Fp2, F3, F4, F7, F8, Fz, C3, C4, Cz, P3, P4, P7, P8, Pz, T7, T8, O1, O2	sLORETA
Schneider et al.	2010a	22 (35.4)	30.6 (7.7)	Single group	Treadmill	Graded with a start at 7.2 km/h and increased every 3 min by 1.4 km/h, until volitional	hr/week min.)	Fp1, Fp2, F3, F4, F7, F8, Fz, C3, C4, Cz, P3, P4, P7, P8, Pz, T7, T8, O1, O2	sLORETA

post-exercise (exact

Control: 23.1

Table 1. Continued.

			$M_{\rm age}$ (SD)					Number of	
Authors	Year	N (% female)	in years	Study design	Experimental task	Intervention	Participants	electrodes	Method of analysis
						exhaustion. EEG was recorded for 5 min before exercise and again immediately after exercise and 15 min post-exercise.			
Schneider et al.	2010b	18 (33.3)	28.8 (6)	Randomised, cross-over	Track running	Low (50–55% VO _{2max}), high (80–85% VO _{2max}), and preferred intensity; duration not stated. EEG was recorded pre- and post-exercise (exact times not specified).	Healthy runners	Fp1, Fp2, F3, F4, F7, F8, Fz, C3, C4, Cz, P3, P4, P7, P8, Pz, T7, T8, O1, O2	SLORETA
*Severtsen & Bruya	1986	10 (100)	19–50 (age range)	Two-arm, randomised	Not specified	15–20 min/day at a self- selected intensity for 7 weeks. EEG was recorded for 15 min before exercise and again 6 weeks thereafter (not specified if before or after exercise).	Healthy adults	Not specified, proportion of alpha and beta waves	Not specified
Spring et al.	2017	20 (0)	30.8 (6.9)	Cross-over	Cycle ergometer and cycle trainer	30-min cycle ergometer exercise at 60% MAP, then a 15-min rest followed by a 10-km time trial on a cycle trainer. EEG was recorded pre- and post-exercise for both exercises (exact times not specified).	Healthy road cyclists/ triathletes	Fp1, Fpz, Fp2, C1, Cz, C2, PO3, POz, PO4	Frequency analysis, microstates analysis
Wollseiffen et al.	2016a	50 (46)	40.9 (11.1)	Five-arm, randomised	Cycle ergometer and boxing	Intervention 1: 20 min of cycling at 70% HR _{max} .	Healthy adults	Fp1, Fp2, FPz	Frequency analysis

						Intervention 2: 3 min of boxing at maximum exhaustion. EEG was recorded pre- and immediately post- exercise.			
Wollseiffen et al.	2016b	11 (45.5)	36.5 (7)	Single group	Outdoor running on asphalt	6 hr at self-selected pace. EEG was recorded for 2 min pre and immediately post each 1-hr period of exercise.	Healthy ultra- marathoners	Fp1, Fp2, F3, Fz, F4, F7, F8, C3, C4, Cz, P3, Pz, P4, O1, Oz, O2	Frequency analysis
Woo et al.	2009	16 (100)	21 (0.9)	Cross-over	Treadmill	15, 30, and 45 min at 60% VO _{2max} . EEG was recorded for 10 min pre- and 15–20 min post-exercise.	Healthy, non- regular exercisers	F3, F4	Frequency analysis, frontal asymmetry
Woo et al.	2010	16 (100)	21 (0.8)	Cross-over	Treadmill	30 min, graded (45, 60, and 75% of VO _{2max}). EEG was recorded for 10 min pre- and 15 min post-exercise.	Healthy and had not exercised aerobically for the previous year	F3, F4	Frequency analysis, frontal alpha asymmetry

Note. Studies are ordered alphabetically. Studies marked with an asterisk (*) indicate those that examined bouts of acute exercise over weeks (i.e. chronic effects of exercise). HR_{max} = maximal heart rate; sLORETA = standardised low-resolution electromagnetic tomography; DMS = delayed match-to-sample; WM = working memory; VAS = visual-attention search; MAP = maximal aerobic power; MICE = moderate-intensity continuous exercise; HIIT = high-intensity interval training.



Table 2. Results From Studies Investigating Pre- and Post-Exercise Effects

Authors	Year	Main findings	Effect size (d, η_p^2)
Bailey et al.	2008	Alpha/beta ratio increased in frontal and central electrodes for baseline vs. immediately post-exercise, and remained significant 10 min post-exercise, with exception of F3 and F4 electrodes.	Alpha-beta ratio (η ² _p): Main effects of time (.58***), and region (.86***)
Bixby et al.	2001	Parietal alpha power was greater pre- and during exercise vs. post-exercise.	P4 and P3 (<i>d</i>): Period (0.16**)
Boutcher & Landers	1988	Bilateral increase in alpha power from pre- to 1–7 min post-task for both the running and reading group.	Non-runners (reading; d): 1–7 min post-task (0.16), 8–14 min post-task (0.21), 15–21 mi post-task (0.15) Runners (reading; d): 1–7 min post-task (0.16), 8–14 min post-task (0.08), 15–21 mi post-task (0.13) Non-runners (running; d): 1–7 min post-task (1.64), 8–14 min post-task (0.13), 15–21 mi post-task (0.72) Runners (running; d): 1–7 min post-task (0.81), 8–14 min post-task (0.40), 15–21 mi post-task (0.38)
Brümmer et al.	2011	Healthy runners: Alpha activity increased from pre- to post-exercise in the frontal and parietal cortices. Beta activity increase in the parietal cortex and decreased across the frontal cortex from pre- to post-exercise. Hand-cycling athletes: Alpha activity decreased in the frontal area from pre- to post-exercise.	Healthy runners, alpha at 50% intensity (d): Treadmill (1.63**), bicycle (2.30**), arm crank (1.68**), isokinetic (2.35**); alpha at 80% intensity (d): Treadmill (1.46), bicycle (1.30), arm crank (1.09), isokinetic (2.12*) Healthy runners, beta at 50% intensity (d): Treadmill (1.16), bicycle (2.12*), arm crank (1.49), isokinetic (1.29); beta at 80% intensity (d): Treadmill (2.24**), bicycle (1.76), arm crank (1.27), isokinetic (1.19) Hand-cycling athletes, alpha (d): Hand bike (9.01*); beta (d): Hand bike (4.16)
Büchel et al.	2021	Alpha-1 activity increased from pre- to post- exercise in the parietal and occipital regions. Alpha-2 activity increased from pre- to post-exercise in the frontal, central, parietal, and occipital regions. No significant changes were found in theta.	Alpha-1 (n _p ²): Parietal (.23**), occipital (.23**) Alpha-2 (n _p ²): Frontal (.29***), central (.30***) parietal (.36***), occipital (.28**)
Chaire et al.	2020	Frontal alpha power increased from pre- to post-exercise intervention during the VAS task after exercise. No significant theta alterations.	Theta (d): DMS frontal (0.02), DMS posterior (0.75), VAS frontal (< 0.01), VAS posterior (0.08) Alpha (d): DMS frontal (< 0.01), DMS posterior (< 0.01), VAS frontal (1.78*), VAS posterior (0.03)
Contreras- Jordán et al.	2022	Control group (no exercise): Frontal and right temporal alpha activity increase. Frontal and frontal-parietal beta power increase. Exercise group: Alpha and beta activity increased from pre- to post-exercise across the right prefrontal, central, and parietal regions. Gamma activity increased across the central area. Theta activity increased across the bilateral prefrontal cortex.	Insufficient information provided
Devilbiss et al.	2019	During rest: Theta activity decreased from pre- to post-exercise across the left prefrontal cortex. No significant changes in alpha and delta frequencies. During cognitive testing: Beta and gamma activities increased, and delta activity increased from pre- to post-exercise across the left prefrontal cortex.	Insufficient information provided

Table 2. Continued.

Authors	Year	Main findings	Effect size (d, η_p^2)
Dishman et al.	2010	No significant changes in the anterior region of the brain. Alpha, beta-2, and theta activities increased from pre- to post-exercise in the posterior regions of the brain.	Anterior regions: Insufficient information provided Posterior regions (η_p^2) : Alpha (.36), insufficient information provided for other frequency bands
Fumoto et al.	2010	Significant decrease in theta waves and increase in alpha-2 for central and parietal cortices from pre- to post-exercise. No significant changes found in alpha-1 and beta.	Theta (<i>d</i>): Cz (1.86*), Pz (1.83*) Alpha-1: Insufficient information provided Alpha-2 (<i>d</i>): Cz (1.97*), Pz (1.67*) Beta: Insufficient information provided
Guimarães et al.	2015	Alpha-2 and beta-2 activities increased in the limbic lobe from pre- to post-exercise.	Insufficient information provided
Gutmann et al.	2015	iAPF increased in the whole brain from pre- to post-exercise.	iAPF (η_p^2) : Main effect of time (.47**)
Gutmann et al.	2018a	Maximum alpha power: iAPF increase from pre- to post-exercise. Frequency analysis: Alpha-1 increased from pre- to immediately-post exercise and alpha-2 increased from pre- to immediately and 10 min post-exercise.	Maximum alpha power (η_p^2) : iAPF $(.34*)$ Frequency analysis (η_p^2) : Alpha-1 $(.47**)$, alpha-2 $(.48**)$
Gutmann et al.	2018b	iAPF increased in the whole brain from pre- to post-exercise. iAPF decreased from immediately post-exercise to after rest only if the rest was > 60 min.	iAPF (η_p^2): Main effect of time (.31***), Time \times Group (.15***)
Hicks et al.	2018	Alpha frontal asymmetry significantly greater from pre- to 22–38 min post-exercise. No significant change from pre- to immediately post-exercise. Frontal alpha power increased significantly	Frontal alpha asymmetry (η _p ²): Main effect of time (.19*) Frequency analysis (η _p ²): Main effect of time (.20*)
Hilty et al.	2011	from pre- to post-exercise. No significant change across post-exercise time periods. Alpha synchronisation: No significant changes from pre- to post-exercise in the whole brain. Frequency analysis: Alpha and beta increased from pre- to post-exercise in the whole	Alpha synchronisation (<i>d</i>): Main effect of time (1.28**) Frequency analysis (<i>d</i>): Alpha (1.60***), beta (1.54**)
Hottenrott et al.	2013	brain. Alpha-1, alpha-2, beta-1, beta-2, and theta activities decreased in the whole brain from pre- to post-exercise.	Insufficient information provided
Kao et al.	2021	Increased in frontal alpha activity from pre- vs. post-exercise.	Insufficient information provided
Kubitz & Mott	1996	No significant changes in alpha and beta power from pre- to post-exercise across the bilateral frontal and temporal cortices.	Insufficient information provided
Lattari et al.	2016	Frontal asymmetry: No significant changes.	Alpha frontal asymmetry (η_p^2) : Condition \times Moment (.03), main effect of condition (.11) and moment (.99)
Mechau et al.	1998	Delta activity increased across the frontal and central cortices from pre- to post-exercise.	Delta (η_p^2) : Main effect of time (.40***)
Mierau et al.	2009	Alpha and beta power increased from pre- to post-tracking in the tracking group. Alpha power remained unchanged and beta power decreased from pre- to post-tracking in the running-followed-by-tracking group. No significant changes in the running group from pre- to post-running in the whole brain.	Group \times Time interaction (η_p^2): Alpha (.24*), beta (.34**)
Moraes et al.	2007	Beta increased in the bilateral frontal and right central lobe from pre- to post-	Insufficient information provided

Table 2. Continued.

