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Concentric versus eccentric cycling at equal power output or effort perception: Neuromuscular alterations and muscle pain

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This study aimed to compare neuromuscular alterations and perceptions of effort and muscle pain induced by concentric and eccentric cycling performed at the same power output or effort perception. Fifteen participants completed three 30-min sessions: one in concentric at 60% peak power output (CON) and two in eccentric, at the same power output (ECC_{POWER}) or same perceived effort (ECC_{EFFORT}). Muscle pain, perception of effort, oxygen uptake as well as rectus femoris and vastus lateralis electromyographic activities were collected when pedaling. The knee extensors maximal voluntary contraction (MVC) torque, the torque evoked by double stimulations at 100 Hz and 10 Hz (Dt100; Dt10), and the voluntary activation level (VAL) were evaluated before and after exercise. Power output was higher in ECC_{EFFORT} than CON (89.1 ± 23.3% peak power). Muscle pain and effort perception were greater in CON than ECC_{POWER} ($p < 0.03$) while muscle pain was similar in CON and ECC_{EFFORT} ($p > 0.43$). MVC torque, Dt100, and VAL dropped in all conditions ($p < 0.04$). MVC torque ($p < 0.001$) and the Dt10/ Dt100 ratio declined further in ECC_{EFFORT} ($p < 0.001$). Eccentric cycling perceived as difficult as concentric cycling caused similar muscle pain but more MVC torque decrease. A given power output induced lower perceptions of pain and effort in eccentric than in concentric yet similar MVC torque decline. While neural impairments were similar in all conditions, eccentric cycling seemed to alter excitation-contraction coupling. Clinicians should thus be cautious when setting eccentric cycling intensity based on effort perception.

KEYWORDS
excitation-contraction coupling, maximal voluntary contraction, performance fatigability, voluntary activation level

1 | INTRODUCTION

Eccentric contractions (ie, active lengthening of the muscle) require less oxygen uptake than concentric contractions performed at same power output.[1] For this reason, eccentric cycle ergometers, on which patients resist the pedals driven backward by a motor, have been developed. Locomotor exercises (eg, cycling or running) differ from single-joint exercises because they require a more complex coordination and involve more muscle mass, affecting individuals' fatigability.[2] Among locomotor exercises, eccentric cycling differs from downhill running because it encompasses no plyometric contraction; it is purely eccentric.[3] Therefore, physiological and perceptual responses to eccentric cycling deserve to be probed in addition to responses to other eccentric exercises.

An 8-week conventional cycling (ie, concentric) training program was reported to improve peak oxygen uptake more than a power-matched eccentric cycling program, yet both increased lower limb maximal voluntary isometric (MVC) torque.[4] On the contrary, after a 12-week training program at the same oxygen uptake, eccentric cycling improved body composition (ie, increase in muscle mass and decrease in fat mass) and MVC torque to a greater extent than concentric cycling.[5] Hence, eccentric cycling has been increasingly used in patients suffering from heart or pulmonary diseases,[1] in order to diminish the stress on cardio-vascular organs during rehabilitation. It could even be efficient to counteract neurodegeneration.[6]

However, these benefits do not guarantee that patients are willing to engage in eccentric cycling exercise that is part of a rehabilitation program. Their adherence to exercise prescription is impaired by fatigue, defined as "a disabling symptom" that impedes physical and cognitive function.[7] Fatigue includes performance fatigability, that is an objective decrease in performance, and the perception of fatigability. The latter is influenced by a high perception of effort and muscle pain (or soreness), which limit people's engagement in regular physical activity, undermining their health in the long run.[8] In addition, an exercise that objectively affects performance (eg, decrease in MVC torque) leads to a greater perception of effort in a subsequent bout[9] and hinders the ability to carry out daily activities, which can affect the willingness to engage in exercise again. As a matter of fact, there is a need to understand performance fatigability and related perceptions in response to eccentric cycling.

Perceptual responses to eccentric cycling seem peculiar and remain poorly understood.[10] Particularly, eccentric cycling is perceived easier[4] and induces a greater cognitive load than concentric cycling at the same power output.[11] In addition, the repetition of lengthening contractions during eccentric cycling often causes muscle damage in unaccustomed individuals.[12] Muscle damage refers to histological (eg, disruption of fibers) and systemic changes (eg, increased blood creatine kinase content), and associated symptoms (eg, delayed-onset muscle soreness and MVC torque loss) lasting several days.[13] Nevertheless, muscle pain is reported minimal when progressively increasing eccentric cycling intensity throughout a training program.[14] As it is feasible to calibrate eccentric cycling intensity based on patients' perception of effort[15] or delayed-onset muscle soreness during previous exercise sessions,[14] these inexpensive and easy-to-monitor responses should be investigated further. Notably, muscle pain was of similar intensity during concentric and eccentric cycling[16] but has never been investigated during a fatiguing eccentric cycling exercise. It is thus unknown whether the intensity of perceptions of effort and muscle pain evolve differently throughout eccentric cycling, such as shown in conventional cycling at a given power output[17] or clamped perception of effort.[18]

Although perceived easier than conventional cycling at the same power output, eccentric cycling was reported to induce a decline in MVC torque of similar magnitude[19]—in participants familiar with eccentric cycling. It is uncertain, however, whether the magnitude and etiology (neural and/or muscular) of MVC decline would differ if eccentric and concentric cycling are matched for perception of effort.

This study aimed to compare acute responses to concentric and eccentric cycling matched for either power output or perception of effort in terms of (i) perceptions of effort and muscle pain during the exercise and (ii) changes in MVC torque and neuromuscular function of the knee extensor muscles, following the exercises. Physiological correlates of perception of effort (ie, activity of the knee extensor muscles[20] and respiratory frequency[21]) were also analyzed.

In accordance with the literature, we expected perception of effort to be lower during eccentric than concentric cycling at the same power output[10] and, therefore, power output to be greater in eccentric when the exercises are matched for perception of effort. The intensity of muscle pain while pedaling was uncertain because it may be caused by distinct factors[22] in the two modalities, such as a greater metabolic rate during concentric cycling, leading to more muscle acidity,[23] or more tissue deformation (stretches) during eccentric cycling. Concerning neuromuscular alterations, we based our hypotheses on Garnier et al. (2019),[24] who reported a decrease in torque evoked by motor nerve stimulation immediately after 45 min of downhill (mostly eccentric) but not uphill (mostly concentric) running at the same speed (ie, similar power output), along with no significant difference in MVC torque loss and maximal voluntary muscle activation. We expected similar outcomes when comparing same-work concentric and eccentric cycling. When matched for perception of effort, we hypothesized that MVC torque loss would be greater following eccentric than concentric cycling due to an exacerbated contractile impairment—itself caused by a greater power output.

2 | METHODS

2.1 | Participants

A required sample size of 13 was calculated based on the difference in MVC torque loss induced by downhill and uphill running (perceived easier),[25] for a two-tailed test, an effect size of d = 0.85—calculated from the raw data provided by the authors—an alpha level of 0.05 and power of 0.8. Therefore, 15 healthy volunteers (10 males and 5 females) participated in this study (age: 27.7 ± 7.7 years, height: 175 ± 7.8 cm, and body mass: 65.7 ± 7.1 kg). None of them was familiar with eccentric cycling. The study was approved by the French ethics committee (CPP EST I) and was registered on ClinicalTrials.gov (Identifier: NCT03280875). It was conducted in accordance with the declaration of Helsinki (2008) and all participants signed a written informed consent.

2.2 | Experimental procedures

The experimental design is illustrated in Figure 1. Each participant completed one familiarization and 3 experimental laboratory sessions at the same time of day (±2 h), separated by one to two weeks. Participants were instructed to abstain from fatiguing exercise for 2 days before each session and to stick to their usual diet.

