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The cost of durability: Breathing pattern shifts towards frequency- dominance during prolonged submaximal running and repeated uphill time trials

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The cost of durability: Breathing pattern shifts towards frequency-dominance during prolonged submaximal running and repeated uphill time trials

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Running head: Breathing Pattern Reconfiguration in Trail Runners

Abstract

Purpose: To characterize how the breathing pattern (respiratory frequency [f_R] and tidal volume [V_T]) and locomotor–respiratory coupling (LRC) respond to prolonged submaximal running and repeated self-paced uphill time trials.

Methods: Twenty-three trained trail runners (11 F) completed a baseline uphill time trial (TT0), then three 60-minute submaximal blocks, each followed by a 12-minute self-paced uphill time trial (TT1–TT3). f_R, V_T, and minute ventilation ($\dot{V}_E$) were computed per breath and aggregated to 30-second bins, while LRC was quantified with an open-source algorithm. Outcomes were log-transformed and analyzed with linear mixed models; time-trial comparisons were additionally adjusted for within-participant external load to isolate load-independent ventilatory responses.

Results: Breathing pattern showed no change within each submaximal block, but it adjusted substantially between blocks: f_R increased +19.3% (block 3 vs 1), V_T decreased −7.2% and $\dot{V}_E$ increased +10.9%. Between time trials at matched external load, f_R was 13.4% greater (TT3 vs TT0), $\dot{V}_E$ +5.6%, and V_T was 6.6% lower. LRC was higher during maximal time trials (56.9%) than submaximal running (40.6%) and increased between submaximal blocks. RPE increased within (+0.6 points [0.3, 0.9]) and between blocks (+2.7 points [2.5, 3.0], block 3 vs. 1).

Conclusions: Breathing pattern adjusted to a more frequency-dominant pattern between (but not within) submaximal blocks, indicating an exposure-dependent relationship between the self-paced time trials and discrete ventilatory adjustments. These insights may be used to improve the application and interpretation of breathing monitoring.

Keywords: *breathing pattern, physiological resilience, fatigability, respiratory frequency, tidal volume, trail running*

f_R	Respiratory frequency
V_T	Tidal volume
$\dot{V}_E$	Minute ventilation
LRC	Locomotor-respiratory coupling
RPE	Rating of perceived exertion
TT	Time trial

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Introduction

Classical determinants of endurance performance, such as maximal oxygen uptake, fractional utilization and economy, are often profiled when athletes are fresh, but they are known to deteriorate during prolonged exercise. As such, the capacity to withstand this deterioration has been proposed as a potential "fourth dimension" of endurance performance (Hunter et al., 2025; Jones & Kirby, 2025). Although the terms "durability" and "physiological resilience" have often been used interchangeably to describe this capacity, recent work has called for clearer definitions (Meixner et al., 2025). Here we choose the physiologically-based definitions proposed by (Zanini et al., 2025). Durability refers to a change in external output (i.e., running speed) as work accumulates and should be described context-specific (i.e., durability of uphill time-trial performance). The ability to repeat high-intensity efforts (repeatability) should be considered a subcomponent of durability. Physiological resilience refers to the change in the physiological determinants that underpin that output, reflecting the robustness of the cardiorespiratory, metabolic and neuromuscular systems to maintain function as work accumulates. Durability thus describes the functional consequence, and physiological resilience its physiological basis. Fatigability is not a synonym for either term; rather, fatigue develops progressively during exercise as a multifactorial phenomenon that includes both physiological and perceptual components (Amann, 2011). In the current study, this distinction maps directly onto the design: the decline in self-paced time-trial performance (distance covered) indexes durability; gas exchange and ventilatory efficiency index physiological resilience, and breathing pattern and perceived exertion provide a window into the fatigue processes that link the two.

Best practice for measuring durability and physiological resilience is still debated. Different exercise protocols (i.e., relative intensity, duration) can induce varying responses (Hunter et al., 2025), and changes in oxygen consumption or ventilatory thresholds show poor test-retest reliability (Malinen et al., 2026). Running economy and heart rate (HR) show moderate reliability, so "decoupling" indices (i.e., HR:speed) are practically useful metrics that might effectively discriminate performance differences (Smyth et al., 2022). There remains a need to better profile psychophysiological changes underpinning the known performance changes during long-duration exercise. Breathing is a candidate marker of the fatigue processes underlying durability, as ventilation ($\dot{V}_E$) and respiratory frequency (f_R) are particularly sensitive to acute changes in fatigue, effort, and other stressors (Nicolo et al., 2017). However, in the literature $\dot{V}_E$ is seldom separated into f_R and V_T for analysis. One counterexample demonstrated that, after 2 h of moderate-intensity cycling, $\dot{V}_E$ at the first ventilatory threshold (VT1) was unchanged but produced with +16% f_R and −16% V_T (Stevenson et al., 2024). Furthermore, Rothschild et al. (2025) found that f_R and HR decoupling (but not $\dot{V}_E$ decoupling) tracked power loss at VT1 across 2.5 h cycling. Not only does f_R drift track fatigue and time-on-task, but it is also sufficiently repeatable between sessions (Rogers et al., 2025). Lloria-Varella et al. (2026) reported that f_R increases