Authors	Year	Main findings	Effect size (d, η _p ²)
Moraes et al.	2011	exercise. No significant changes in alpha power in the whole brain. Frequency analysis: Alpha, beta-1, and beta-2 increased from pre- to post-exercise. sLORETA: Alpha (anterior cingulate gyrus), beta-1 (anterior cingulate gyrus), beta-2 (posterior cingulate gyrus) increased from pre- to post-exercise in young adults. There were no significant between-group differences (pre- vs. post-exercise).	Frequency analysis: Insufficient information provided sLORETA pre- vs. post-exercise (young; d): Alpha (2.51*), beta-1 (2.51*), beta-2 (2.62*) delta (1.12), theta (1.66) sLORETA pre- vs. post-exercise (elderly; d): Alpha (1.65), beta-1 (1.92), beta-2 (2.97), delta (1.89), theta (2.47)
Ohmatsu et al.	2014	sLORETA: Decrease in alpha-2 in the anterior cingulate cortex from pre- to post-exercise. No significant difference for beta-1, beta-2, delta, and theta. Frontal asymmetry: Increase in alpha-1 from pre- to post-exercise. No significant difference for beta-1, beta-2, delta, and theta.	Insufficient information provided
Petruzzello & Landers	1994	Alpha activity increased in the left frontal cortex and was greater in the frontal than in the anterior temporal areas from pre- to 5 min post-exercise. Alpha activity was increased from 10 min to 30 min post-exercise in the right frontal area.	Pre- vs. 5 min post-exercise (η_p^2) : Main effect of time (.15) and site (.91***) 10-min vs. 30 min post-exercise (η_p^2) : Main effect of time (.40**)
Petruzzello & Tate	1997	Frontal asymmetry: No significant changes. Frequency analysis: No significant changes in the bilateral frontal and parietal cortices.	Insufficient information provided
Schneider et al.	2009a	Frequency analysis: Alpha-1 increased across the parietal and occipital cortices from pre- to post-exercise. Beta-1 decreased across the right frontal and temporal cortices from pre- to post-exercise.	Frequency analysis (η_p^2) : Alpha-1 (.14*), beta-1 (.34***), insufficient information provided for other frequencies Frontal asymmetry (η_p^2) : Alpha-1 (.12), alpha-2 (.03) beta-1 (.08), beta-2 (.07)
Schneider et al.	2009b	Frontal asymmetry: No significant changes. Treadmill: Alpha activity increased in the frontal and limbic lobes, and beta activity increased in the parietal lobe from pre- to post-exercise. Bike: Alpha and beta activity increased in the parietal lobe from pre- to post-exercise. Alpha activity increased in the frontal and limbic lobes from pre- to 15 min post-exercise. Arm crank: Alpha activity increased in the frontal lobe and beta activity increased in the parietal lobe from pre- to post-exercise. Alpha and beta activity increased in the bilateral temporal lobes from pre- to 15 min post-exercise. Beta activity increased in the temporal lobe from pre- to 15 min post-exercise and in the limbic lobe from pre- to	Pre- vs. post-treadmill (<i>d</i>): Alpha (2.03*), beta (2.55**) Pre- vs. post-bike (<i>d</i>): Alpha (2.06**), beta (2.09**) Pre- vs. post-arm crank (<i>d</i>): Alpha (1.35*), beta (1.68*) Pre- vs. post-15-min treadmill (<i>d</i>): Alpha (1.72), beta (1.57) Pre- vs. post-15-min bike (<i>d</i>): Alpha (1.61*), beta (1.55) Pre- vs. post-15-min arm crank (<i>d</i>): Alpha (1.68*), beta (1.55*) Pre- vs. post-30-min treadmill (<i>d</i>): Alpha (1.71), beta (1.26) Pre- vs. post-30-min bike (<i>d</i>): Alpha (1.68), beta (1.18) Pre- vs. post-30-min arm crank (<i>d</i>): <i>t</i> value not the state of the state of (1.18)
Schneider et al.	2010a	30 min post-exercise. Increase in (a) left middle frontal gyrus alpha- 1, (b) widespread delta and (c) left and right temporal theta, from pre- to post- exercise. Decrease in (a) left inferior temporal gyrus alpha-2, (b) left inferior, middle, and superior temporal gyri beta-1, (c) left part of cuneus gamma, from pre- to 15 min	reported for alpha, beta (1.81) Pre vs. post (<i>d</i>): Alpha-1 (1.48**), alpha-2 (0.99), beta-1 (1.00), beta-2 (0.92), gamma (0.97), delta (1.83**), theta (1.32*) Pre- vs. post-15 min (<i>d</i>): Alpha-1 (0.80), alpha-2 (1.20*), beta-1 (1.47**), beta-2 (1.16), gamma (1.67**), delta (1.77**), theta (1.10)
Schneider et al.	2010b	post-exercise. Delta activity increased in the frontal and limbic lobes from pre- to post-exercise.	Insufficient information provided

Table 2. Continued.

Authors	Year	Main findings	Effect size (d, η_p^2)
Severtsen & Bruya	1986	Alpha activity increased from pre- to post- exercise (insufficient information provided regarding the brain area of interest). No significant change for beta activity.	Insufficient information provided
Spring et al.	2017	Frequency analysis: Delta decreased from pre- to post-cycle ergometer. Theta, alpha, and beta power increased from pre- to post-cycle trainer. Microstate analysis: Global variance explained, mean duration of, time coverage for, and frequency of occurrence of, microstate class C (i.e. frontal to occipital activity) was significantly increased from pre- to post-cycling tasks.	Frequency analysis pre- vs. post-cycle ergometer (η ² _p): Delta (.24**) Frequency analysis pre- vs. post-cycle trainer (η ² _p): Theta (.21*), alpha (.69***), beta (.40***) Microstate analysis (η ² _p) time effect: GEV (.67***), time coverage (.38***) Microstate analysis (η ² _p) maps effect: GEV (.77***), mean duration (.67***), time coverage (.69***)
Wollseiffen et al.	2016a	Prefrontal alpha-2 activity was significantly increased after (a) boxing and biking in comparison with the usual break and no break, and (b) the massage chair intervention when compared to the usual break and no-break condition, from pre- to post-exercise.	Pre- vs. post-exercise (n ² _p): Alpha-1 (.07), alpha-2 (.22*), beta-1 (.07), beta-2 (.03)
Wollseiffen et al.	2016b	Significant increase in frontal alpha activity in the measurement performed after 4 and 5 hr of running compared to measurement before and after 1 and 2 hr of running. Frontal beta activity decreased after 1, 5, and 6 hr of running compared to preexercise.	Main effect of time (n²): Main effects of time for alpha (.22*), insufficient information provided for beta
Woo et al.	2009	Frequency analysis: Delta, theta (only right hemisphere), and alpha increased in the bilateral frontal cortex from pre-exercise to 15 min of exercise. Asymmetry analysis: Higher delta, theta, and alpha frontal asymmetry after 30 min of exercise vs. pre-exercise.	Frequency analysis (η_p^2) : Alpha (.29**), insufficient information provided for beta-1, delta (.41***), theta (.44***) Asymmetry analysis (η_p^2) : Alpha (.48***), beta-1 (.25*), delta (.58***), theta (.58***)
Woo et al.	2010	Frequency analysis: Alpha power decreased in the left frontal cortex from pre- to post-exercise. Right-frontal alpha power was greater than left-frontal alpha power from pre- to post-exercise. Asymmetry analysis: Increased fontal asymmetry from pre- to post-exercise.	Frequency analysis (η_p^2) : Main effect of time $(.62^{***})$ Asymmetry analysis (η_p^2) : Main effect of time $(.63^{***})$

Note. Studies are ordered alphabetically. Significant results are indicated using asterisks (*p < .05, **p < .01, ***p < .001). Cohen's d effect sizes are reported as absolute values. sLORETA = standardised low-resolution electromagnetic tomography; DMS = delayed match-to-sample; VAS = visual-attention search; BA = Brodmann area; iAPF = individual alpha peak frequency.

to EEG (see Parr et al., 2021). The modified QATQS allows researchers to assess study quality with reference to 11 components¹ (i.e. selection bias, study design, confounders, blinding, data collection method, withdrawals and dropouts, artefact handling, temporal precision, brain wave definition², regional specificity, and controls to volume conduction). Each component is attached to a scale ranging from 1 (strong) to 3 (weak). The quality rating for each component was assessed and scores then averaged to assign each study with a global quality score of 1 (high quality), 2 (moderate quality), or 3 (low quality). It is noteworthy that double-blind or placebo-controlled designs are not adopted in this literature (see e.g. Renjith, 2017; Sedlmeier et al., 2012). Nonetheless,

Table 3. Results From Studies Investigating Effects During Exercise

Authors	Year	Main findings	Effect size (d, η_p^2)
Bailey et al.	2008	Alpha-1, alpha-2, beta-1, beta-2, and theta activity increased across the bilateral frontal and parietal cortices from during to immediately post-exercise. Values returned to baseline within 10 min post-exercise.	Main effect of time (n _p ²): Alpha-1 (.48***), alpha-2 (.69***), beta-1 (.76***), beta-2 (.75***), theta (.72***)
Bixby et al.	2001	Frequency analysis: Frontal alpha power increased during vs. pre- and post-exercise. F4 and F3 activity was more important in the left side of the brain. F8 and F7 activity was more important in the right side of the brain. Asymmetry analysis: Higher right-frontal alpha activity compared to left-frontal alpha activity during vs. pre- and post-exercise.	Frequency analysis (η_p^2) , F4 and F3: Period (0.53^{***}) , hemisphere (0.36^{***}) ; F8 and F7 Period (0.74^{***}) , hemisphere (0.76^{***}) , Period \times Hemisphere (0.14^*) Asymmetry analysis (η_p^2) : Alpha $(.12^*)$
Ciria et al.	2018	Whole-brain delta and centro-occipital beta activities increased from pre-exercise to during exercise. No significant results for alpha and theta activities.	Insufficient information provided
Ciria et al.	2019	Whole-brain delta and parieto-occipital alpha and beta activities increased from pre- exercise to during exercise.	Insufficient information provided
Enders et al.	2016b	Alpha, beta, and gamma activity increased in left frontal cortex from the first to the last 20% of the exercise session. Clusters in supplementary motor area and left parietal cortex showed a significant increase in the alpha and beta activity. Alpha activity increase in the parietal cortex.	Insufficient information provided
Fumoto et al.	2010	Significant decrease in theta activity. Increase in alpha-2 for central and parietal cortices from pre- to post-exercise, as well as during exercise. No significant changes found in alpha-1 and beta.	Theta (d): Cz (1.86*), Pz (1.83*) Alpha-2 (d): Ca (1.97*), Pz (1.67*) Insufficient information provided for alpha-1 and beta
Gwin & Ferris	2012	Significant beta- and gamma-range coherence between contralateral motor cortex EEG signals and lower limb EMG during exercise. Gamma-range coherence was significantly greater for isotonic vs. isometric exercise.	Insufficient information provided
Hilty et al.	2011	Alpha synchronisation between intra- hemispheric insular and motor cortex increased from the beginning to end of exercise. Alpha synchronisation decreased from the end of exercise to recovery. Frequency analysis: Alpha power decreased in the insular cortex from beginning and end of cycling to recovery.	Alpha synchronisation (<i>d</i>): Beginning vs. end (0.57**), end vs. recovery (1.57***) Frequency analysis (<i>d</i>): Alpha (1.60***), beta (1.54**)
Hottenrott et al.	2013	Alpha-1, alpha-2, beta-1, beta-2, and theta activities increased in the whole brain from pre- to during-exercise.	Insufficient information provided
Kubitz & Mott	1996	Alpha activity decreased across the bilateral frontal and temporal cortices from pre- to during-exercise. Beta activity increased from pre- to during-exercise.	Insufficient information provided
Ludyga et al.	2016	Alpha/beta ratio increased from pre- to during- exercise the central cortex. Alpha and beta activities increased from pre- to during-exercise across the bilateral frontal, central and parietal cortices.	Insufficient information provided
Ludyga et al.	2017	Frontal alpha/beta ratio increased from warm up to during exercise.	Insufficient information provided

Table 3. Continued.

Authors	Year	Main findings	Effect size (d, η_p^2)
Mechau et al.	1998	Alpha-1, alpha-2, beta-1, beta-2, delta, and theta activities increased across the whole brain from pre- to during-exercise.	Frequency analysis (η _p ²): Alpha-1 (.38***), alpha-2 (.25***), beta-1 (.33***), beta-2 (.18***), delta (.40***), theta (.43***)
Mott et al.	1995	Alpha coherence increased from during vs. pre-/post-exercise across the bilateral frontal and temporal cortices. No significant changes in beta coherence.	Insufficient information provided
Nielsen et al.	2001	Significant increases in frontal alpha and beta activity from pre- to during exercise. Alpha activity levelled off after the first 5 min of exercise. Beta activity significantly declined throughout the exercise session.	Insufficient information provided

Note. Studies are ordered alphabetically. Significant results are indicated using asterisks (*p < .05, **p < .01, ***p < .001). Cohen's d effect sizes are reported as absolute values. EEG = electroencephalography; EMG = electromyography.

blinding represents ~9% of the total QATQS score, which, invariably, has a bearing upon the quality rating assigned to studies in this literature.

Eligibility criteria

The criteria for studies to be considered for inclusion were as follows: (a) full papers published in English; (b) studies using healthy human adults as participants³; (c) studies conducted in an individual exercise or sport setting (indoor [n = 44] and outdoor [n = 3]); (d) studies comprised of physical exercise interventions that entailed analysis of cortical oscillatory activity through the use of EEG.

Studies were excluded if they were characterised by aims that were too specific and thus unrelated to the purpose of the present review; for example, motor memory (Dal Maso et al., 2018), motor imagery (Wriessnegger et al., 2020), motor learning (Gallicchio et al., 2017), and the effects of exercise on sleep (Menicucci et al., 2016). Given that a full complement of methodological detail was needed from each study for an in-depth review and synthesis of results, full published papers were the focus of this study, while published abstracts were not considered for inclusion. Theses were also not considered for inclusion due to the fact that they are not subject to peer review.