During the familiarization session, a concentric incremental ramp test (starting at 50 W with an increase of 1 W/3 s) served to determine peak oxygen uptake, peak heart rate, and peak power output at exhaustion (ie, when pedaling cadence dropped below 50 rpm for more than 5 s). After a 15-min recovery period, participants performed 15 min of eccentric cycling (60% concentric peak power output), preceded and followed by an assessment of the knee extensors neuromuscular function and of perceptions (ie, leg pain while walking and subjective feeling of fatigue). The aim of this session was to familiarize the volunteers with the experimental procedures and trigger a repeated-bout effect.[13,26]

During the experimental sessions, participants completed three 30-min cycling sessions at 60 rpm: one in concentric at 60% peak power output (CON), one in eccentric at the same power output (ECC_{POWER}) and one in eccentric at the same perception of effort as in concentric, adjusted every 3 min (ECC_{EFFORT}). Isopower mode (60% peak power output) was used in CON and ECC_{POWER}, while isocadence mode (60 rpm) was used in ECC_{EFFORT}. Sessions were completed in a random order, except that CON had to take place before ECC_{EFFORT} so the perception of effort during the former could be matched during the latter.

2.3 | Cycling exercises

Two semi-recumbent cycle ergometers were used for concentric (Ergoline GmbH, Ergoselect 600) and eccentric (Cyclus 2, Cyclus GmbH) cycling. The right knee and hip joint angles were measured at maximal right leg extension on each bicycle, and the seat seatback and incline were adjusted so that there was fewer than 10° of difference between either of the two joint angles between the two bikes.

Muscle activity (electromyography, EMG), heart rate, and respiratory gas exchanges were continuously assessed during the exercises, and perception of effort and muscle pain were both rated by the participants every 3 min in a random order. The three sessions began with a 10-min warm-up at 40% peak power output in concentric cycling, followed by 30 s at peak power output during which EMG was recorded. We assessed neuromuscular function, subjective feeling of fatigue, and muscle pain walking before and immediately after the 30-min pedaling exercises. The time latency between the end of the cycling exercise and the onset of the neuromuscular function tests was 1 min.

2.4 | Effort matching

In the ECC_{EFFORT}session, participants were instructed to pedal at the same intensity of effort perception as in CON. Their target perception of effort was orally given to them 10 s before each 3-min section (during which the target changed or not) with the associated anchor (eg, "between hard and very hard") on the Borg CR100 scale—which was placed on the wall in front of them (for more details see the "perceptual parameters" section). Prior to exercise, participants were explained that in this condition, pedaling cadence was set by the cycle ergometer and that to perceive more effort they were probably going to have to increase their power output by resisting harder against the pedals, and vice versa—they received no feedback upon their power output. At this point, they were also reminded that perception of effort is not a reflect of power output but of their difficulty to breathe and control their legs. Following successful pre-trials, we opted not to report participants' perception of effort in ECC_{EFFORT} but to ask them whether they were able to pedal at the instructed pedaling intensity or not—they all were, except one participant who was 10 a.u. above target during most of the exercise. Her data for this condition were excluded (see "data analysis").

2.5 | Electromyography

The EMG activity of the right vastus lateralis (VL) and rectus femoris (RF) muscles was recorded during the neuromuscular tests and cycling exercises. A pair of pre-gelled

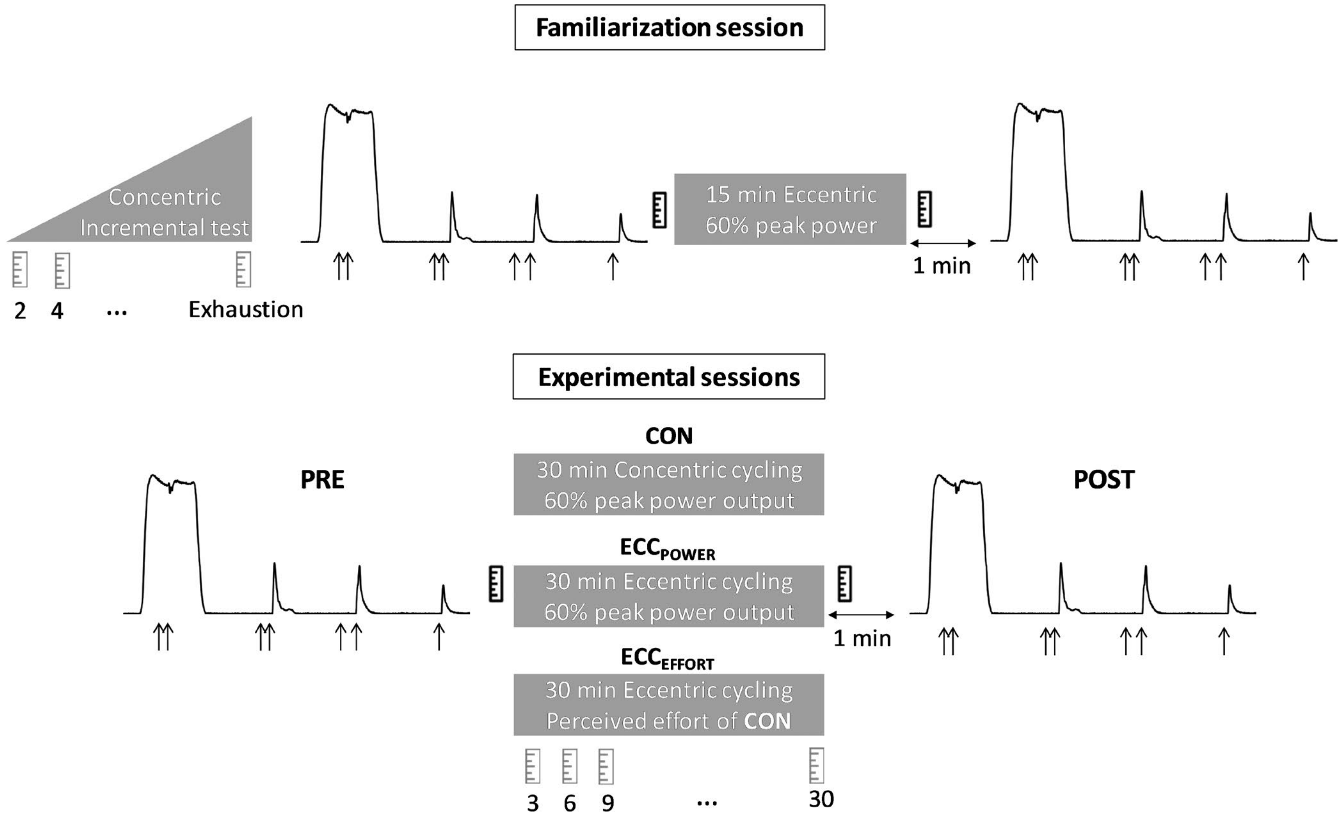

FIGURE 1 Overview of the experimental protocol. Shapes with a gray background illustrate the cycling exercises, during which the activity of vastus lateralis and rectus femoris muscles was measured, as well as gas exchanges and heart rate. Gray items below the exercises indicate that perception of effort and muscle pain were asked at regular time intervals from exercise onset, specified by the numbers below the items (ie, "1" means 1 min after exercise onset). Black items before and after the exercises mean that participants reported their subjective feeling of fatigue and leg muscle pain while walking. The raw trace shows the torque of a typical participant during neuromuscular testing of the right knee extensor muscles. Two joined arrows show high-frequency double electrical stimulations (100 Hz) applied to the femoral nerve during a maximal voluntary contraction or at rest. Two spaced arrows indicate low-frequency stimulation (10 Hz) and a single arrow shows single stimulation

Ag/AgCl bipolar surface electrodes (10 mm^2, center-to-center distance of 20 mm) was placed over the muscle belly according to SENIAM recommendation (seniam.org), with a reference electrode on the patella. During the neuromuscular assessments, EMG and torque were recorded at 2000 Hz with a Biopac MP150 unit and stored on AcqKnowledge 4.2 software (Bipoac Systems Inc.) for offline analysis. EMG during cycling was recorded using a Biopac M160 unit (Bipoac Systems Inc.) at the same sampling rate. All EMG signals were amplified by a thousand, bandpass- (10–390 Hz) and notch-filtered (50 Hz, 1 Hz width).

2.6 | Neuromuscular function

Participants were seated on an isokinetic dynamometer (System pro 4, Biodex Medical System) with a 90° hip flexion, the right knee at a 90° angle (0° being full extension), the knee joint axis in line with the rotation axis of the dynamometer, the leg strapped to the lever arm 2 cm above the malleoli, and the torso strapped against the seat. Percutaneous electrical stimulations were delivered at a 90° knee angle using a high-voltage constant-current stimulator (model DS7AH, Digitimer) via a ball probe cathode (0.5 cm diameter) manually pressed by the experimenter on the femoral nerve using a stylus. A self-adhesive anode (8 × 4 cm) was placed in the gluteal fossa. Stimulation intensity was progressively increased until both M-wave and the torque responses plateaued. We then used 150% of this intensity (1 ms, 400 V, 123 ± 29 mA) to assess maximal M-wave (M_{MAX}) and associated muscle twitch properties.

Participants performed maximal voluntary isometric knee extensor contractions (MVC) with their right leg, during which they were strongly encouraged and visualized the torque they developed on a screen. Two MVCs were performed before each cycling exercise (three if the peak torque difference between the two first was greater than 5%)—the trial with the greatest peak torque was analyzed—and one immediately after the exercise. A double stimulation (100 Hz) was triggered manually at the torque plateau of each MVC, followed by two more double stimulations evoked at rest (100 Hz—Dt100 and 10 Hz—Dt100, respectively) and one single stimulation. The voluntary activation level (VAL) was obtained using Strojnik and Komi's formula (1998),[27] which includes the torque value at the moment of the stimulation ($MIVC_{stim}$) and the torque added by the stimulation (Dtsup).

$$VAL = \left[1 - \left(\left(\frac{MVIC_{stim}}{MVIC}\right) \times \left(\frac{Dt\,sup}{Dt100}\right)\right)\right] \times 100$$

2.7 | Cardiorespiratory responses during the exercises

Heart rate was obtained using a chest-belt heart rate monitor (Ergoline GmbH, Ergoselect 600, Bitz, Germany) and reported by the experimenter 2 min 45 s after exercise onset and then every 3 min throughout exercise. Gs exchanges—oxygen uptake (ml/min/kg) and respiratory frequency (bpm)—were recorded using a $K4B^2$ metabolic system (Cosmed). The gas analyzer was calibrated before each session according to the manufacturer guidelines.

2.8 | Perceptual parameters

Participants reported their perception of effort (ie, their difficulty to breathe and to drive their legs to pedal[28]) and muscle pain (ie, how much it globally hurt in their leg muscles, except the buttocks muscle, that may have been sore by rubbing against the seat). The two perceptions were reported every 3 min during the exercise, using Borg's CR100 scale.[29] Participants were familiarized with these perceptual ratings during the incremental test (day 1). Muscle pain was also asked at rest while sitting on the bike prior to exercise onset, and immediately before and after cycling exercises while walking between the isokinetic ergometer and the bicycle. Memory anchoring was performed for effort perception and muscle pain, meaning that a rating of 100 on the CR100 scale corresponded to the most intense effort or muscle pain they had experienced running or pedaling. Subjective feeling of fatigue (ie, feelings of tiredness and lack of energy, from both physical or mental origin) was reported using a 10 cm visual analog scale while sitting on the bicycle, right before and at the end of the exercises.[25] The left extremity of the visual analog scale corresponded to "not fatigued at all" and its right extremity to "extremely fatigued." Finally, participants self-reported muscle pain walking and subjective feeling of fatigue sitting 24 h, 48 h, and 72 h after the end of each session.

2.9 | Data analysis

Physiological data were considered as outliers and excluded if they were 2.5 standard deviations below or above the mean value (3.13% of data). The perception of effort of one female participant and all her data in ECC_{EFFORT} were excluded because her perception of effort highly differed from the other participants' (perception of effort of 1 a.u. for most of the exercise), and she was not able to match effort perception in ECC_{EFFORT}. Another female participant did not tolerate double stimulations, which were thus only applied to the other 14 volunteers. EMG root mean square (RMS) during cycling was normalized to the EMG RMS obtained during pedaling at peak power output at the end of the warm-up and will be referred to as $EMG_{CYCLING}$. Oxygen uptake during the exercise was expressed as a percentage of peak oxygen uptake (maximum average value over 15 s during the incremental test). Heart rate was expressed as a percentage of the peak value reached prior to exhaustion during the incremental test. $EMG_{CYCLING}$ and oxygen uptake were averaged over the last 30 s of every 3-min section during cycling exercises (10 time points) to match the time window of perceptual data. All data corresponding to 3-min sections were averaged by pairs so that only 5 time-points remained, allowing to preserve statistical power. Power output during ECC_{EFFORT} was thus averaged over each 6-min section of the pedaling exercises. Muscle pain sitting on the cycle ergometer before the exercise was subtracted from muscle pain while pedaling.

EMG RMS during MVC was measured 250 ms on each side of MVC peak torque and divided by M_{MAX} amplitude (EMG_{MAX} RMS/ M_{MAX}) to estimate the magnitude of maximal voluntary neural drive. Maximal torque amplitude was analyzed for single twitch, Dt100 and Dt10. For the M_{MAX} of the RF and VL muscles, the peak-to-peak amplitude and peak-to-peak duration were analyzed. The change in the Dt10/ Dt100 ratio was used as an index of modification of the excitation-contraction coupling.[30] The rate of torque development (RTD, N/s) of Dt100 and Dt10 was measured from the onset of torque increase to its peak value, while the half-relaxation rate (HRR, N/s) was measured from the end of the peak torque plateau—when applicable—to the point it fell to half its peak value.

2.10 | Statistical analyses

In accordance with our hypotheses, data from the CON session were compared with those from the ECC_{POWER} and the ECC_{EFFORT} sessions, but the two eccentric sessions were not compared with one another. Two-way repeated-measure ANOVAs (CONDITION – CON, ECC_{POWER} or CON, ECC_{EFFORT} – x TIME) were used in case of normal data distribution (Shapiro-Wilk test) and homogeneous variance (Levene's test). When significance was reached, these tests were followed by Tukey honest significant difference post hoc tests. Parameters measured during the exercises were tested at 5 time-points (every 6 min), so were muscle pain walking and subjective feeling of fatigue (before, immediately after exercise, 24 h, 48 h, and 72 h after exercise). Other data were tested at 2 time points (PRE, POST). All data confirmed the assumptions of normality and homogeneity of variance except heart rate, muscle pain during the exercise, muscle pain walking, Dt10/ Dt100, and VL M_{MAX} amplitude. Abnormally distributed data were compared with Friedman's non-parametric ANOVAs, followed up by Wilcoxon's matched pairs tests in case of significant outcome ($p < 0.05$) and corrected with Bonferroni's method. The effect of CONDITION on the changes in the Dt10/ Dt100 ratio, VL M_{MAX} amplitude, and muscle pain walking (from baseline to each time point) was assessed by the latter non-parametric tests. The PRE values of the parametric variables were compared in the order in which the sessions were carried out using a one-way ANOVA—and those of other variables using previously cited non-parametric tests—to check for an order effect. Effect sizes (dz) were calculated for followed-up analyses (G*Power software version 3.1.9.4; Kiel University). Spearman's individual rank correlation coefficients were calculated between perception of effort and its physiological correlates, that is $EMG_{CYCLING}$[20] and respiratory frequency,[20] for each condition (5 time points). Spearman's rank correlation coefficients were also computed between perception of effort and muscle pain to assess to what extent the two perceptions evolved similarly within each exercise modality.