Analyses

To illustrate the meaningfulness of each effect reported herein, we include effect sizes. Where authors provided sufficient information (i.e. means and standard deviations), we calculated Cohen's d using an online calculator (https://www.polyu.edu.hk/mm/ effectsizefags/calculator/calculator.html). In other instances, where we had an F ratio, we calculated partial eta squared (η_p^2) , again by use of an online calculator (https:// effect-size-calculator.herokuapp.com). Effect sizes presented as Cohen's d were interpreted according to Cohen's (1988) guidelines. Accordingly, d < 0.5 was considered small, $d \ge 0.5$ was considered medium, and $d \ge 0.8$ was considered large. In instances where an effect size was 0.45, we rounded it up to one decimal point (i.e. 0.5), thus considering it medium in size. Where effect sizes were presented as partial eta squared (η_p^2) , in

Table 4. Results From Studies Investigating Effects of Exercise Intensity

Authors	Year	Main findings	Effect size (d, η_p^2)
Low vs. moderate intensity			
Ciria et al.	2018	Whole-brain delta and centro-occipital beta activities were higher in high- vs. low- intensity exercise.	Insufficient information provided
Dishman et al.	2010	Alpha activity in the posterior regions of the brain was higher following low- vs. moderate-intensity exercise.	Insufficient information provided
Hicks et al.	2018	No significance differences.	Frontal alpha asymmetry (η_p^2) : Main effect of intervention (< .01), Intervention × Time (.07)
Low vs. high			
intensity Bixby et al.	2001	No significant effect of exercise intensity.	Insufficient information provided
Ciria et al.	2019	Greater increase in whole-brain delta and parieto-occipital alpha and beta activities during exercise in high vs. low-intensity exercise.	Insufficient information provided
Gutmann et al. Moderate vs.	2018b	Whole-brain iAPF increased from pre- to post- exercise in high-vs. low- intensity exercise.	iAPF (η_p^2) : Time × Group (.15***)
high intensity			
Gutmann et al.	2015	Whole-brain iAFP increased from pre- to post- exercise during high- but not moderate- intensity exercise.	iAPF (η_p^2) : Protocol × Time (.33*)
Gutmann et al.	2018b	Whole-brain iAPF increased from pre- to post- exercise during high- vs. moderate- intensity exercise.	iAPF (η_p^2) : Time \times Group (.15***)
Petruzzello & Tate	1997	Frontal asymmetry: No significant changes. Frequency analysis: Frontal alpha activity decreased from pre- to 20 and 30 min post-exercise only during the high-intensity exercise. No significant changes in the bilateral parietal cortices.	Insufficient information provided
Woo et al. Low intensity	2010	No significant differences.	Insufficient information provided
Brümmer et al.	2011	Alpha activity increased from pre- to post- treadmill, bicycle, arm crank, and isokinetic exercise in parietal and frontal areas. Beta activity increased from pre- to post-bicycle	Alpha (d): Treadmill (1.63**), bicycle (2.30**), arm crank (1.68**), isokinetic (2.35**) Beta (d): Treadmill (1.16), bicycle (2.12*),
Büchel et al.	2021	exercise in the parietal area. No significant changes in alpha-1, alpha-2, and theta alterations from pre- to post-	arm crank (1.49), isokinetic (1.29) Insufficient information provided
Ciria et al.	2018	exercise. Whole-brain delta and temporo-occipital beta activities increased during exercise.	Insufficient information provided
Dishman et al.	2010	Alpha activity increased in the posterior regions of the brain from pre- to post-exercise.	Low-intensity exercise (η_p^2) : Alpha (.36*)
Guimarães et al.	2015	No significant changes in alpha-2 and beta-2 from pre- to post-exercise.	Insufficient information provided
Gwin & Ferris	2012	Significant beta- and gamma-range coherence between contralateral motor cortex EEG signals and lower-limb EMG during exercise.	Insufficient information provided
Hicks et al.	2018	No significant changes from pre- to post- exercise in alpha frontal asymmetry. Frontal alpha power increased significantly from pre- to immediately post-exercise, and	Alpha frontal asymmetry (η_p^2) : Pre- vs. post- exercise (< .01) Frontal alpha power: Insufficient information provided



Table 4. Continued

Authors	Year	Main findings	Effect size (d, η_p^2)
		from immediately post-exercise to 22-30	
Kao et al.	2020	min post-exercise. Frontal alpha activity increased following exercise vs. rest. No significant difference for alpha activity in the posterior and occipital cortices, and for theta activity in	Insufficient information provided
Kao et al.	2021	the frontal and central areas. Larger increased in frontal alpha activity following exercise.	Insufficient information provided
Lattari et al.	2016	No significant changes from pre- to post- exercise.	Alpha frontal asymmetry (η_p^2) : Main effect of condition (.11)
Ohmatsu et al.	2014	sLORETA: Decrease in alpha-2 in the anterior cingulate cortex from pre- to post-exercise. No significant difference for beta-1, beta-2, delta, and theta. Frontal asymmetry: Increase in alpha-1 from pre- to post-exercise. No significant difference for beta-1, beta-2, delta, and theta.	Insufficient information provided
Schneider et al. Moderate	2010b	No significant changes from pre- to post- exercise.	Insufficient information provided
intensity			
Bixby et al.	2001	Frontal alpha activity increased during exercise.	Frequency analysis (d): Pre- vs. during exercise (6.11***), post-exercise vs. during (4.63***)
Fumoto et al.	2010	Theta activity decreased and alpha-2 activity increased across central and parietal cortices from pre- to post-exercise. No significant changes found in alpha-1 and beta.	Theta (d): Cz (1.86*), Pz (1.83*) Alpha-1: Insufficient information provided Alpha-2 (d): Cz (1.97*), Pz (1.67*) Beta: Insufficient information provided
Hottenrott et al.	2013	Whole brain alpha-1, alpha-2, beta-1, beta-2, and theta activities were higher at 120 vs. 60 rpm.	Insufficient information provided
Kubitz & Landers	1993	Lower alpha activity across the bilateral frontal cortex following 8 weeks of exercise vs. no exercise. No significant differences in beta activity.	Frequency analysis: Alpha (.33*), insufficien information provided for beta
Kubitz & Mott	1996	No significant changes in alpha and beta power from pre- to post-exercise. Alpha activity decreased across the bilateral frontal and temporal cortices from pre- to during-exercise. Beta activity increased from pre- to during-exercise.	Insufficient information provided
Ludyga et al.	2017	Frontal alpha/beta ratio increased from warm up to during exercise only for moderate-intensity exercise, but not for high-intensity exercise.	Insufficient information provided
Mott et al.	1995	Alpha coherence increased from during vs. pre-/post-exercise across the bilateral frontal and temporal cortices. No significant	Insufficient information provided
Nielsen et al.	2001	changes emerged in beta coherence. Significant increases in frontal alpha and beta activity from pre- to during exercise. Alpha activity levelled off after the first 5 min of exercise. Beta activity significantly declined throughout the exercise session.	Insufficient information provided
Schneider et al.	2009a	Alpha-1 activity increased from pre- to immediately post-exercise across parietal and occipital regions.	Frequency analysis (η_p^2): Alpha-1 (.14*)
Spring et al.	2017	Delta decreased from pre- to post-exercise.	Frequency analysis pre- vs. post-exercise (η_p^2) : Delta (.24**)

Table 4. Continued.

Authors	Year	Main findings	Effect size (d, η_p^2)
Wollseiffen et al. Woo et al.	2016a 2009	Prefrontal alpha-2 activity increased from pre- to post-exercise. Frequency analysis: Delta, theta (only right hemisphere), and alpha increased in the	Pre- vs. post-exercise (η_p^2) : Alpha-1 (.07), alpha-2 (.22*), beta-1 (.07), beta-2 (.03) Frequency analysis (η_p^2) : Alpha (.29**), insufficient information provided for beta
		bilateral frontal cortex from pre-exercise to 15 min of exercise. Asymmetry analysis: Higher delta, theta, and alpha frontal asymmetry after 30 min of exercise vs. pre-exercise.	1, delta (.41***), theta (.44***) Asymmetry analysis (n _p ²): Alpha (.48***), beta-1 (.25*), delta (.58***), theta (.58***
Woo et al.	2010	Frequency analysis: Alpha power decreased in the left frontal cortex from pre- to post-exercise. Right-frontal alpha power was greater than left-frontal alpha power from pre- to post-exercise. Asymmetry analysis: Increased fontal asymmetry from pre- to post-exercise.	Frequency analysis (η _p ²): Main effect of time (.62***) Asymmetry analysis (η _p ²): Main effect of time (.63***)
High intensity		., ., . ,,	
Bailey et al.	2008	Alpha/beta ratio increased in frontal and central electrodes for baseline vs. immediately post-exercise, and remained significant 10 min post-exercise, with exception of F3 and F4 electrodes. Alpha-1, alpha- 2, beta-1, beta-2, and theta activity increased across the bilateral frontal and parietal cortices from during to immediately post-exercise. Values returned to baseline within 10 min post-exercise.	Main effect of time (η _p ²): Theta (.72***), alpha-1 (.48***), alpha-2 (.69***), beta-1 (.76***), beta-2 (.75***)
Bixby et al.	2001	Frontal alpha activity increased during exercise.	Frequency analysis (d): Pre- vs. during exercise (6.11***), post-exercise vs. during (4.63***)
Boutcher & Landers	1988	Bilateral increase in alpha power from pre- to 1–7 min post-exercise.	Nonrunners (running; d): 1–7 min post-tasl (1.64), 8–14 min post-task (0.13), 15–21 min post-task (0.72). Runners (running; d): 1–7 min post-task (0.81), 8–14 min post-task (0.40), 15–21 min post-task (0.38)
Brümmer et al.	2011	Alpha activity increase pre- vs. post-isokinetic in the frontal areas. Beta activity decreased across the frontal area pre- vs. post-treadmill.	Alpha (d): Treadmill (1.46), bicycle (1.30), arm crank (1.09), isokinetic (2.12*) Beta (d): Treadmill (2.24**), bicycle (1.76), arm crank (1.27), isokinetic (1.19)
Büchel et al.	2021	Alpha-1 activity increased from pre- to post- exercise in the parietal and occipital regions. Alpha-2 activity increased from pre- to post-exercise in the frontal, central,	Alpha-1 (η_p^2): Parietal (.23**), occipital (.23**). Alpha-2 (η_p^2): Frontal (.29***), central (.30***), parietal (.36***), occipital (.28**)
Chaire et al.	2020	parietal, and occipital regions. No significant changes found in theta. Frontal alpha power increased from pre- to post-exercise. No significant theta	Theta (d): DMS frontal (0.02), DMS posterio (0.75), VAS frontal (< 0.01), VAS posterio
		alterations.	(0.08) Alpha (d): DMS frontal (< 0.01), DMS posterior (< 0.01), VAS frontal (1.78*), VAS posterior (0.03)
Ciria et al.	2018	Whole-brain delta and temporo-occipital	Insufficient information provided
Devilbiss et al.	2019	beta activities increased during exercise. Theta activity decreased from pre- to post- exercise across the left prefrontal cortex.	Insufficient information provided
Dishman et al.	2010	Anterior and posterior beta and theta activities decreased from pre- to post-exercise.	Insufficient information provided
Enders et al.	2016b	Alpha, beta, and gamma activity increased in left frontal cortex from the first to the last 20% of the exercise session. Alpha and beta	Insufficient information provided



Table 4. Continued.