3 | RESULTS

All data are expressed as mean ± standard deviation in the text and mean ± standard error in the figures. The mean concentric peak power output was 275 ± 77.2 (170–390) W, corresponding to 4.2 ± 1 (2.6–5.8) W/kg, for a maximal heart rate of 180.1 ± 11.7 (157–203) bpm, a peak oxygen consumption of 45.5 ± 13.7 (30–63) ml/kg/min, an effort perception of 87.7 ± 10 (70–100) a.u., and a muscle pain of 74.4 ± 27.9 (17–100) a.u. Based on their absolute (W) and relative (W/kg) peak power outputs, two individuals had a performance level of 1, five a level of 2, four a level of 3, and four a level of 4.[31,32]

All ANOVA main effects are available in supplementary material.

3.1 | Baseline values

One-way ANOVAs indicated no significant difference between the baseline levels of any variable of the session carried out first, second, and third (all $p > 0.3$; all $\eta_p^2 < 0.065$; expect for RF M_{MAX} amplitude and subjective feeling of fatigue; all $p > 0.06$; all $\eta_p^2 < 0.13$). No significant difference was found in non-parametric variables either (all $p > 0.47$; all dz < 0.67).

3.2 | Response during the exercise

3.2.1 | CON versus ECC_{POWER}

Perception of effort ($p < 0.001$; $\eta_p^2 = 0.61$) and muscle pain (all $p < 0.03$; all dz > 1.24) were more intense in CON than ECC_{POWER} (Figure 2, panels A and C). Changes in effort perception ($p = 0.15$; $\eta_p^2 = 0.06$) and muscle pain (all $p > 0.36$; all dz < 0.15) were not different between these two conditions.

Table 1 depicts the physiological responses during the exercises. ANOVAs showed that oxygen uptake and respiratory frequency were higher in CON than ECC_{POWER} (all $p < 0.001$; all $\eta_p^2 > 0.43$) and increased with TIME (all $p < 0.001$; all $\eta_p^2 > 0.39$). Respiratory frequency exhibited a TIME × CONDITION effect ($p = 0.03$; $\eta_p^2 = 0.1$). Wilcoxon's matched pairs test indicated that heart rate was higher in CON at all time points (all $p < 0.01$; all dz > 3.03) and increased more from the first 6-min time interval to the third time interval than in ECC_{POWER} ($p = 0.04$; dz = 0.59). $EMG_{CYCLING}$ of the RF muscle was not significantly affected by TIME or CONDITION (all $p > 0.21$; all $\eta_p^2 < 0.07$) whereas $EMG_{CYCLING}$ of the VL muscle exhibited a TIME x CONDITION effect ($p = 0.01$; all $\eta_p^2 = 0.13$).

3.2.2 | CON versus ECC_{EFFORT}

As shown in Figure 2, muscle pain (panel D) did not differ between the two conditions (all $p > 0.43$; all dz < 0.18). Power output (panel B) decreased throughout ECC_{EFFORT} ($p < 0.001$; $\eta_p^2 > 0.53$). Changes in muscle pain were not different between the two conditions (all $p > 0.61$; all dz < 0.23).

Oxygen uptake and respiratory frequency (Table 1) were higher in CON than ECC_{EFFORT} (all $p < 0.01$; all $\eta_p^2 > 0.26$) and augmented with TIME (all $p < 0.001$; all $\eta_p^2 > 0.39$). There was a TIME x CONDITION effect on re-

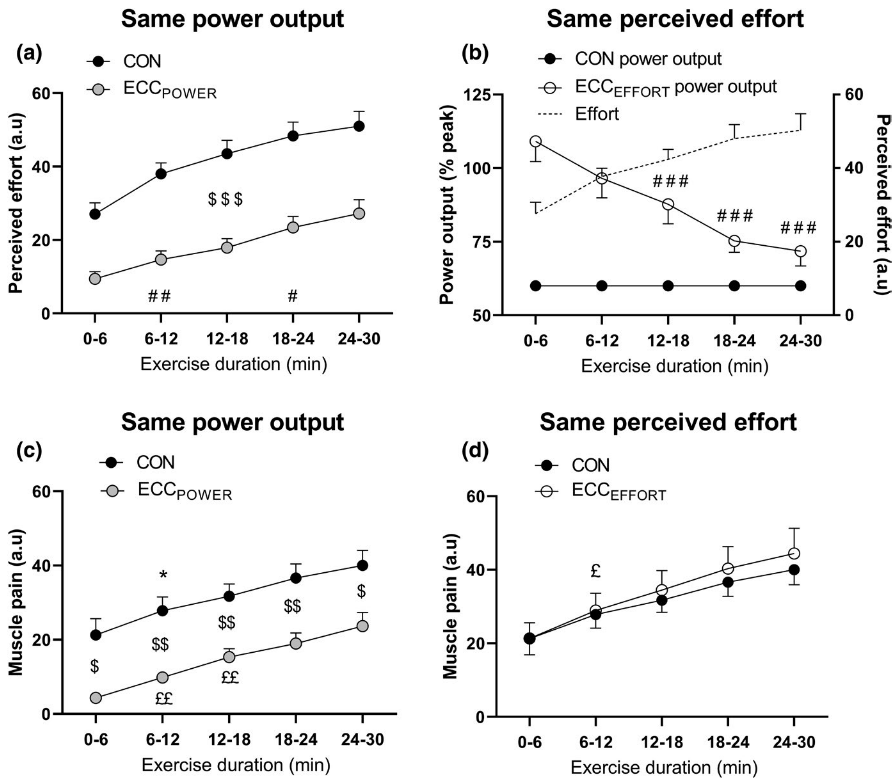

FIGURE 2 Perceived effort, muscle pain and power output during the cycling exercises. This figure displays two statistical comparisons: concentric cycling (CON) at 60% peak power output versus eccentric cycling at the same power output (ECC$_{POWER}$) and CON versus eccentric cycling at the same perceived effort (ECC$_{EFFORT}$). Panels A and B show the evolution of perceived effort and muscle pain, respectively, in CON and ECC$_{POWER}$. Panels B and D illustrate power output and muscle pain, respectively, in CON and ECC$_{EFFORT}$. The dashed line represents perceived effort, common to the conditions. In panel A, $ indicates that effort was perceived more intense in CON than ECC$_{POWER}$ overall. # means that perceived effort was greater than during the previous six-min time interval for the combined conditions CON and ECC$_{POWER}$. In panel B, # shows a decrease in power output compared with the six first min of exercise. In panel C, $ indicates or a difference in muscle pain between CON and ECC$_{POWER}$, for every time interval. An increase in muscle pain from one interval of time to the next one is indicated by * in CON and by £ in ECC$_{POWER}$. In panel D, £ means that, in ECC$_{EFFORT}$, muscle pain was more intense than during the previous time interval. For every symbol, one sign means $p < 0.05$, two signs mean $p < 0.01$ and three signs mean $p < 0.001$). Error bars represent the standard error

spiratory frequency ($p < 0.001$; $\eta_p^2 = 0.19$). Non-parametric tests revealed a greater heart rate (Table 1) in CON at all time points (all $p < 0.01$; all dz > 1.68), but no difference in its increase between the two conditions (all $p > 0.59$; all dz < 0.53). EMG$_{CYCLING}$ of the RF muscle was unaffected by TIME or CONDITION (all $p > 0.41$; all $\eta_p^2 < 0.04$) while EMG$_{CYCLING}$ of the VL muscle showed a TIME x CONDITION effect ($p = 0.02$; all $\eta_p^2 = 0.12$) and rose in ECC$_{EFFORT}$ (all $p < 0.04$; all dz > 0.91).

3.3 | Correlates of perception of effort

The correlation between perception of effort and muscle pain was strong in ECC$_{POWER}$ ($p < 0.001$; d = 0.65), moderate in CON ($p < 0.001$; d = 0.49), and small in ECC$_{EFFORT}$ ($p = 0.01$; d = 0.3). Perception of effort was correlated with respiratory frequency in CON ($p < 0.001$; d = 0.43) but not in the eccentric conditions (all $p > 0.22$; all d < 0.11). Finally, perception of effort showed no correlation with the EMG RMS of either muscle in any condition (all $p > 0.07$; all d < 0.17).