	Year	Main findings	Effect size (d, η_p^2)
		activities increased across clusters in the	
		supplementary motor area and left parietal	
		cortex. Alpha activity increased in the parietal cortex.	
Guimarães et al.	2015	Alpha-2 and beta-2 activities increased in the	Insufficient information provided
		limbic lobe from pre- to post-exercise.	·
Gutmann et al.	2018a	Maximum alpha power: iAPF increase from	Maximum alpha power (η_p^2): iAPF (.34*)
		pre- to post-exercise.	Frequency analysis (η_p^2): Alpha-1 (.47**),
		Frequency analysis: Alpha-1 increased from pre- to immediately-post exercise, and	alpha-2 (.48**)
		alpha-2 increased from pre- to immediately	
		and 10-min post-exercise.	
Hicks et al.	2018	Alpha frontal asymmetry significantly greater	Alpha frontal asymmetry (η_p^2): Pre- vs. post-
		from pre- to 22–38 min post-exercise. No	exercise (< 0.01)
		significant change from pre- to immediately post-exercise.	Frontal alpha power: Insufficient information provided
		Frontal alpha power increased significantly	mornation provided
		from pre- to post-exercise. No significant	
		change across post-exercise time periods.	
Hilty et al.	2011	Alpha synchronisation: No significant	Alpha synchronisation (d): Beginning vs.
		changes from pre- to post-exercise in the whole brain. Alpha synchronisation	end of exercise (1.28**), end of exercise vs. recovery (1.57***)
		between intra-hemispheric insular and	Frequency analysis (d): Alpha (1.60***), beta
		motor cortex increased from the beginning	(1.54**)
		to the end of exercise. Alpha	
		synchronisation decreased from the end of	
		exercise to recovery. Frequency analysis: Alpha and beta increased	
		from pre- to post-exercise in the whole	
		brain. Alpha power decreased in the insular	
		cortex from 1 min after exercise began to	
		the final minute of the 15-min active cool down, and from 5 min before exercise	
		ended to the final minute of the 15-min	
		active cool down.	
Kao et al.	2021	Larger increased in frontal alpha activity	Insufficient information provided
Ludius at al	2016	following exercise.	las (Caiant information are ideal
Ludyga et al.	2016	Alpha/beta ratio increased from pre- to during-exercise the central cortex.	Insufficient information provided
		Alpha and beta activities increased from pre-	
		to during-exercise across the bilateral	
	4000	frontal, central, and parietal cortices.	D 1: (2) 11: (5)
Mechau et al.	1998	Delta activity increased across the frontal and	Delta (η_p^2) : Main effect of time (.40)
Mechau et al.	1998	Delta activity increased across the frontal and central cortices from pre- to post-exercise.	Frequency analysis (η_p^2): Alpha-1 (.38***),
Mechau et al.	1998	Delta activity increased across the frontal and	
Mechau et al.		Delta activity increased across the frontal and central cortices from pre- to post-exercise. Alpha-1, beta-1, beta-2, delta, and theta activities increased across the whole brain from pre- to during-exercise.	Frequency analysis (n _p ²): Alpha-1 (.38***), alpha-2 (.25***), beta-1 (.33***), beta-2 (.18***), delta (.40***), theta (.43***)
Mechau et al. Mierau et al.	1998	Delta activity increased across the frontal and central cortices from pre- to post-exercise. Alpha-1, beta-1, beta-2, delta, and theta activities increased across the whole brain from pre- to during-exercise. Alpha and beta power increased from pre- to	Frequency analysis (η_p^2) : Alpha-1 (.38***), alpha-2 (.25***), beta-1 (.33***), beta-2 (.18***), delta (.40***), theta (.43***) Group \times Time interaction (η_p^2) : Alpha (.24*),
		Delta activity increased across the frontal and central cortices from pre- to post-exercise. Alpha-1, beta-1, beta-2, delta, and theta activities increased across the whole brain from pre- to during-exercise. Alpha and beta power increased from pre- to post-tracking in the tracking group. Alpha	Frequency analysis (n _p ²): Alpha-1 (.38***), alpha-2 (.25***), beta-1 (.33***), beta-2 (.18***), delta (.40***), theta (.43***)
		Delta activity increased across the frontal and central cortices from pre- to post-exercise. Alpha-1, beta-1, beta-2, delta, and theta activities increased across the whole brain from pre- to during-exercise. Alpha and beta power increased from pre- to post-tracking in the tracking group. Alpha power remained unchanged and beta	Frequency analysis (η² _p): Alpha-1 (.38***), alpha-2 (.25***), beta-1 (.33***), beta-2 (.18***), delta (.40***), theta (.43***) Group × Time interaction (η² _p): Alpha (.24*),
		Delta activity increased across the frontal and central cortices from pre- to post-exercise. Alpha-1, beta-1, beta-2, delta, and theta activities increased across the whole brain from pre- to during-exercise. Alpha and beta power increased from pre- to post-tracking in the tracking group. Alpha	Frequency analysis (η_p^2) : Alpha-1 (.38***), alpha-2 (.25***), beta-1 (.33***), beta-2 (.18***), delta (.40***), theta (.43***) Group \times Time interaction (η_p^2) : Alpha (.24*),
		Delta activity increased across the frontal and central cortices from pre- to post-exercise. Alpha-1, beta-1, beta-2, delta, and theta activities increased across the whole brain from pre- to during-exercise. Alpha and beta power increased from pre- to post-tracking in the tracking group. Alpha power remained unchanged and beta power decreased from pre- to post-tracking in the running-followed-by-tracking group. No significant changes in the running	Frequency analysis (η_p^2) : Alpha-1 (.38***), alpha-2 (.25***), beta-1 (.33***), beta-2 (.18***), delta (.40***), theta (.43***) Group \times Time interaction (η_p^2) : Alpha (.24*),
		Delta activity increased across the frontal and central cortices from pre- to post-exercise. Alpha-1, beta-1, beta-2, delta, and theta activities increased across the whole brain from pre- to during-exercise. Alpha and beta power increased from pre- to post-tracking in the tracking group. Alpha power remained unchanged and beta power decreased from pre- to post-tracking in the running-followed-by-tracking group. No significant changes in the running group from pre- to post-running in the	Frequency analysis (η_p^2) : Alpha-1 (.38***), alpha-2 (.25***), beta-1 (.33***), beta-2 (.18***), delta (.40***), theta (.43***) Group \times Time interaction (η_p^2) : Alpha (.24*),
Mierau et al.	2009	Delta activity increased across the frontal and central cortices from pre- to post-exercise. Alpha-1, beta-1, beta-2, delta, and theta activities increased across the whole brain from pre- to during-exercise. Alpha and beta power increased from pre- to post-tracking in the tracking group. Alpha power remained unchanged and beta power decreased from pre- to post-tracking in the running-followed-by-tracking group. No significant changes in the running group from pre- to post-running in the whole brain.	Frequency analysis (η_p^2) : Alpha-1 (.38***), alpha-2 (.25***), beta-1 (.33***), beta-2 (.18***), delta (.40***), theta (.43***) Group \times Time interaction (η_p^2) : Alpha (.24*), beta (.34**)
Mierau et al.		Delta activity increased across the frontal and central cortices from pre- to post-exercise. Alpha-1, beta-1, beta-2, delta, and theta activities increased across the whole brain from pre- to during-exercise. Alpha and beta power increased from pre- to post-tracking in the tracking group. Alpha power remained unchanged and beta power decreased from pre- to post-tracking in the running-followed-by-tracking group. No significant changes in the running group from pre- to post-running in the	Frequency analysis (η_p^2) : Alpha-1 (.38***), alpha-2 (.25***), beta-1 (.33***), beta-2 (.18***), delta (.40***), theta (.43***) Group \times Time interaction (η_p^2) : Alpha (.24*),
Mierau et al.	2009	Delta activity increased across the frontal and central cortices from pre- to post-exercise. Alpha-1, beta-1, beta-2, delta, and theta activities increased across the whole brain from pre- to during-exercise. Alpha and beta power increased from pre- to post-tracking in the tracking group. Alpha power remained unchanged and beta power decreased from pre- to post-tracking in the running-followed-by-tracking group. No significant changes in the running group from pre- to post-running in the whole brain. Beta increased in the bilateral frontal and	Frequency analysis (η_p^2) : Alpha-1 (.38***), alpha-2 (.25***), beta-1 (.33***), beta-2 (.18***), delta (.40***), theta (.43***) Group \times Time interaction (η_p^2) : Alpha (.24*), beta (.34**)
	2009	Delta activity increased across the frontal and central cortices from pre- to post-exercise. Alpha-1, beta-1, beta-2, delta, and theta activities increased across the whole brain from pre- to during-exercise. Alpha and beta power increased from pre- to post-tracking in the tracking group. Alpha power remained unchanged and beta power decreased from pre- to post-tracking in the running-followed-by-tracking group. No significant changes in the running group from pre- to post-running in the whole brain. Beta increased in the bilateral frontal and right central lobe from pre- to post-	Frequency analysis (η_p^2) : Alpha-1 (.38***), alpha-2 (.25***), beta-1 (.33***), beta-2 (.18***), delta (.40***), theta (.43***) Group \times Time interaction (η_p^2) : Alpha (.24*), beta (.34**)

Table 4. Continued.

Authors	Year	Main findings	Effect size (d, η_p^2)
		sLORETA: Alpha (anterior cingulate gyrus), beta-1 (anterior cingulate gyrus), and beta- 2 (posterior cingulate gyrus) increased from pre- to post-exercise in young adults.	sLORETA pre- vs. post-exercise (young; d): Alpha (2.51*), beta-1 (2.51*), beta-2 (2.62*), delta (1.12), theta (1.66) sLORETA pre- vs. post-exercise (elderly; d): Alpha (1.65), beta-1 (1.92), beta-2 (2.97), delta (1.89), theta (2.47)
Petruzzello & Landers	1994	Alpha activity increased in the left frontal cortex and was greater in the frontal than in the anterior temporal areas from pre- to 5 min post-exercise. Alpha activity was increased from 10 min to 30 min post-exercise in the right frontal area.	Pre- vs. 5 min post-exercise (η_p^2) : Main effect of time (.15) and site (.91***) 10 min vs. 30 min post-exercise (η_p^2) : Main effect of time (.40**)
Schneider et al.	2009a	Alpha-1 activity decreased from pre- to 15 min post-exercise across parietal and occipital regions. Whole-brain beta-2 activity decreased from pre- to immediately post-exercise and 15 min post-exercise.	Frequency analysis (n _p ²): Alpha-1 (.14*), beta-2 (.14*)
Schneider et al.	2009b	Treadmill: Alpha activity increased in the frontal and limbic lobes, and beta activity increased in the parietal lobe from pre- to post-exercise.	Pre- vs. post-treadmill (<i>d</i>): Alpha (2.03*), beta (2.55**) Pre- vs. post-bike (<i>d</i>): Alpha (2.06**), beta (2.09**)
		Bike: Alpha and beta activity increased in the parietal lobe from pre- to post-exercise.	Pre- vs. post-arm crank (<i>d</i>): Alpha (1.35*), beta (1.68*)
		Alpha activity increased in the frontal and limbic lobes from pre- to 15 min post-	Pre- vs. post-15-min treadmill (<i>d</i>): Alpha (1.72), beta (1.57)
		exercise. Arm crank: Alpha activity increased in the	Pre- vs. post-15-min bike (d): Alpha (1.61*) beta (1.55)
		frontal lobe and beta activity increased in the parietal lobe from pre- to post-exercise.	Pre- vs. post-15-min arm crank (d): Alpha (1.68*), beta (1.55*)
		Alpha and beta activity increased in the bilateral temporal lobes from pre- to 15 min post-exercise. Beta activity increased in the	Pre- vs. post-30-min treadmill (<i>d</i>): Alpha (1.71), beta (1.26) Pre- vs. post-30-min bike (<i>d</i>): Alpha (1.68),
		temporal lobe from pre- to 15 min post- exercise and in the limbic lobe from pre- to 30 min post-exercise.	beta (1.18) Pre- vs. post-30-min arm crank (<i>d</i>): <i>t</i> value not reported for alpha, beta (1.81)
Schneider et al.	2010a	Increase in (a) left middle frontal gyrus alpha- 1, (b) widespread delta, and (c) left and right temporal theta, from pre- to post- exercise. Decrease in (a) left inferior temporal gyrus alpha-2, (b) left inferior, middle and superior temporal gyri beta-1, and (c) left part of cuneus gamma, from pre- to 15 min post-exercise.	Pre vs. post (d): Alpha-1 (1.48**), alpha-2 (0.99), beta-1 (1.00), beta-2 (0.92), gamma (0.97), delta (1.83**), theta (1.32*) Pre- vs. post-15-min (d): Alpha-1 (0.80), alpha-2 (1.20*), beta-1 (1.47**), beta-2 (1.16), gamma (1.67**), delta (1.77**), theta (1.10)
Schneider et al.	2010b	Delta activity increased in frontal and limbic lobes from pre- to post-exercise.	Insufficient information provided
Spring et al.	2017	Theta, alpha, and beta power increased from pre- to post-exercise.	Frequency analysis pre- vs. post-exercise (η_p^2) : Theta (.21*), alpha (.69***), beta (.40***)
Wollseiffen et al.	2016a	Prefrontal alpha-2 activity increased from pre- to post-exercise.	Pre- vs. post-exercise (η _p ²): Alpha-1 (.07), alpha-2 (.22*), beta-1 (.07), beta-2 (.03)
Woo et al.	2010	Frequency analysis: Alpha power decreased in the left frontal cortex from pre- to post-exercise. Right-frontal alpha power was greater than left-frontal alpha power from pre- to post-exercise. Asymmetry analysis: Increased fontal asymmetry from pre- to post-exercise.	Frequency analysis (η_p^2) : Main effect of time (.62***) Asymmetry analysis (η_p^2) : Main effect of time (.63***)

Note. Studies are ordered alphabetically. Significant results are indicated using asterisks (*p < .05, **p < .01, ***p < .001). Cohen's d effect sizes are reported as absolute values. iAPF = individual alpha peak frequency; sLORETA = standardised low-resolution electromagnetic tomography.

Table 5. Results Fr	ana Cturdiae Inc	restination Effects	of Eversies us	No Eversise
Table 5. Results Fr	om Studies in	vestidating Effects	of Exercise vs.	No Exercise

Authors	Year	Main findings	Effect Size (d, η_p^2)
Dishman et al.	2010	Alpha-1, alpha-2, beta-2, and theta activities in the posterior regions of the brain were higher for the exercise vs. no-exercise group.	Insufficient information provided
Kao et al.	2020	Frontal alpha activity was greater for the exercise vs. no-exercise group. No significant difference for alpha activity in the posterior and occipital cortices, and for theta activity in the frontal and central areas.	Insufficient information provided
Kubitz & Landers	1993	Lower alpha activity across the bilateral frontal cortex for the 8-week exercise vs. no-exercise group. No significant difference in beta activity.	Exercise group (d): Left alpha (0.45*), right alpha (0.18*), left beta (0.46), right beta (0.02)
		No-exercise group (d): Left alpha (0.21*), right alpha (0.14*), left beta (0.16), right beta (< 0.01)	
Kubitz & Mott	1996	Higher beta activity across the bilateral frontal and temporal areas for the exercise vs. no-exercise group. No significant differences in alpha activity.	Insufficient information provided
Mott et al.	1995	Alpha coherence increased for the exercise group across the bilateral frontal and temporal cortices. No significant changes in beta coherence.	Insufficient information provided
		Beta-1 coherence decreased across the right frontal and temporal cortices in the no-exercise group. No significant changes in alpha coherence.	
Severtsen & Bruya	1986	No significant changes in alpha and beta activity for the 6-week exercise vs. no-exercise group (insufficient information provided regarding the brain region of interest).	Insufficient information provided

Note. Studies are ordered alphabetically. Significant results are indicated using asterisks (*p < .05, **p < .01, ***p < .001). Cohen's d effect sizes are reported as absolute value. ERD = event-related desynchronisation; AE = aerobic exercise.

accord with Cohen's (1988) guidelines, $\eta_p^2 = .01$ is considered small, $\eta_p^2 = .06$ is considered medium, and $\eta_p^2 = .14$ is considered large.