3.4 | Neuromuscular and perceptual changes from before to immediately after the exercise

3.4.1 | CON versus ECC$_{power}$

As shown in Figure 3, MVC torque (−18.8 ± 7.9%) and VAL (−2.2 ± 5.1%) decreased with TIME (all $p < 0.02$; $\eta_p^2 > 0.2$) but were not significantly influenced by CONDITION (all $p > 0.56$; all $\eta_p^2 < 0.01$). ANOVAs revealed no significant effect of TIME or CONDITION (all $p > 0.07$; all $\eta_p^2 < 0.13$) on EMG RMS$_{MAX}$ /M$_{MAX}$ for the RF and the VL muscles.

TABLE 1 Evolution of physiological variables during the exercises

Variable	Main effect	Condition	0–6 min	6–12 min	12–18 min	18–24 min	24–30 min
Heart rate (% peak)	Non-parametric Testing	ECC_{POWER}	$52 \pm 7.5^{\$\$}$	$55.7 \pm 9.2^{\#\#,\$\$}$	$57.4 \pm 9.9^{\#\#,\$\$}$	$59.8 \pm 13.2^{\#\#,\$\$}$	$59.9 \pm 11.1^{\#\#,\$\$}$
		CON	80 ± 4.7	$85.7 \pm 5.6^{\#\#}$	$88.1 \pm 6.6^{\#}$	$89 \pm 7.2^{\#}$	$91.2 \pm 7.3^{\#\#}$
		ECC_{EFFORT}	$60.2 \pm 9.3^{\$\$}$	$64.7 \pm 13.7^{\$\$}$	$67.2 \pm 16^{\$\$}$	$67.9 \pm 16.4^{\$\$}$	$70 \pm 16.7^{\$\$\$}$
Oxygen uptake (% peak)	CONDITION*** Interaction***	ECC_{POWER}	22.9 ± 5.6	24.9 ± 5.5	$27.7 \pm 7.2^{\$}$	$29.7 \pm 6.6^{\$\$}$	$31.2 \pm 8.8^{\$\$}$
		CON	73.3 ± 5.3	76.2 ± 8.9	$77.4 \pm 8.7^{\#\#}$	$78.2 \pm 8.7^{\#\#\#}$	$78.6 \pm 9.1^{\#\#\#}$
	CONDITION*** Interaction***	ECC_{EFFORT}	26.8 ± 4.1	28.2 ± 2.1	31.3 ± 5.1	$33.1 \pm 4.7^{\$\$}$	$34.2 \pm 5.2^{\$\$}$
Respiratory frequency (bpm)	Interaction*	ECC_{POWER}	19.7 ± 3.1	20.4 ± 4.7	$20.8 \pm 3.5^{\$}$	$20.8 \pm 4.6^{\$\$}$	$21.2 \pm 4.7^{\$\$}$
	Interaction***	CON	26.8 ± 4.1	28.2 ± 2.1	$31.3 \pm 5.1^{\#\#}$	$33.1 \pm 4.7^{\#\#\#}$	$34.2 \pm 5.2^{\#\#\#}$
		ECC_{EFFORT}	21.7 ± 6.5	23.1 ± 8.2	22.5 ± 6.7	$21.7 \pm 7^{\$\$}$	$21 \pm 6.8^{\$\$}$
Vastus lateralis $EMG_{CYCLING}$ (%)	Interaction***	ECC_{POWER}	49 ± 39	59.6 ± 47.5	$64 \pm 51.8^{\#\#}$	$66 \pm 53.9^{\#\#\#}$	$67.5 \pm 56.8^{\#\#\#}$
	Interaction**	CON	81.2 ± 46.6	83.1 ± 48.1	84.3 ± 49.1	83.8 ± 48	82.5 ± 47.3
		ECC_{EFFORT}	69.1 ± 31.2	$77.4 \pm 37.2^{\#}$	$77.7 \pm 36.2^{\#}$	$81.5 \pm 37.8^{\#\#\#}$	$81.8 \pm 41.1^{\#\#\#}$
Rectus femoris $EMG_{CYCLING}$ (%)	No effect	ECC_{POWER}	25.8 ± 15.9	27.4 ± 15.6	29.2 ± 13.3	29.2 ± 11.7	29.6 ± 13.4
	No effect	CON	35.1 ± 17.9	36.3 ± 16.7	37 ± 16.5	36.8 ± 19.4	38.1 ± 20.1
		ECC_{EFFORT}	39.9 ± 20.9	40.5 ± 18.1	42.2 ± 19.5	44 ± 22.4	39 ± 21.1

Two comparisons are illustrated: For each variable, main effects corresponding to CON versus ECC_{POWER} are above the horizontal line and those corresponding to CON versus ECC_{EFFORT} are below that line. "Interaction" indicates a TIME × CONDTION effect. $: different from CON during the same time interval; #: different from the 0–6 min time interval. One sign means $p < 0.05$, two signs mean $p < 0.01$; three signs mean $p < 0.001$.

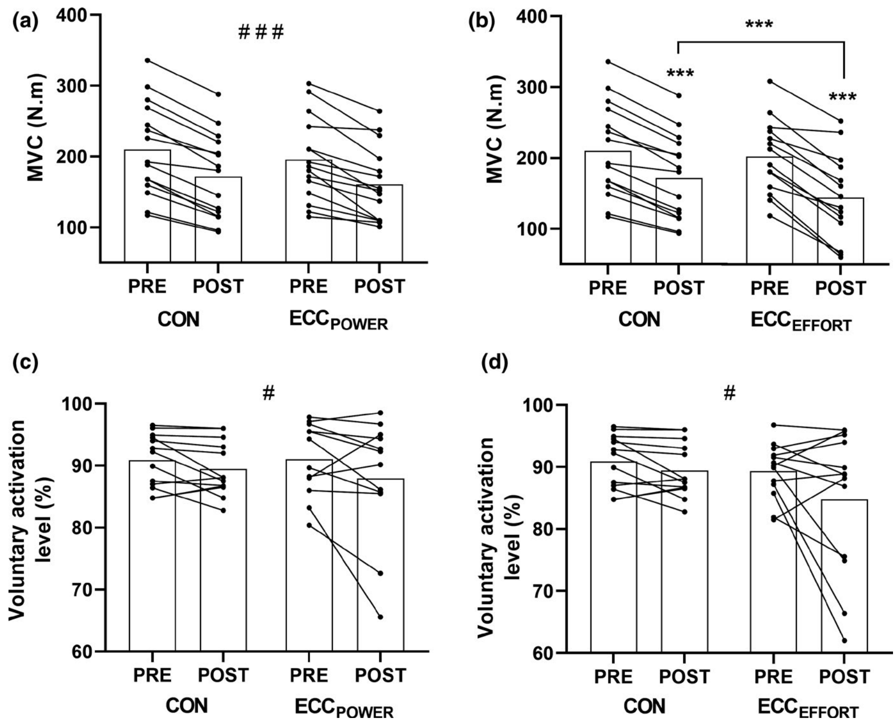

FIGURE 3 Neuromuscular fatigue before and after the pedaling exercises. This figure illustrates two statistical comparisons: concentric cycling (CON) versus eccentric cycling at the same power output (ECC_{POWER}) and CON versus eccentric cycling at the same perceived effort (ECC_{EFFORT}). The panels A and B show the maximal voluntary (MVC) torque and the panels C and D depict the voluntary activation level (VAL), before (PRE) and after (POST) each exercise. *indicates a reduction within a condition or a greater reduction in one condition than in another and # shows a decrease independent of CONDITION. For every symbol, one sign means $p < 0.05$ and three signs mean $p < 0.001$)