Results

Of the 81 abstracts and journal articles retrieved from the searches, five were duplicates and 29 were deemed irrelevant for (a) not meeting the inclusion criteria (review [n=1]; (b) applying an intervention that was not exercise/physical activity/sport related [n=7]; (c) targeting the wrong population (i.e. children) [n=6]; (d) stating aims that did not align with those of the present review (i.e. investigating sleep-related oscillations) [n=10]; and (e) not investigating oscillations [n=5]), leaving 47 relevant studies. The screening and selection process is illustrated in Figure 1. The selected 47 studies were then categorised as follows: (a) pre- vs. post-exercise condition (n=37); (b) pre-/post- vs. during-exercise condition (n=15); (c) comparisons among different exercise intensities (n=43); (d) exercise vs. control group (n=6). The quality rating for each study, along with relevant descriptive statistics, can be found in Supplemental Material 1.

Exercise intervention and analytical methods of included studies

The intervention procedures from the 47 included studies, along with their main findings and associated effect sizes are shown in Tables 2–5. Given that some studies investigated several exercise modes/intensities and/or applied multiple analytical techniques, it is the

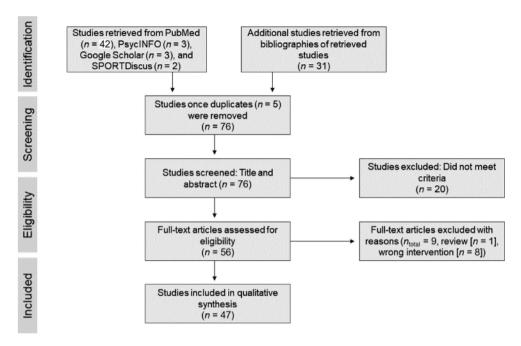


Figure 1. Process of Selection of the Studies According to PRISMA.

number of effects that is most relevant herein, rather than the number of studies per se. The number of effects will be expressed by use of 'k' hereafter.

The most frequently investigated exercise mode was cycle ergometry (k = 27), followed by treadmill walking/running (k = 12), track running (k = 3), outdoor running (k = 3), cycle trainer (k = 2), arm crank (k = 1), isokinetic dynamometer wrist flexion (k = 1), isometric and isotonic movements (k=1), aerobic (callisthenic-type) exercise (k=1), and outdoor cycling (k = 1; see Figure 2). Most studies (n = 39) used acute exercise interventions, while the remaining eight studies used acute exercise interventions over the course of 4–16 weeks, with the exception of one study that used a long-duration acute intervention (Wollseiffen et al., 2016b; see Table 1).

The markers used in terms of exercise intensity were: (a) $\dot{V}O_{2max}$ (k = 14); (b) percentages of maximal heart rate (HR_{max}; k = 12); (c) exercising until volitional exhaustion (k= 8); (d) rating of perceived exertion using a version of Borg's RPE Scale; (k = 3); (e) maximal aerobic/anaerobic power (k = 2); (f) reaching lactate threshold (k = 1); (g) reaching the ventilatory breakpoint (k = 1). The remaining studies did not report a marker for exercise intensity (k = 5). In order to analyse the effects of different exercise intensities on electrical activity in the brain, studies were categorised into high (≥ 70% VO₂ max), moderate (56–69% VO₂ max), and low-intensity exercise (≤ 55% VO₂ max) bands, according to the American College of Sports Medicine (ACSM, 2013) guidelines. Given that some studies used heart-rate based parameters to establish exercise intensity, we used data from Swain et al. (1994) and thus associated 63%, 76%, 89%, and 92% HR_{max} with 40%, 60%, 80%, and 85% VO_{2max}, respectively. The most common analytical method used within the included studies was frequency analysis (k = 35), followed by asymmetry (k= 9), low resolution electromagnetic tomography ([s]LORETA; k = 8), individual peak alpha frequency (k = 3), alpha/beta ratio (k = 3), coherence (k = 2), and microstates (k = 1).

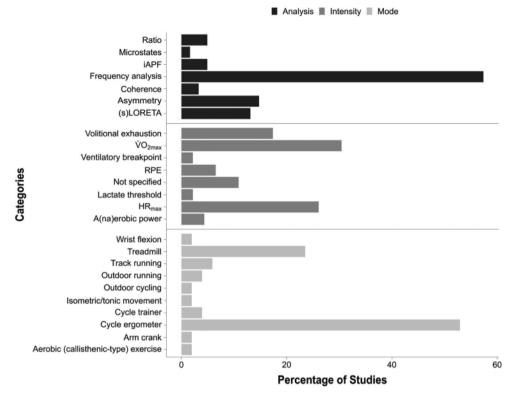


Figure 2. Total Percentage of Studies Across Methods of Analysis, Exercise Intensity and Exercise Mode. Note. (s)LORETA = (standardised) low-resolution electromagnetic tomography; iAPF = individual alpha peak frequency; RPE = rating of perceived exertion; HRmax = maximal heart rate.

Pre- and post-exercise studies

Alpha activity

The most common effect observed among the studies investigating the effect of pre- vs. post-exercise was a significant increase in alpha brainwave activity (see Table 2). Of the 37 studies in the pre- vs. post-exercise category, 24 reported increases in alpha peak and/or power across the bilateral frontal cortex (k = 7; e.g. Brümmer et al., 2011; Chaire et al., 2020), left frontal cortex (k = 2; Petruzzello & Landers, 1994; Schneider et al., 2010a), right prefrontal cortex (k = 1; Contreras-Jordán et al., 2022), bilateral frontal and central cortices (k = 1; Bailey et al., 2008), anterior cingulate cortex (k = 1; Moraes et al., 2011), limbic lobe (k = 1; Guimarães et al., 2015), bilateral parietal cortex (k = 3; e.g. Brümmer et al., 2011), bilateral central and parietal cortices (k = 3; e.g. Fumoto et al., 2010), bilateral temporal cortex (k = 1; Boutcher & Landers, 1988), posterior regions (k = 1; Dishman et al., 2010), occipital cortex (k = 2; Büchel et al., 2021; Schneider et al., 2009a), and whole brain (k = 6; e.g. Gutmann et al., 2018a; Wollseiffen et al., 2016b). Four studies reported increased frontal alpha asymmetry (e.g. Hicks et al., 2018; Woo et al., 2009), while three studies found no differences (e.g. Petruzzello & Tate, 1997). All studies observing increases in alpha peak and/or power reported large effect sizes ($d \ge 0.8$; $\eta_p^2 \ge .14$ [Cohen, 1988]), with the exception of Boutcher and Landers (1988), who reported a large effect for their

running task (non-runners: d = 1.64 and runners: d = 0.81), and a small effect for the nonexercise task (reading; non-runners and runners: d = 0.16 [see Table 2]).

Three studies found a decrease in alpha across the left frontal cortex (Woo et al., 2010), bilateral frontal cortex (for athletes with spinal cord injuries; Brümmer et al., 2011), and in the whole brain (Hottenrott et al., 2013). In addition, Ohmatsu et al. (2014) and Schneider et al. (2010a) reported a decrease in alpha-2 in the anterior cingulate cortex and left inferior temporal gyrus, respectively. All studies that observed a decrease in alpha reported large effect sizes, which ranged from d = 0.99 (Schneider et al., 2010a) to d =2.35 (Brümmer et al., 2011), and included η_p^2 = .62 (Woo et al., 2010; see Table 2). Seven studies reported no significant changes in alpha activity pre- vs. post-exercise in the left prefrontal cortex (Devilbiss et al., 2019), anterior region of the brain (Dishman et al., 2010), bilateral frontal and temporal cortices (Kubitz & Mott, 1996), bilateral frontal and parietal cortices (Petruzzello & Tate, 1997), and in the whole brain (k=3; e.g. Mierau et al., 2009).

Beta activity

Eleven studies reported an increase in beta activity across the left prefrontal cortex (k = 1; Devilbiss et al., 2019), right frontal cortex (k = 1; Contreras-Jordán et al., 2022), bilateral frontal and right central cortex (k = 1; Moraes et al., 2007), bilateral cingulate cortex (k= 1; Moraes et al., 2011), limbic lobe (k=2; Guimarães et al., 2015; Schneider et al., 2009b), bilateral parietal cortex (k = 3; e.g. Schneider et al., 2009b), central regions (k = 3) 1; Contreras-Jordán et al., 2022), posterior regions (k=1; Dishman et al., 2010), and whole brain (k = 2; Hilty et al., 2011; Spring et al., 2017). All studies observing an increase in beta activity that reported effect sizes, found these to be large (e.g. d = 1.16 [Brümmer et al., 2011]; d = 2.97 [Moraes et al., 2011]; $\eta_0^2 = .40$ [Spring et al., 2017]; see Table 2). Six studies reported a decrease in beta activity across the bilateral frontal cortex (Brümmer et al., 2011; Wollseiffen et al., 2016b), right frontal and temporal cortices (Schneider et al., 2009a), bilateral temporal cortex (Schneider et al., 2010a), and whole brain (Hottenrott et al., 2013; Mierau et al., 2009). All studies observing a decrease in beta activity that included effect sizes, reported large effects that ranged from d = 0.92 (Schneider et al., 2010a) to d = 2.12 (Brümmer et al., 2011), with two exceptions: Schneider et al. (2009a), who reported medium effects ($\eta_p^2 = .08$ and $\eta_p^2 = .07$ for beta-1 and beta-2, respectively), and Wollseiffen et al. (2016a) who reported a medium effect (η_p^2 = .07) for beta-1 and a small effect ($\eta_p^2 = .03$) for beta-2 (see Table 2). Three studies reported no significant changes in beta power across the bilateral prefrontal cortex (Wollseiffen et al., 2016a), bilateral frontal and temporal cortices (Kubitz & Mott, 1996), and in the whole brain (only for beta-2; Schneider et al., 2010a).

Delta activity

For delta activity, four studies reported an increase in the bilateral frontal cortex (Woo et al., 2009), frontal and central cortices (Mechau et al., 1998), limbic lobe (Schneider et al., 2010b), and in the whole brain (Schneider et al., 2010a), while Spring et al. (2017) reported a decrease across the whole brain. Two studies observing delta changes reported large effects of $\eta_p^2 = .24$ (Spring et al., 2017) and $\eta_p^2 = .58$ (Woo et al., 2009; see Table 2). Two studies reported no significant changes in delta activity (Devilbiss et al., 2019; Moraes et al., 2011).

Gamma activity

Two studies reported a reduction in gamma activity in the left prefrontal cortex (Devilbiss et al., 2019) and left cuneus (Schneider et al., 2010a). Three studies reported no significant changes for theta activity (e.g. Moraes et al., 2011), while four reported an increase after exercise in the bilateral frontal cortex (k = 2; Contreras-Jordán et al., 2022; Woo et al., 2009), temporal cortex (Schneider et al., 2010a) and whole brain (Spring et al., 2017). Among the studies that observed changes in gamma activity, only one (Schneider et al., 2010a) provided effect sizes, and these were large: d = 0.97 for the pre- vs. immediately post-exercise comparison and d = 1.67 for the pre- vs. post-15-min exercise comparison (see Table 2).

Theta activity

Three studies found a decrease in theta waves across the left prefrontal cortex (Devilbiss et al., 2019), central and parietal cortices (Fumoto et al., 2010), and in the whole brain (Hottenrott et al., 2013). Only one study reported effect sizes (Fumoto et al., 2010), and these were found to be large in relation to both central and parietal cortices (d = 1.86and d = 1.83, respectively). In addition, Contreras-Jordán et al. (2022) reported an increase in theta activity across the bilateral prefrontal cortex from pre- to post-exercise. One study reported no significant changes in theta activity (Büchel et al., 2021).

The overall quality of studies comparing pre- and post-exercise conditions was rated as moderate (M = 2.01, SD = 0.21; see Supplemental Material 1).

Studies taking during-exercise measures of EEG

Alpha activity

The most common effect found within studies investigating changes in cortical activity during exercise was an increase in alpha activity (see Table 3). More precisely, 13 studies reported an increase in alpha activity across the central and parietal cortices (k = 1; Fumoto et al., 2010 [only alpha-2]), left frontal cortex (k = 1; Enders et al., 2016b), bilateral frontal cortex (k = 3; e.g. Ludyga et al., 2017), bilateral frontal and parietal cortices (k = 3) 3; e.g. Bailey et al., 2008), bilateral frontal and temporal cortices (k = 1; Mott et al., 1995), insular cortex (k = 1; Hilty et al., 2011), bilateral parietal cortex (k = 1; Ludyga et al., 2016), parieto-occipital cortex (k = 1; Ciria et al., 2019), and in the whole brain (k = 2; Hottenrott et al., 2013; Mechau et al., 1998 [only alpha-1]). Four studies included effect sizes for alpha activity and these were all large, ranging from d = 1.60 (Hilty et al., 2011) to d = 1.97(Fumoto et al., 2010), and from $\eta_p^2 = .38$ for alpha-1 to $\eta_p^2 = .25$ for alpha-2 (Mechau et al., 1998) to $\eta_p^2 = .48$ for alpha-1 and $\eta_p^2 = .69$ for alpha-2, respectively (Bailey et al., 2008; see Table 3). Two studies found a decrease in alpha activity across the bilateral frontal and temporal cortices (Kubitz & Mott, 1996), and insular cortex (Hilty et al., 2011). Ciria et al. (2018) reported no significant alpha changes across the whole brain, and Fumoto et al. (2010) reported no significant changes in alpha-1 across central and parietal cortices.

Beta activity

Ten studies found an increase in beta activity across the left frontal cortex (k = 1; Enders et al., 2016b), bilateral frontal cortex (k=1; Nielsen et al., 2001), bilateral frontal and



parietal cortices (k = 2; Bailey et al., 2008; Ludyga et al., 2016), supplementary area and left parietal cortex (k = 1; Enders et al., 2016b), bilateral frontal and temporal cortices (k = 1; Kubitz & Mott, 1996), bilateral parietal cortex (k = 1; Ludyga et al., 2016), centro- and parieto-occipital regions (k = 2; Ciria et al., 2018, 2019), and in the whole brain (k = 2; Hottenrott et al., 2013; Mechau et al., 1998). Notably, Nielsen et al. (2001) reported that frontal beta activity increased during exercise but steadily declined from 2 min into the exercise bout. All reported effect sizes for beta activity were large, including d = 1.54 (Hilty et al., 2011), $\eta_p^2 = .75$ (Bailey et al., 2008), and $\eta_p^2 = .18$ (Mechau et al., 1998; see Table 3). Two studies reported no significant changes in beta activity (Fumoto et al., 2010; Mott et al., 1995).

Delta activity

Only three studies examined delta activity (Ciria et al., 2018; 2019; Mechau et al., 1998) and reported an increase across the whole brain. Among these, only Mechau et al. (1998) reported an effect size, which was large $(\eta_p^2 = .40)$.

Theta activity

Three studies reported that theta activity increased across the bilateral frontal and parietal cortices (Bailey et al., 2008), and in the whole brain (Hottenrott et al., 2013; Mechau et al., 1998), while one reported that it decreased across central and parietal cortices (Fumoto et al., 2010). All studies observing changes in theta activity that included effect sizes, reported large effect sizes. These ranged between d = 1.83 and d = 1.86 for parietal and central cortices, respectively (Fumoto et al., 2010). Studies that reported effect sizes using partial eta squared indicated a range between $\eta_p^2 = .43$ (Mechau et al., 1998) and $\eta_p^2 = .72$ (Bailey et al., 2008; see Table 3). Ciria et al. (2018) found no significant change in theta activity across the whole brain.

Gamma activity

Gwin and Ferris (2012) reported small-but-significant coherence between contralateral motor cortex EEG signals and lower-limb EMG in the gamma bands during exercise.

Study quality

The overall quality of studies taking during-exercise measures of EEG was rated as moderate (M = 2.02; SD = 0.21; see Supplemental Material 1).

Exercise intensity studies

Alpha activity

The most common finding observed among studies investigating the effects of different exercise intensities on cortical oscillations concerned an increase in alpha activity, regardless of intensity (see Table 4). Of the 33 studies examining brain oscillations during highintensity exercise, 25 reported increased alpha activity across the prefrontal cortex (k = 2; Devilbiss et al., 2019; Wollseiffen et al., 2016a), bilateral frontal cortex (k = 8; e.g. Kao et al., 2021), left frontal cortex (k = 1; Petruzzello & Landers, 1994), central cortex (k = 3; e.g. Ludyga et al., 2016), parietal cortex (k = 6; e.g. Schneider et al., 2009b), bilateral temporal

cortex (k = 3; e.g. Schneider et al., 2010a), parieto-occipital regions (k = 1; Ciria et al., 2019), centro-occipital regions (k = 1; Ciria et al., 2018), occipital regions (k = 1; Büchel et al., 2021), limbic regions (k = 3; e.g. Guimarães et al., 2015), and in the whole brain (k = 6; e.g. Ciria et al., 2019). Six studies reported a decrease in alpha activity across the left prefrontal cortex (k = 1; Devilbiss et al., 2019), bilateral frontal cortex (k = 3: e.g. Woo et al., 2010), posterior cortex (k = 1; Dishman et al., 2010), and parieto-occipital regions (k = 1; Schneider et al., 2009a). Two studies reported no change across the bilateral frontal and right central brain regions (Moraes et al., 2007), and in the whole brain (Mierau et al., 2009). Chaire et al. (2020) reported small effects for alpha during a delayed match-to-sample working memory task (d < 0.01) and a visual-attention task (d = 0.03), and Wollseiffen et al. (2016a) reported medium effects for alpha-1 ($\eta_p^2 = .07$). All other studies observing the effects of high-intensity exercise on alpha activity that included effect sizes, reported large effects. These ranged between d = 0.81 (Boutcher & Landers, 1988) and d = 6.11 (Bixby et al., 2001), as well as between $\eta_p^2 = .14$ for alpha-1 (Schneider et al., 2009a) and $\eta_p^2 = .22$ for alpha-2 (Wollseiffen et al., 2016a) and $\eta_p^2 = .48$ and $\eta_p^2 = .69$ for alpha-1 and alpha-2, respectively (Bailey et al., 2008; see Table 4).

Of the 12 studies examining brain activity during moderate-intensity exercise, six reported an increase in alpha activity across the prefrontal cortex (k = 1; Wollseiffen et al., 2016a), bilateral frontal cortex (k = 3; e.g. Nielsen et al., 2001), parietal cortex (k =3; e.g. Fumoto et al., 2010), central regions (k = 1; Fumoto et al., 2010), temporal cortex (k = 1; Kubitz & Mott, 1996), occipital cortex (k = 1; Schneider et al., 2009a), and in the whole brain (k = 1; Hottenrott et al., 2013). Four studies reported a decrease in alpha activity across the bilateral frontal (k = 3; e.g. Woo et al., 2010) and in the whole brain (k = 1; Hottenrott et al., 2013), while two studies reported no changes (k = 2; Gutmann)et al., 2015; Ludyga et al., 2017). With the exception of Wollseiffen et al. (2016a) who reported a medium effect for alpha-1 ($\eta_p^2 = .07$) as well as a large effect for alpha-2 (η_p^2 = .22), all studies investigating the effects of moderate-intensity exercise on alpha activity that included effect sizes, reported large effects. These ranged from from d = 1.67 (for alpha-2; Fumoto et al., 2010) to d = 6.11 (Bixby et al., 2001), as well as between $\eta_p^2 = .14$ for alpha-1 (Schneider et al., 2009a) and η_p^2 = .62 (Woo et al., 2010; see Table 4).

During low-intensity exercise, five studies reported an increase in alpha activity across the frontal cortex (k = 3; e.g. Hicks et al., 2018), parietal cortex (k = 1; Brümmer et al., 2011), centro-occipital regions (k = 1; Ciria et al., 2018), posterior cortex (k = 1; Dishman et al., 2010), and in the whole brain (k = 1; Ciria et al., 2018). Another five effects related to a decrease across the frontal cortex (k = 3; e.g. Kao et al., 2021), temporal cortices (k = 1; Kubitz & Mott, 1996), and the anterior cingulate gyrus (k = 1; Ohmatsu et al., 2014). In four instances, there were no reported changes (k = 1; Guimarães et al., 2015). Two studies exploring the effects of low-intensity exercise on alpha activity included effect sizes. Dishman et al. (2010) reported a large effect of $\eta_p^2 = .36$, while Brümmer et al. (2011) also reported large effects across all conditions (treadmill: d = 1.16; bicycle: d =2.12; arm crank: d = 1.49; isokinetic: d = 1.29; see Table 4).

Beta activity

The second most observed frequency band activity was that of beta. Of the 18 studies examining brain activity during high-intensity exercise, 13 reported an increase in beta frequency across the bilateral frontal cortex (k = 5; e.g. Bailey et al., 2008), central cortex (k = 3; e.g. Moraes et al., 2007), parietal cortex (k = 3; e.g. Enders et al., 2016b), parieto-occipital regions (k = 2; Ciria et al., 2018, 2019), the limbic regions (k = 3; e.g. Schneider et al., 2009b), temporal cortex (k = 1; Schneider et al., 2009b), and in the whole brain (k = 4; e.g. Mechau et al., 1998). Five studies showed a decrease across the frontal cortex (k = 2; Brümmer et al., 2011; Schneider et al., 2010a), parietal cortex (k = 2; Brümmer et al., 2011; Schneider et al., 2009a), temporal cortex (k = 1; Schneider et al., 2010a), posterior brain regions (k = 1; Dishman et al., 2010), and occipital cortex (k = 1; Schneider et al., 2009a). With the exception of Wollseiffen et al. (2016a), who reported a medium effect size for beta-1 ($\eta_p^2 = .07$) and a small effect for beta-2 ($\eta_p^2 = .03$), all studies exploring the effects of high-intensity exercise on beta activity reported large effect sizes. These ranged from d = 1.00 to d = 0.92 for beta-1 and beta-2, respectively, to d = 1.92 and d = 2.97 for beta-1 and beta-2, respectively (Moraes et al., 2011). Studies reporting partial eta squared indicated a range between $\eta_p^2 = .33$ and $\eta_p^2 = .14$ for beta-1 (Mechau et al., 1998) and beta-2 (Schneider et al., 2009a), respectively, to $\eta_p^2 = .76$ and $\eta_p^2 = .75$ for beta-1 and beta-2 respectively (Bailey et al., 2008).

Of the six studies examining brain activity during moderate-intensity exercise, five reported an increase in beta frequency across the bilateral frontal (k = 4; e.g. Nielsen et al., 2001), temporal cortex (k = 1; Kubitz & Mott, 1996), and in the whole brain (k = 1; Hottenrott et al., 2013). One study found a decrease in beta activity in the whole-brain (Hottenrott et al., 2013). Only one study (Wollseiffen et al., 2016a) that investigated the effects of moderate-intensity exercise on beta activity reported effect sizes; these were medium for beta-1 ($\eta_p^2 = .07$) and small for beta-2 ($\eta_p^2 = .03$). With reference to low-intensity exercise, only two studies observed an increase in beta activity across the frontal and parietal cortices (Brümmer et al., 2011), and in the whole-brain (Ciria et al., 2018). Only Brümmer et al. (2011) reported effect sizes, which were large for all activity conditions (treadmill: d = 1.16; bicycle: d = 2.12; arm crank: d = 1.49; isokinetic: d = 1.29). Three studies reported no changes (e.g. Ohmatsu et al., 2014).

Delta activity

With reference to high-intensity exercise, five studies reported an increase in delta activity across the left prefrontal cortex (k = 1; Devilbiss et al., 2019), frontal cortex (k = 1) = 2; Schneider et al., 2010a, 2010b), the centro-occipital regions (k = 1; Ciria et al., 2018), limbic regions (k = 1; Schneider et al., 2010b), temporal cortex (k = 1; Schneider et al., 2010a), and in the whole brain (k = 2; Ciria et al., 2018; Mechau et al., 1998). Of the two studies exploring effects of high-intensity exercise on delta activity that reported effect sizes, both found large effect sizes. Schneider et al. (2010a) reported d = 1.83 for the pre- vs. immediately post-exercise comparison, and d = 1.77 for the pre- vs. post-15-min exercise comparison, while Mechau et al. (1998) reported $\eta_0^2 = .40$ (see Table 4). Moderate-intensity exercise was found to engender an increase in delta activity in one instance across the bilateral frontal region of the brain (Woo et al., 2009), and a decrease in another instance (Spring et al., 2017). Both studies reported large effect sizes for delta ($\eta_p^2 = .24$; Spring et al., 2017; $\eta_p^2 = .41$; Woo et al., 2009). Low-intensity exercise did not appear to have any meaningful effect on delta activity (Ohmatsu et al., 2014).

Gamma activity

Three effects pertaining to high-intensity exercise on gamma activity were observed. One study reported an increase across the frontal and parietal brain regions (Enders et al., 2016b), while the other two reported a decrease across the left prefrontal cortex (Devilbiss et al., 2019), and the left middle frontal gyrus and temporal cortex (Schneider et al., 2010a). Notably, gamma activity was not investigated in studies using moderate or low-intensity exercise. Of the studies that did investigate changes in gamma activity, only one reported effect sizes (Schneider et al., 2010a), and these were large for both the pre- vs. immediately post-exercise comparison (d = 0.97) and the pre- vs. post-15min exercise comparison (d = 1.67; see Table 4).

Theta activity

Theta activity was observed to increase with high-intensity exercise in seven studies across the frontal cortex (k = 3; e.g. Bailey et al., 2008), central regions (k = 1; Bailey et al., 2008), temporal cortex (k = 1; Schneider et al., 2010a), centro-occipital cortex (k = 1) 2; Ciria et al., 2018, 2019), and in the whole brain (k = 3; Ciria et al., 2018; 2019; Mechau et al., 1998). A decrease was observed in two instances, across the left prefontal cortex (Devilbiss et al., 2019) and posterior brain region (Dishman et al., 2010). Two studies observed no changes in theta activity following high-intensity exercise. One of these took measures across the frontal area (Chaire et al., 2020), and another from the whole brain (Büchel et al., 2021). Studies that explored the effects of high-intensity exercise on theta activity and reported effect sizes, showed large effects in all instances. Moraes et al. (2011) reported effect sizes of d = 1.66 and d = 2.47 for young and elderly groups, respectively, while Bailey et al. (2008) reported an effect size of η_p^2 = .72. Mechau et al. (1998) reported an effect of η_p^2 = .44 (see Table 4).