Table 2 depicts neuromuscular parameters before and immediately after the exercises. M_{MAX} peak-to-peak amplitude and duration of the RF muscle decreased with TIME (all $p < 0.02$; all $\eta_p^2 > 0.18$), but not the VL muscle peak-to-peak duration (all $p < 0.92$; all $\eta_p^2 < 0.01$). VL muscle peak-to-peak amplitude did not change with TIME ($p = 0.99$; dz = 0.3) nor CONDITION ($p = 0.79$; dz < 0.01). Dt100 (−12.1 ± 6.8%), Dt10 (−29.8 ± 2.7%), and single twitch amplitudes (−25.1 ± 16.7%) decreased with TIME (all $p < 0.02$; $\eta_p^2 > 0.2$) but were not significantly influenced by CONDITION (all $p > 0.68$; all $\eta_p^2 < 0.01$). Non-parametric tests showed reduced Dt10/ Dt100 ratios after ECC_{POWER} ($p = 0.01$; dz = 2.28) but not CON ($p = 0.11$; dz = 0.21), nonetheless without a significant effect of CONDITION on the change in this ratio ($p = 0.18$; dz = 0.49). The RTDs of Dt100 and Dt10 decreased with TIME (all $p < 0.027$; all $\eta_p^2 > 0.19$), the HRRs of Dt100 and Dt10 exhibited a TIME x CONDITION effect (all $p < 0.01$; all $\eta_p^2 > 0.33$), and the HRR associated with Dt100 increased in ECC_{POWER} ($p < 0.001$; dz = 1.1).

Table 3 describes subjective feeling of fatigue and muscle pain walking levels before and up to 72 h following the exercise. Wilcoxon's matched pairs tests indicated that muscle pain walking increased more from before to immediately after exercise in CON than ECC_{POWER} ($p = 0.04$; dz = 0.83) but increased less from before to 24 h to 72 h after exercise in CON than ECC_{POWER} (all $p < 0.02$; all dz > 0.56). Subjective feeling of fatigue was neither modulated by TIME nor CONDITION (all $p > 0.17$; all $\eta_p^2 < 0.07$).

3.4.2 | CON versus ECC_{EFFORT}

Changes in MVC and VAL are illustrated in Figure 3. ANOVA exhibited a TIME x CONDITION effect on MVC torque ($p = 0.01$; $\eta_p^2 > 0.22$). MVC declined after both conditions (all $p < 0.001$; all dz > 2.56) yet to a greater extent after ECC_{EFFORT} than CON (−30.2 ± 15.8% vs −19 ± 6.5%; $p = 0.03$; dz = 1.2). VAL decreased with TIME (−2.6 ± 6.5%; $p = 0.04$; $\eta_p^2 < 0.16$) but was unaffected by CONDITION ($p = 0.19$; $\eta_p^2 > 0.06$). Non-parametric tests showed no change with TIME or CONDITION (all $p > 0.33$; all $\eta_p^2 > 0.09$) in EMG RMS_{MAX} /M_{MAX} of the RF or the VL muscles.

Neuromuscular parameters are displayed in Table 2. M_{MAX} peak-to-peak amplitude and duration of the RF muscle decreased with TIME (all $p < 0.03$; all $\eta_p^2 > 0.17$).

TABLE 2 Changes in neuromuscular parameters from PRE-to-POST cycling exercises

Variable	Main effect	Condition	PRE	POST	Effect size (dz)
Vastus lateralis M_{MAX} amplitude (mV)	Non-parametric testing	ECC_{POWER}	5.9 ± 3.1	5.5 ± 3.2	0.3
		CON	6 ± 2.8	5.7 ± 2.7	0.21
		ECC_{EFFORT}	6 ± 3.2	5.6 ± 3.2	0.29
Vastus lateralis M_{MAX} duration (ms)	No effect	ECC_{POWER}	6.6 ± 2.7	8 ± 4	0.52
	TIME*	CON	9.6 ± 4.8	8.7 ± 4.2	0.3
		ECC_{EFFORT}	8.8 ± 4.3	7.6 ± 3.7	0.57
Rectus femoris M_{MAX} amplitude (mV)	TIME**	ECC_{POWER}	6.1 ± 3	5.4 ± 2.7	0.48
	TIME*	CON	5.9 ± 2.5	4.7 ± 2.1	0.59
		ECC_{EFFORT}	5.8 ± 2.6	5.5 ± 2.7	0.24
Rectus femoris M_{MAX} duration (ms)	TIME*	ECC_{POWER}	8.2 ± 4.7	7.5 ± 3.8	0.35
	TIME*	CON	8.7 ± 4.5	7.2 ± 3.7	0.54
		ECC_{EFFORT}	6.9 ± 3.3	6.1 ± 2.8	0.29
Single twitch Amplitude (N.m)	No effect	ECC_{POWER}	42.7 ± 17	33 ± 15.6	1.45
	No effect	CON	43.2 ± 14.7	31.4 ± 10.9	1.39
		ECC_{EFFORT}	45.1 ± 11.9	29.8 ± 12.2	1.69
Dt10 amplitude (N.m)	TIME***	ECC_{POWER}	69.3 ± 20	49.9 ± 16.6	1.95
	TIME***	CON	67.4 ± 22.2	45.87 ± 17.30$^{###}$	1.93
	Interaction*	ECC_{EFFORT}	73.4 ± 13.7	38.8 ± 18.9$^{##}$	2.56
Dt10 RTD (N/s)	TIME***	ECC_{POWER}	426.6 ± 120.9	349.3 ± 158.1	0.85
	TIME***	CON	420.3 ± 308.4	308.4 ± 137.1	1.04
		ECC_{EFFORT}	427 ± 91.7	250 ± 90.4	2.25
Dt10 HRR (N/s)	Interaction***	ECC_{POWER}	469.8 ± 132.1	564.2 ± 221.4	0.64
	TIME*	CON	499.9 ± 201	382.9 ± 149.4	0.87
		ECC_{EFFORT}	573.9 ± 217.2	474.4 ± 244.3	0.4
Dt100 amplitude (N.m)	TIME***	ECC_{POWER}	72 ± 17.6	64.4 ± 17.1	1.0
	Interaction*	CON	72.4 ± 22.2	61.4 ± 18.1	1.28
		ECC_{EFFORT}	73.2 ± 14.6	54.6 ± 18.3	2.03
Dt100 RTD (N/s)	TIME*	ECC_{POWER}	769.4 ± 222.9	728.4 ± 197.1	0.42
	TIME**	CON	755 ± 218.2	705 ± 198.6	0.59
		ECC_{EFFORT}	745.6 ± 176.9	631.9 ± 198.5	0.58
Dt100 HRR (N/s)	TIME**	ECC_{POWER}	415.2 ± 150.2	601 ± 250.5$^{###,\$}$	1.1
	Interaction***	CON	429 ± 236.2	367.3 ± 155.6	0.57
	Interaction*	ECC_{EFFORT}	469 ± 190.8	608.5 ± 263$^{###,\$}$	0.63
Dt10/ Dt100 ratio	Non-parametric testing	ECC_{POWER}	1.02 ± 0.15	0.79 ± 0.13$^{#}$	2.28
		CON	0.89 ± 0.17	0.73 ± 0.1	0.91
		ECC_{EFFORT}	1.01 ± 0.08	0.7 ± 0.18$^{##,££}$	1.85

Two comparisons are illustrated: For each variable, main effects corresponding to CON versus ECC_{POWER} are above the horizontal line and those corresponding to CON versus ECC_{EFFORT} are below that line. "Interaction" indicates a TIME × CONDTION effect. #: different from PRE; $: POST-value different from CON. £: change from PRE different from CON for non-parametric testing; one sign means $p < 0.05$, two signs mean $p < 0.01$; three signs mean $p < 0.001$. The effect size concerns the PRE-to-POST difference. RTD: rate of torque development; HRR: half-relaxation rate.

VL muscle peak-to-peak amplitude (all $p > 0.77$; all dz < 0.29) and duration (all $p = 0.55$; all $\eta_p^2 = 0.01$) did not change with CONDITION. VL muscle peak-to-peak duration decreased with TIME ($p = 0.03$; $\eta_p^2 = 0.16$). Contrary to Dt100 amplitude (−20.1 ± 13.9%; all $p < 0.001$), which dropped in both conditions, and to the twitch response, which decreased with TIME (−30.7 ± 18.4%; $p = 0.72$), Dt10 decreased more following ECC_{EFFORT} than CON

TABLE 3 Evolution of muscle pain walking and fatigue following the cycling exercises

Variable	Main effect	Condition	PRE	POST	POST 24 h	POST 48 h	POST 72 h
Muscle pain walking (a.u)	Non-parametric testing	ECC_{POWER}	1.8 ± 1.9	6.7 ± 7.5 $^{£}$	27.5 ± 23.3 $^{\#\ ££}$	30.5 ± 31.2$^{££}$	15.1 ± 24.3$^{£}$
		CON	2.9 ± 6.4	15.1 ± 14.8$^{\#}$	7.1 ± 8.7	4 ± 6.1	2.3 ± 4.3
		ECC_{EFFORT}	4.2 ± 5.9	17.7 ± 15.4$^{\#}$	35.9 ± 11$^{\#,\$,£}$	43.1 ± 16$^{\#,\$,£}$	22 ± 12.1$^{\$,£}$
Subjective feeling of fatigue (a.u)	No effect	ECC_{POWER}	3.8 ± 3.4	4.2 ± 1.5	3 ± 2.2	2.7 ± 2	2.5 ± 2.1
	No effect	CON	2.8 ± 1.5	4.9 ± 1.5	3.3 ± 1.3	2.8 ± 1.9	2.5 ± 2
		ECC_{EFFORT}	3.1 ± 1.4	4.8 ± 1.6	3.3 ± 1.5	3.2 ± 1.8	2.7 ± 1.7

Two comparisons are illustrated: For each variable, main effects corresponding to CON versus ECC_{POWER} are above the horizontal line and those corresponding to CON versus ECC_{EFFORT} are below that line. \$: Different from CON at the same time point; #: Different from PRE. £: change from PRE different from CON for non-parametric testing. One sign means $p < 0.05$, two signs mean $p < 0.01$; three signs mean $p < 0.001$.

(48.8 ± 20.8 vs 27.8 ± 12%; $p = 0.01$). Wilcoxon's matched pairs tests showed depressed Dt10/ Dt100 ratios following ECC_{EFFORT} ($p = 0.01$; dz = 1.97) but not CON ($p = 0.11$; dz = 0.21), with a greater decline in ECC_{EFFORT} ($p < 0.001$; dz = 0.89). ANOVA exhibited TIME x CONDITION effects on Dt100 and Dt10 (all $p < 0.03$; all $\eta_p^2 > 0.17$). The RTDs of Dt100 and Dt10 decreased with TIME (all $p < 0.01$; all $\eta_p^2 > 0.23$). The HRR of Dt10 also slowed with TIME ($p < 0.05$; $\eta_p^2 = 0.18$) and that of Dt100 showed a TIME × CONDITION effect ($p = 0.02$; all $\eta_p^2 = 0.2$), increasing in ECC_{EFFORT} ($p = 0.02$; dz = 0.63).

As reported in Table 3, Wilcoxon's matched pairs tests indicated that muscle pain walking increased from 4.2 ± 5.9 a.u. before ECC_{EFFORT} to 17.7 ± 15.4 a.u. immediately after it and up to 39.5 ± 14 a.u. 48 h after (all $p < 0.04$; all dz > 0.85). Muscle pain walking raised similarly from before to immediately after exercise in CON and ECC_{EFFORT} ($p = 0.87$; dz = 0.06) and increased less from before to 24 h to 72 h after exercise in CON than ECC_{EFFORT} (all $p < 0.042$; all dz > 0.92). Subjective feeling of fatigue was neither modulated by TIME nor CONDITION (all $p > 0.11$; all $\eta_p^2 < 0.09$).

4 | DISCUSSION

This study compared responses to concentric cycling (CON) with those to eccentric cycling performed at the same power output (ECC_{POWER}, 60% peak aerobic power output) or perception of effort (ECC_{EFFORT}). It focused on performance fatigability (ie, MVC torque loss), associated neuromuscular alterations, as well as on the perceptions of effort and muscle pain during the exercises. Despite no detectable increase in the subjective feeling of fatigue after either pedaling bout, performance fatigability and perceptual responses differed between the experimental conditions. ECC_{POWER} was less painful and perceived easier than CON, and as previously shown in individuals familiar with eccentric cycling,[19] caused similar MVC torque decline. ECC_{EFFORT} elicited similar pedaling muscle pain but a more pronounced MVC torque impairment than CON. Neural alterations associated with MVC torque loss appeared similar in all conditions whereas specific muscular impairments were found immediately after ECC_{EFFORT}, despite no difference in knee extensors torque amplitude evoked by peripheral nerve stimulation (Dt100). ECC_{EFFORT} specifically impaired excitation-contraction coupling and both eccentric sessions probably damaged the muscle more than concentric cycling. The investigation of fatiguing concentric and eccentric cycling at the same perception of effort is a novel approach, providing clinical perspectives.

4.1 | Perceptions of effort and muscle pain during the exercise

Perception of effort was higher during CON than ECC_{POWER}. Conversely, the average power output was greater in ECC_{EFFORT} than CON (Figure 2, panels A and B). Furthermore, the stronger correlation between perception of effort and muscle pain during the cycling bout of ECC_{POWER} than CON suggests that different mechanisms underpin one or both perceptions in the two exercise modalities.

Perception of effort, thought to result from a copy of efference (ie, voluntary cortical motor command) to active muscles,[9] reaches respiratory centers at the medulla level[33] and is correlated with respiratory frequency during conventional pedaling.[21] The greater respiratory frequency in CON than ECC_{POWER}, along with the presence of a moderate correlation between perception of effort and respiratory frequency during CON but not ECC_{POWER}, could hint at a significant contribution of respiratory drive to perception of effort in concentric but not eccentric cycling. This contribution would partly explain the lower perception of effort in ECC_{POWER} than CON. However, respiratory frequency was higher in CON than ECC_{EFFORT}, despite the same effort perception, showing that other factors contributed significantly to effort perception in ECC_{EFFORT}. For instance, matching a fluctuating effort in this condition may have required additional focus, thereby increasing effort perception.[34] In the CON condition, individuals had to match a pedaling cadence of 60 rpm instead, but this probably required less attention than matching effort perception in ECC_{EFFORT}, where cadence was steady. During the first 6 min of the ECC_{EFFORT} exercise, the power output was largely higher than in CON (109 ± 24% vs 60% peak concentric power output) for the same effort perception. Then, the efficacy of the vastus lateralis muscle waned, as suggested by an increased EMG (more neural drive was required to produce less power).

Because the EMG of a muscle reflects the movement-related cortical potentials (MRCP, obtained with electroencephalography),[35] studies showed perception of effort to be correlated with the EMG of the main muscles involved in a single-joint task.[20] Given the low cardiorespiratory demand of eccentric cycling,[1] we expected leg EMG to be correlated with perception of effort. We see three main potential explanations for the absence of such a correlation. First, the relationship between EMG and MRCPs might be less during eccentric cycling than isometric single-joint movements. Indeed, MRCPs were of greater magnitude during eccentric than concentric single-joint contractions despite a lower EMG in eccentric.[36] Moreover, this relationship may be further diminished during locomotor exercise as the result of the contribution of central pattern generators to muscle command.[37] Second, it has previously been evidenced that the EMG of muscles not directly involved in pedaling (ie, biceps brachii) raises during eccentric cycling at higher power outputs, likely to stabilize the upper body,[38] increasing overall muscle command. Third, the cognitive load of eccentric cycling[11] probably influences perception of effort regardless of the intensity of the motor command.