Effects on theta activity pertaining to moderate-intensity exercise included a bilateral frontal cortex increase (Woo et al., 2009), a whole-brain decrease (Hottenrott et al., 2013) and, in one instance, no changes (Chaire et al., 2020). Only Woo et al. (2009) reported an effect size, and this was large ($\eta_p^2 = .44$). One study reported an increase in theta activity, due to low-intensity exercise, across the centro-occipital region and in the whole brain (Ciria et al., 2018), while the remaining studies observed no such changes (Chaire et al., 2020; Ohmatsu et al., 2014).

Study quality

The overall quality of studies exploring exercise intensity was rated as moderate (M = 2.01, SD = 0.20; see Supplemental Material 1).

Exercise vs. no exercise studies

Alpha activity

Among the six studies investigating changes in cortical activity for exercise vs. no-exercise group (see Table 5), two found an increase in alpha activity for the exercise group in relation to the frontal cortex (Kao et al., 2020) and posterior regions (Dishman et al., 2010). Kubitz and Landers (1993) reported lower alpha activity in the exercise group for the bilateral frontal cortex, as well as medium effect sizes for left alpha (d = 0.45) and



small effects for right alpha (d = 0.18). Three studies did not find significant differences for exercise vs. no-exercise groups across the frontal and temporal cortices (Kubitz & Landers, 1993), and posterior and occipital cortices (Kao et al., 2020).

Beta activity

Two studies reported greater beta activity in the bilateral frontal cortex (Kubitz & Mott, 1996) and posterior regions of the brain (beta-2; Dishman et al., 2010) for the exercise group. One other study reported no significant differences across the bilateral frontal cortex (Kubitz & Landers, 1993), along with a medium effect size for left beta (d = 0.46) and a small effect for right beta (d = 0.02) in the exercise group, in comparison to small effect sizes for left beta (d = 0.16) and right beta (d < 0.01) in the non-exercise group. Notably, a further study did not report the brain region of interest (Severtsen & Bruya, 1986).

Theta activity

Dishman et al. (2010) reported greater theta activity for the exercise group in relation to the posterior regions of the brain, while Kao et al. (2020) found no significant differences.

Study quality

The overall quality of studies that compared exercise with no exercise was rated as moderate (M = 2.05, SD = 0.21; see Supplemental Material 1).

Discussion

This systematic review was conducted with the aim of investigating the effects of exercise on EEG-recorded neural oscillatory activity. After the screening and selection process, 47 studies met the inclusion criteria for the synthesis that ensued. The results showed that, in general, studies were conducted among young and healthy adults ($M_{\text{age}} = 27.3$), and employed an acute exercise intervention. It also emerged that studies were generally small in scope, as the average number of participants was only 24 (see Table 1). The most commonly used EEG analysis methodology was frequency analysis (n = 35), followed by (s)LORETA (n = 8).

Changes in alpha frequency

Thirty-five studies (pre- vs. post-exercise = 24; pre-/post- vs. during-exercise = 11) found exercise to cause an increase in alpha-band activity, while four reported a decrease (see Table 2 and Table 3). The alpha activity pertaining to the effect of exercise was located mainly across the frontal areas (k = 18; e.g. Enders et al., 2016b; Gutmann et al., 2018a), with left lateralisation (k = 3; e.g. Petruzzello & Landers, 1994), and central regions of the brain (k = 12; e.g. Bailey et al., 2008; Fumoto et al., 2010). Over the last two decades, experimental evidence has suggested that physical exercise improves neuropsychological performance outcomes that include memory and executive functioning (Blomstrand & Engvall, 2021; Smith et al., 2010). Thus, the notable frontal alpha activity found in the present review might be reflective of the execution of cognitive functions

(e.g. pace judgement, attentional focus, and recovery strategies) during and following exercise. It should be noted that such functions can also be enhanced by alpha activity (Escolano et al., 2014).

Enhanced alpha activity has been associated with a decrease in neuro-connectivity from somatosensory afferents (Gundlach et al., 2020). More specifically, alpha waves play a central role in regulating the timing of information processing within the cerebral cortex (see Klimesch et al., 2007). This can partially explain the increase in alpha activity observed in this review across the central sites of the brain, as these sites overlay regions of the sensorimotor cortex that receive afferent feedback during exercise (Crabbe & Dishman, 2004). Another possible reason for the increase in alpha activity concerns the cortical inhibition caused by brainstem and subcortical activation (Koriath et al., 1987; Lacey & Lacey, 1978). This might have a direct bearing on cardiovascular regulation during exercise. Nonetheless, only two studies reported enhanced alpha activity both during and post-exercise across the limbic lobe (Guimarães et al., 2015; Hilty et al., 2011).

Although an overall increase in alpha activity was observed in the selected studies, most focused on just one or two brain regions, meaning that oscillatory alpha activity in other regions would have been missed. Some studies (e.g. Hottenrott et al., 2013; Mierau et al., 2009) did not identify the cerebral regions of interest and examined the electrical activity of the brain as a whole. Such a generalised approach can lead to inconsistent results, given that detailed analysis of individual brain regions is not conducted. Nonetheless, the fact that most studies reported an increase in alpha activity may relate to the notion that such activity is present during processes that are germane to exercise, such as attention (Saalmann et al., 2012) and the delay of afferent feedback (Klimesch et al., 2007).

Among the seven studies reporting a decrease in alpha activity, two reported a decrease only in the alpha-2 range (Ohmatsu et al., 2014; Schneider et al., 2010a). Notably, five of these studies did not differentiate between alpha-1 and alpha-2 ranges (e.g. Hilty et al., 2011; Woo et al., 2010). Thus, it is possible that only alpha-2 frequency decreases during and after exercise, highlighting the importance associated with differentiating between alpha-1 and alpha-2 ranges. A decrease in alpha-2 would be consistent with the transient hypo-frontality hypothesis (Dietrich, 2006) and the dual-mode theory of exercise-related affect (Ekkekakis et al., 2005). These theoretical frameworks propose that acute exercise leads to a redistribution of brain activity – towards those areas responsible for preparing and performing motor commands (e.g. motor and sensory cortices) due to limited cortical resources.

Changes in beta frequency

Oscillations in the beta frequency band were, primarily, found to increase due to exercise, as reported in 20 studies (pre- vs. post-exercise = 10; pre-/post- vs. during-exercise = 10). Only four studies reported a decrease (see Table 2 and Table 3). This activity was mainly identified across the central and parietal brain regions (k = 10; e.g. Brümmer et al., 2011), and limbic lobe (k = 3; e.g. Guimarães et al., 2015). Beta waves across the sensorimotor areas are usually associated with movement planning and production (Pogosyan et al., 2009). More specifically, the peripheral sensory sampling hypothesis posits that beta activity moderates the operation of sensory feedback loops to update the motor

commands (Chung et al., 2017). In the present review, four studies reported a decrease in beta frequency pre- vs. post-exercise, while none that compared pre-/post- vs. duringexercise reported such a reduction. This finding supports the proposition that enhanced beta activity is associated with the production of movement per se and occurs only during task execution (Jenkinson & Brown, 2011).

EEG data have shown that emotional processing increases beta activity in the limbic structures (Cannon et al., 2005). Specifically, unpleasant audio-visual stimuli have been found to induce cerebral electrical activity in the beta frequency range (Hayashi et al., 2009). In the present review, the enhanced beta activity reported during and post-exercise across the limbic lobe might be reflective of affective responses to exercise (Hall et al., 2007). This is corroborated by the fact that the three studies reporting increased beta activity in this region employed a high-intensity exercise protocol (e.g. Guimarães et al., 2015).

There is much work in affective science to show marked affective decline at exercise intensities that exceed 70% VO2_{max} (e.g. Box et al., 2020; Ekkekakis et al., 2005). A notable limitation of the present suite of studies is that affective responses to exercise were not measured. We would predict that high levels of beta activity would be associated with subjective displeasure during exercise (i.e. low scores for affective valence).

Similar to alpha activity, some studies calculated beta power as a mean across all electrodes, and reported any activity occurred within a range of 12.5-35 Hz as beta activity (e.g. Mierau et al., 2009; Schneider et al., 2009b). By considering beta activity to be any activity within such a large range, such studies fail to consider differences between beta-1 and beta-2 frequencies that could help explain between-group differences. While beta-1, or low beta waves (12-15 Hz), are mainly associated with focused concentration, beta-2, or mid-range beta waves (15-20 Hz), are linked to increases in energy and performance (Abhang et al., 2016). Accordingly, calculating beta power as a mean across all electrodes can lead to inaccurate results.

Inconsistent results for other frequency bands

It was observed in six studies that delta activity increased (pre- vs. post-exercise = 4; pre-/ post- vs. during-exercise = 2; e.g. Ciria et al., 2019; Schneider et al., 2010b) and it decreased in one study pre- to post-exercise (Spring et al., 2017; see Table 2 and Table 3). There was no explanation offered by Spring et al. (2017) for the decrease, which perhaps overlooks a hypothesis offered by Hatfield (1991) that cortical activity reaches a point at which an inhibitory mechanism is activated in the brainstem. This mechanism is believed to then influence the reticular formation in a way that reduces the transmission of somatic afferents to the cortex, thereby reducing cortical activity. Another possible explanation for the post-exercise decreases in delta activity has been advanced by Lacey and Lacey (1978). Specifically, the notion that brain activation decreases during exercise due to neuro-regulatory feedback mechanisms that pertain to communication between the heart and brain.

Schneider et al. (2010a) asserted that the delta activity increases they observed were reflective of changes in cortical activity. The increases could be due to the oscillatory after-effects of running or artefacts stemming from the cardiovascular system. Conversely, Mechau et al. (1998) suggested the increases in delta activity are associated with the

predominant involvement of the motor cortex in the performance of running. The present discussion seeks to reflect the variety of reasons put forward in regard to increases in delta activity as a consequence of exercise engagement (e.g. Mechau et al., 1998; Schneider et al., 2010b).

Theta activity was seen to increase in seven studies (pre- vs. post-exercise = 4; pre-/ post- vs. during-exercise = 3; e.g. Bailey et al., 2008; Spring et al., 2017) and to decrease pre- vs. post-exercise in three (e.g. Devilbiss et al., 2019). In addition, five studies reported no significant changes in theta activity (e.g. Ciria et al., 2018; Moraes et al., 2011; see Table 2 and Table 3). It is important to note, however, that some studies observed theta activity during the execution of cognitive tasks (e.g. Chaire et al., 2020). Cognitive activity may have influenced results, as elevated theta activity has been observed in executive cognitive function tasks, such as those that involve attention and working memory (Arski et al., 2021; Sirota et al., 2008).

Decreases in theta activity have been suggested to be indicative of impaired cognitive performance immediately after exercise, as well as the absence of relaxation (Devilbiss et al., 2019; Lambourne & Tomporowski, 2010). This means that contrasting findings may also be a consequence of the difference in timing of EEG recordings (i.e. during, immediately after exercise, or 15-30 min later). Thus, careful attention needs to be given to the methodological heterogeneities evident in the field of exercise science when interpreting the patterns of brain activity observed during exercise-related tasks.

To date, only the review of Gramkow et al. (2020) has synthesised results pertaining to gamma activity in the domain of exercise and physical activity. In so doing, these authors exposed how limited the knowledge base is in regard to this frequency band. From among the 47 studies included in the present review, only five examined gamma activity (see Table 2 and Table 3). Gwin and Ferris (2012) explored gamma-range coherence and the other three studies reported contrasting results; specifically, an increase in gamma activity during exercise (Devilbiss et al., 2019; Enders et al., 2016b), and both an increase (Contreras-Jordán et al., 2022) and a decrease (Schneider et al., 2010a) from pre- to postexercise.

It might be argued that increases in gamma activity during exercise result from the increased arousal that is germane to exercise performance (Abhang et al., 2016; Lambourne & Tomporowski, 2010). Contrastingly, post-exercise decreases in gamma activity have been linked to a decrease in cortical arousal (Schneider et al., 2010a). However, due to the limited number of studies observing gamma activity, it is not possible to arrive at firm conclusions regarding the effects of exercise on oscillatory gamma frequency-band activity at the present time.

It is noteworthy that the average quality of the studies included in the present systematic review was rated as moderate (see Supplemental Material 1). Given that participants cannot be blinded to the presence or absence of an exercise intervention, the quality rating of studies used is limited (i.e. double-blind or placebo-controlled designs are not used in this literature; e.g. Renjith, 2017; Sedlmeier et al., 2012). Additionally, with the exception of three studies (Ciria et al., 2018; Dishman et al., 2010; Hilty et al., 2011), the articles included in the present review failed to control for volume conduction, thus limiting the interpretation of EEG-recorded regional effects produced by local neurons (Parr et al., 2021). This could provide a meaningful explanation for the inconsistent results found for some frequency bands (i.e. delta, theta, gamma). Moreover, the study



quality could have impacted our results, as some of the trends are predicated on weak studies (see Supplemental Material 1).

Exercise intensity

We found that alpha, beta, and delta activity mostly increased as a consequence of highintensity exercise, when compared to both moderate and low-intensity exercise. Previous research has found that heat stress caused by exhaustive exercise can lead to an increase in cortical activity (Nakata et al., 2016; Shibasaki et al., 2017), which might explain, in part, the relationship between exercise intensity and alpha, beta, and delta activity. Another possible explanation for the increase observed in beta activity, in particular at the fronto-central regions, is its association with higher levels of psychomotor arousal (Nielsen & Nybo, 2003) and increased cortical activation due to voluntary movements (Halliday et al., 1998; Moraes et al., 2007). An increase in theta activity has also been linked to the processing of novel information (Demiralp et al., 2001; Pesonen et al., 2007), thus the observed theta findings may relate to the control and regulation of attentional resources (Sauseng et al., 2010).