In CON, pedaling muscle pain was higher than in ECC_{POWER} but not different from that reported in ECC_{EFFORT}. Nonetheless, distinct mechanisms are likely to induce muscle pain with repeated concentric or eccentric contractions. That is, the metabolic rate of CON (~ 77% peak oxygen uptake) let think that the anaerobic metabolism was involved[39] to a greater extent during this exercise than during ECC_{EFFORT} (~36% peak oxygen uptake), thereby increasing muscle acidity through the accumulation of metabolites.[23] This would result in an increased firing of type III/IV metabosensitive nociceptive afferent.[22] On the contrary, the greater power output in ECC_{EFFORT} than CON (89 ± 23% vs 60% peak power output), combined with repeated stretches of the muscle, may have triggered more type III/IV mechanosensitive nociceptive afferent firing.[40] Provided that power output decreased throughout the ECC_{EFFORT} exercise, the accumulation of muscle stretches seems to account more for eccentric cycling-induced muscle pain than a mechanism related to transient power output (eg, intramuscular pressure).

4.2 | Muscular alterations following exercise

There was no effect of condition on the decrease in amplitude and rate of torque development of Dt100. However, the depressed power output at the end of the ECC_{EFFORT} exercise, along with a higher vastus lateralis EMG, highlights a reduced muscle efficiency—so does the higher vastus lateralis EMG at the end of ECC_{POWER} despite a steady power output.[41] Such a reduction in muscle efficacy to produce power output was not found in CON. Possibly related to this discrepancy, the low-to-high frequency stimulation response (Dt10 /Dt100 ratio) decreased in ECC_{POWER}, but not significantly more than in CON, and declined more in ECC_{EFFORT} than CON. This suggests an altered excitation-contraction coupling in ECC_{EFFORT} but not in CON.[30] Low-frequency response was found to be similar immediately after concentric and eccentric single-joint knee extensor contractions[42,43] whereas, in line with our results, it decreased after downhill but not uphill running at the same speed.[25] Consequently, locomotor eccentric exercise may particularly alter excitation-contraction coupling. Of note as well, the presence of muscle pain the days following the two eccentric cycling bouts is an indirect evidence of inflammatory processes, probably in response to histological damage—although the two are not systematically related[44]—affecting maximal voluntary torque immediately after eccentric exercises.[13] Contrary to the muscle wisdom hypothesis,[45] the half-relaxation rate of Dt100 increased after both eccentric exercises. Potential explanatory mechanisms include an elevated muscle temperature, as proposed after running,[27] and a quicker calcium reuptake.[45] The absence of influence of either experimental condition on M_{MAX} properties suggests a preserved sarcolemmal excitability in all conditions.

4.3 | Neural alterations following the exercises

The maximal voluntary activation level (VAL) decreased immediately after all cycling exercises and maximal vastus lateralis and rectus femoris EMG (EMG RMS_{MAX}/M_{MAX}) was unaltered, suggesting no difference in the impairment in the neural mechanisms of maximal voluntary torque production between the conditions. The significantly raised muscle pain level walking immediately after CON and ECC_{EFFORT} let assume that type III/IV nociceptive afferents were discharging at this moment,[40] likely inhibiting the motor command to the knee extesnor muscles[46] and thereby contributing to the depressed VAL. Nonetheless, this was certainly not the main factor since VAL was similarly depressed in ECC_{POWER} despite no increase in muscle pain walking. The high interindividual variability in VAL modifications in ECC_{POWER}, and even more in ECC_{EFFORT} (Figure 3), suggests that its underpinning mechanisms may have differed more between participants following eccentric and concentric cycling. Notably, the increase in VAL exhibited by 5 of 13 participants in ECC_{EFFORT} might be related to an increased vigilance as previously shown following an eccentric cycling exercise.[11] As vigilance is known to be proportional to corticospinal excitability,[47] it could have compensated for neural alterations in these individuals.[46]

In line with our findings, VAL decreased similarly immediately after 45 min of uphill or downhill running.[25] Yet it should also be noted that the time delay between the end of a locomotor exercise and the evaluation of VAL (one min in this study) provides time for partial recovery.[48] This limitation may have precluded the identification of an effect of condition on neural alterations. In single-joint settings, where this time delay between the exercise and neuromuscular function assessment is typically shorter, similar decreases in VAL were reported following same-work eccentric and concentric submaximal knee extensor contractions.[42] On the contrary, maximal eccentric leg extensions caused VAL depression but their concentric counterpart did not.[43,49] Then, while conclusions from single-joint exercise cannot be applied to locomotor exercises without being specifically tested,[2,50] eccentric exercise intensity domain (maximal versus submaximal) seems to highly influence the resulting neural alterations.

4.4 | Limitations

We must acknowledge several limitations inherent to the experimental design of this study. First, the use of a within-subject design may have attenuated participants' fatigability following the eccentric session performed second, due to a protective effect conferred by the first.[13] As trials were randomized and counterbalanced, however, we assume that such a confound had a limited impact on the current results. This supposition is supported by similar baseline levels in all data before each condition, regardless of the order in which they were performed. Furthermore, two considerations related to effort perception matching should be noted. First, while most participants declared matching the target effort perception easily, suggesting this had a minimal influence on their perception of effort, this additional task requirement is a confound when comparing the response to ECC_{EFFORT} with those to CON. Second, in CON, participants rated their effort perception at the end of every 3 min section, while in ECC_{EFFORT}, they matched this effort perception constantly. Because effort perception drifted upward during CON, it may have been higher at the beginning of each 3-min time-interval during ECC_{EFFORT}. We believe, however, that this likely had little impact on the data collected during the exercise at the end of every 3-min time interval, because 1) the average perception of effort over 3 min is probably be very close to that at any time within these 3 min—as exercise intensity was not extreme—and 2) even if effort perception was higher in ECC_{EFFORT} than CON at the onset of each 3-min interval, participants likely adjusted their power output throughout the time interval in order for their effort perception not to increase above target. To avoid these issues related to effort matching, it would be relevant to compare perceptual and neuromuscular responses to concentric and eccentric cycling at the same steady effort perception in future studies. We also acknowledge that the assessment of muscle pain walking (before and after the exercises) probably underestimated the actual muscle pain intensity as individuals may have modified their walking pattern, precisely to attenuate pain. Finally, since several weeks of eccentric cycling training are expected to induce more pronounced modality-specific changes in neuromuscular function (eg, decrease in leg EMG[51]), the outcomes of the comparison CON vs ECC_{POWER} only apply to individuals merely familiar with eccentric cycling. On the contrary, given that eccentric cycling practice increases power output for a given perception of effort,[52] we argue that the more pronounced MVC torque loss in ECC_{POWER} than CON may be reproducible in trained individuals. Nonetheless, this hypothesis remains to be tested.

5 | CONCLUSION

When performed at the same power output, eccentric cycling elicited less intense perceptions of effort and muscle pain than concentric cycling, but participants showed a similar performance fatigability (ie, MVC torque decline). In contrast, eccentric cycling perceived as difficult as concentric cycling induced similar muscle pain but more MVC torque decline. While all exercises impaired neural function similarly, only eccentric cycling hindered excitation-contraction coupling.

6 | PERSPECTIVES

The comparison of performance fatigability following concentric and eccentric cycling perceived as difficult is new and opens clinical perspectives. In fact, from a clinician's standpoint, the propensity of participants to exhibit more neuromuscular performance decline after eccentric than concentric cycling perceived as difficult should prompt to be cautious when setting eccentric cycling intensity based on perception of effort. In other words, eccentric cycling should always feel easier than concentric cycling if basing exercise prescription on guidelines upon conventional cycling. These conclusions have still to be tested among patients and with more functional performance fatigability markers.

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DATA AVAILABILITY STATEMENT

The data presented in this study are available upon request to the corresponding author.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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