It is difficult to be certain of the exact cause of effects of high-intensity exercise on cortical activity due to the physiological effects that also manifest (e.g. elevated body temperature and blood circulation), which in turn may influence oscillatory activity. However, effects of moderate-intensity exercise are less likely to be affected by such factors, as, for example, body temperature is not elevated to the same degree (Takeda & Okazaki, 2018). Results from moderate-intensity exercise showed the most common finding to be an increase in alpha and beta activity across multiple brain regions (e.g. frontal, parietal, occipital, whole brain). This can be attributed to the fact that alpha-band activity is related to wakefulness (Cantero et al., 2002), while beta activity is essential to maintaining exercise at a steady state (Plattner et al., 2014).

When analysing the effects caused by low-intensity exercise on cortical activity, no meaningful patterns emerged, as the most common effect observed was that of no changes in oscillatory bands, except alpha. The effects of low-intensity exercise on alpha-band activity included increases and decreases as well as no changes. Nonetheless, no effect was seen to stand out, as there was an increase in five studies (e.g. Brümmer et al., 2011), a decrease in five studies (e.g. Kao et al., 2020), and no changes in five (e.g. Gutmann et al., 2018b). Similar to moderate-intensity exercise studies, those investigating low-intensity exercise focused primarily on alpha-band activity, thus limiting discussion in regard to other oscillatory bands.

Findings emanating from high-quality studies

Focusing exclusively on the high-quality studies based on QATQS ratings (i.e. M < 2.00), findings, on the whole, mirror those evident in the studies of moderate quality (i.e. M =2.00-3.00; see Supplemental Material 1). There are, however, a few notable exceptions, albeit these are of a minor order. First, higher-quality studies tended to focus on the full range of brainwaves as well as differentiating between alpha-1 and alpha-2 (e.g. Büchel et al., 2021; Gutmann et al., 2018a; 2018b). Second, along similar lines, the higher-quality studies generally went beyond examining only frontal brain regions,

thus providing a more holistic representation of brainwave activity (e.g. Hilty et al., 2011; Hottenrott et al., 2013). Third, with the exception of eight studies (e.g. Guimarães et al., 2015; Ludyga et al., 2016), the higher-quality studies provided sufficient statistical detail to facilitate calculation of effect sizes (e.g. Contreras-Jordán et al., 2022; Wollseiffen et al., 2016a; 2016b). More specifically, while eight out of 20 (40%) of the higher-quality studies did not provide sufficient information for such calculations, almost half of lower-quality studies (13 out of 27; 48.2%) lacked such statistical detail (e.g. Ciria et al., 2018; 2019).

From among the 20 high-quality studies, the most common effect of exercise on oscillatory activity was an increase in alpha activity from pre- to post-exercise (k = 15; e.g. Büchel et al., 2021; Contreras-Jordán et al., 2022) and from pre- to during exercise (k = 2; Hottenrott et al., 2013; Ludyga et al., 2016). Interestingly, this increase was observed across the frontal area of the brain in six studies (e.g. Contreras-Jordán et al., 2022; Hicks et al., 2018) and the whole brain in six studies (e.g. Gutmann et al., 2015; Hilty et al., 2011). In the five remaining studies, the increase in alpha frequency was reported across various brain areas without any clear trend (i.e. parietal and occipital cortices [k = 2], posterior cortex [k=1], limbic lobe [k=1], and anterior and posterior cingulate gyrus [k=1]). It is noteworthy that only one high-quality study observed a decrease in the frontal brain region (Kubitz & Mott, 1996), which serves to question the veracity of the analogous decrease reported in six lower-quality studies (e.g. Hilty et al., 2011; Schneider et al., 2010a). With respect to other frequency bands, findings from high-quality studies were equivocal in nature; similar to those with a QAQTS mean rating of ≥ 2.0 .

Considerations for use of EEG in exercise science

The inconsistent findings found in the present review for most of the EEG frequency ranges can also be attributed to the use of a variety of EEG devices. Given that the accuracy of EEG recordings increases in accord with the number of electrodes used (Lau et al., 2012), differences in this number can explain some of the differences reported in the present systematic review. While Engchuan et al. (2019) used a commercially available lightweight EEG device that required the application of only one electrode, Schneider et al. (2010a) used a 64-channel portable EEG device. Thus, researchers need to consider the EEG device that they use and the number of electrodes most suitable in testing their research hypotheses.

When selecting the most suitable technique for the measurement of brain activity, aspects such as temporal and spatial resolution must be considered (Liu et al., 2006). EEG may be a suitable tool in identifying cognitive processes that arise over brief time periods, such as observation and shifts in attention (e.g. Luck et al., 2000; Vecchiato et al., 2010). It is not, however, considered the most suitable technique for detecting activity in the deeper areas of the brain, such as the thalamus or the posterior cingulate cortex (Bigliassi et al., 2021). Instead, EEG is recommended for signals that originate from more peripheral areas of the brain such as the prefrontal cortex (Darvas et al., 2004; Dickter & Kieffaber, 2013).

EEG is considered to provide excellent temporal resolution but its spatial resolution is limited (Britton et al., 2016). This pertains to a mathematical issue known as the inverse problem, which entails the prediction of exact brain activity locations through surface

electrodes placed on the scalp (Grech et al., 2008; Purves et al., 2008). Even if this limitation can be countered by the use of source reconstruction analysis that estimates the brain activation sources (see Luck, 2014), researchers might prefer brain-imaging methods that offer higher spatial resolution (e.g. functional near-infrared spectroscopy; Leff et al., 2011).

It is expected that different forms of physical exercise and different intensities will lead to different outcomes in terms of electrical activity in the brain (Gramkow et al., 2020). This is because each exercise type involves specific variances related to sensorimotor execution, cognition, and functional neural networks. These variances serve to activate different parts of the brain and different oscillatory bands. For instance, Brümmer et al. (2011) found that exercise leads to a significant increase in alpha activity. While this change occurred under four exercise modes (i.e. treadmill running, indoor cycling, arm crank, and isokinetic exercises) during moderate-intensity exercise (50% maximum capacity), a significant increase in alpha activity was only observed in the isokinetic exercise protocol when participants worked at a high-intensity (80% maximum capacity). Furthermore, a significant increase in beta activity was only observed during the bicycle exercise when the intensity was moderate, and beta activity was seen to significantly decrease after high-intensity treadmill running (Brümmer et al., 2011). Notably, it has been suggested that the most significant alterations in cortical activity occur when the individual can self-select their exercise intensity, rather than use heart-rate limits to determine intensity (Schneider et al., 2009b). Future research should, therefore, take into consideration the variability that different exercise modes and intensities can elicit in brain activity; this will avoid the erroneous conglomeration of different outcomes.

Physically active young adults have shown higher activity of neural oscillations at 22-34 Hz when compared to physically inactive controls, thus implying that higher aerobic fitness levels are associated with enhanced top-down cognitive control regulation (Kamijo et al., 2010; Kamijo & Takeda, 2010). Additionally, participants with higher levels of aerobic fitness have been found to achieve faster reaction times and superior variation of oscillatory theta and beta power during a cognitive task. These findings further support the notion that superior aerobic fitness levels are associated with greater attentional control in regard to visuo-spatial processing, shown through greater motor preparation and upregulation of attentional processing (Wang et al., 2015). Thus, participants' fitness level should be reported in future studies to facilitate the interpretation of findings.

Strengths and limitations

The present review is subject to a number of limitations and has served to illustrate some of the weaknesses in this body of literature. Firstly, the average number of participants in the studies included in this review was 22. Such a low sample size can detrimentally affect statistical analyses and interpretation of results; in particular, due to false-positives and over-estimation of the magnitude of an association (Hackshaw, 2008). Secondly, given that most studies conducting multiple tests failed to adjust for multiple comparisons (i.e. through Bonferroni adjustment), there is a risk of erroneous inferences, which calls into question the reliability of the findings presented in this review (Chen et al., 2017). Future research should, therefore, aim to design studies that are adequately powered and that make suitable adjustment for multiple comparisons.

This review contains a qualitative synthesis of results, given that we assumed that studies would exhibit large heterogeneity, based on previous reviews on the subject (Crabbe & Dishman, 2004; Gramkow et al., 2020). Although it could be argued that a guantitative synthesis might provide more exacting results, this would necessitate the exclusion of many studies that are incompatible with this approach. By extension, important data would be excluded and the generalisability of findings would be limited. Also, performing a meta-analysis when the differences among studies are so stark, as was the case in the present review, would mean that results are combined in a somewhat meaningless manner, as suggested by Gopalakrishnan and Ganeshkumar (2013).

This review offers a quantitative synthesis to some extent, through the analysis of effect sizes that are displayed in Tables 1-5. Although not all studies provided the detail necessary to facilitate calculation of effect sizes, the review showed that most studies observed oscillatory changes of practical significance, as illustrated through the majority of effect sizes being large (cf. Bhandari, 2021). Future researchers might consider a more complex approach that employs both quantitative and qualitative analytical methods in order to optimise reliability and generalisability (Harden, 2010). There is also a need to consider the relevance of items pertaining to blinding (e.g. item 4 in the QATQS) for experiments wherein blinding of conditions is very difficult or impossible.

This review aimed to include all studies that took EEG measurements before, during, and after exercise-related interventions. Previous reviews on the subject of exercise and brain activity have had other foci, such as the effects of exercise on mood states (Lattari et al., 2014), the use of the event-related potentials technique (Rahman et al., 2019), and the use of studies that could be evaluated by meta-analytic methods (Crabbe & Dishman, 2004). The review closest in aim to this systematic review is that of Gramkow et al. (2020), yet they did not calculate effect sizes given that they adopted a qualitative approach. Moreover, they grouped healthy and clinical populations in part of their analysis. This makes it challenging to distinguish changes in cerebral electrical activity brought by facets of exercise and those that might be accounted for by psychological or physical pathologies.

It is important to note that although we have synthesised effects according to four main categories, there were various limitations to the categorisation of these studies due to the variability among them. For example, although some studies used biological parameters such as $\dot{V}O_{2max}$ to measure exercise intensity, others used age predicted HR_{max}, which has been shown to have low accuracy (Shookster et al., 2020). Also, some studies used volitional exhaustion but failed to account for the physiological limits/ fitness level of individuals, which can result in significant variance in terms of the actual intensity of exercise performed (Edvardsen et al., 2014). Future studies might assess relevant aspects of fitness (aerobic capacity) and report them.

Many of the studies explored in the present review failed to account for gender-dependent factors that can perpetuate differences in neural activity that would, ultimately, limit the accuracy and generalisability of findings (Cantillo-Negrete et al., 2016). For instance, Sheel et al. (2016) found that, even when matched for lung size, women's conducting airways are smaller than men's, which could lead to a significant difference in ventilatory resistance and an associated difference in neural responses (Guyenet & Bayliss, 2015).

Moreover, age-related differences such as reduced muscle mass and strength in older participants were not considered by many studies that included a broad age range (Suryadinata et al., 2020). It is also important to note that, while exercise took place indoors for most studies, three studies examined exercise in outdoor settings, which could have had a bearing on cardiovascular and metabolic parameters that, in turn, led to differences in oscillatory activity (Li et al., 2011). Accordingly, there are several factors that future studies should take into consideration.

The present conclusions do not concur with those reached by Crabbe and Dishman (2004), who found an overall increase of activity in all frequency bands due to exercise. When analysing and considering all available data, the outcomes of the present review bear some similarity to those reported by Gramkow et al. (2020). These authors also found a tendency for increases in alpha-band activity. Differences between the two studies may have resulted from differences in the process of study selection, as well as the inclusion of multiple studies that have been published over the intervening 2 years or were not included by Gramkow et al. (k = 6).

Conclusions

Research on the effects of exercise on cortical oscillatory activity recorded by EEG is growing rapidly. Today, EEG can be applied in settings wherein participants perform whole-body movements. This has greatly increased the number of EEG studies that explore brain activity in the field of exercise science. This systematic review was conducted with the aim to enhance knowledge regarding the effects of exercise on EEGrecorded cortical oscillatory activity. Following a review of 47 studies, results showed mostly inconsistent outcomes - even in the 20 high-quality studies - except for an increase in alpha and beta frequency-band activity due to exercise. Albeit this finding is supported by previous reviews, the qualitative synthesis showed that many of the included studies (27) were of moderate quality, therefore somewhat limiting the conclusions that can be drawn. In order to increase reliability and generalisability, future research should not only consider more robust designs, but also the recruitment of larger samples.

Notes

- 1. One component was removed from Parr et al.'s (2021) original 12 components, namely 'secondary measures of verbal and conscious processing' (p. 8), as this was not relevant to the present review.
- 2. This is a slight modification of Parr et al.'s (2021) 'alpha definition' (p. 7) given that all EEG frequency bands are of interest in the present review.
- 3. The review included one study comparing healthy adults with hand cyclists (Brümmer et al., 2011), but otherwise excluded studies in which participants had medical conditions, diseases or disorders.

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