during a simulated trail running race despite constant load and energy cost of running. Current ventilatory control theories suggest that f_R and V_T might diverge during intense or prolonged exercise, since f_R is driven more by central command and muscle afferent feedback and closely tracks ratings of perceived exertion (RPE) (Nicolo & Sacchetti, 2023). RPE increases at fixed submaximal intensity during prolonged exercise (Foster et al., 2025; Jaen-Carrillo, Bruce, Gobbo, et al., 2026). While some studies have proposed f_R as a marker to track internal load during repeated intervals, until now no study has investigated decomposed $\dot{V}_E$ across prolonged running with maximal efforts. Rather, it is unknown if breathing pattern changes monotonically with time-on-task, and how within-bout responses differ from between-bout changes.

Trail running combines prolonged submaximal running with repeated climbs, leading to performance decrements of ~7% over 3 h (Jaen-Carrillo, Bruce, Gobbo, et al., 2026). In this cohort, HR and RPE increased with concomitant biomechanical changes, but OXYGEN CONSUMPTION and energy cost were stable. Breathing pattern was not yet examined. Since the fixed submaximal speed led to negligible metabolic changes, any breathing pattern changes could be linked to perceptual changes, time-on-task, or exposure to higher-intensity efforts. Given the observed stride biomechanics changes, and the theoretical f_R response, there might also be changes in locomotor-respiratory coupling (LRC). An estimated 40-80% of runners express some degree of LRC, usually at ratios of 4:1 or 6:1 steps per breath (Stickford & Stickford, 2014). Some evidence suggests it is more prevalent at higher relative intensities (Bechbache & Duffin, 1977; Fulton et al., 2018); this could be an adaptive response since LRC may contribute up to 10-12% minute ventilation (Daley et al., 2013). While this ventilatory mechanism might affect physiological or perceptual responses, there is a paucity of LRC data reports during prolonged exercise, so it is unclear how it relates to longer efforts.

The aim of this study was to characterize breathing pattern (f_R, V_T, $\dot{V}_E$ and LRC) during a trail-running specific treadmill task, and to examine the within and between-bout responses to submaximal and time trial runs, interpreting them in relation to the durability of time-trial performance and the physiological resilience of gas exchange.

Methods

This study is a secondary planned analysis of a previous study (Jaen-Carrillo, Bruce, Gobbo, et al., 2026; Jaen-Carrillo, Bruce, Lawley, et al., 2026); refer there for full participant and protocol details.

Participants

Twenty-three trained runners (11F) completed this study (Table 1). Participants provided written informed consent, and the protocol was approved by the University of Innsbruck Ethics Committee

(approval no. 109/2024) following the Declaration of Helsinki. Participants were eligible if they were at least 18 years old, had a minimum of 2 years trail-running experience, trained ≥50 km·week^{-1} with ≥800 m of accumulated elevation gain, and had no current musculoskeletal injuries.

Experimental design

Participants attended the laboratory for three visits within 14 days. They avoided caffeine, alcohol, and strenuous exercise for 24 hours before each visit, wore the same running shoes, and were asked to replicate their dietary intake and exercise routine within 48 hours before each visit. Running tests were performed on a motorized treadmill (HP Cosmos Pulsar 4P, HP Cosmos Sports & Medical) under standardized environmental conditions (21–24°C, 45–55% relative humidity), with airflow standardized by a fan (2.55 m·s^{-1}) positioned 1.5 m from the chest.

Figure 1 visualizes the complete running protocol. During the first visit anthropometry was collected, participants were familiarized with the protocol, and a graded exercise test was performed to determine the lactate threshold (LT) and establish the reference intensity for subsequent trials. To ensure sustainable physiological conditions during prolonged exercise, the reference intensity for subsequent trials was set at 85% of the speed at LT + 0.5 mmol·L^{-1} lactate (Jaen-Carrillo, Bruce, Gobbo, et al., 2026). Visit 2 was performed ~72 h later, comprising a single 12-minute uphill time trial at +12% gradient in an unfatigued state (TT0). Speed was self-selected and manually adjusted in real time by an investigator based on the runner's hand signals. TT0 is used henceforth as a reference for every load-matched and between-trial comparison reported here.

Visit 3 included a submaximal 180-minute treadmill run at 85% of the speed at LT + 0.5 mmol·L^{-1}, interspersed with three 12-minute uphill time trials at +12% gradient, performed immediately after each 60-minute submaximal block (TT1, TT2, TT3). Participants consumed 90 g carbohydrate (either as gels and/or formula) and were permitted to drink water ad libitum. RPE was collected using the Borg 6-20 scale at min 20, 40, and 60 of each submaximal block at the end of each time trial. HR was monitored continuously with a Polar H10 (Polar Electro, Finland) and summarized at the same intervals (60 s average at min 20, 40, 60). Respiratory data was collected during visits 2 and 3: TT0-TT3 had continuous data, while submaximal runs had data collected during minutes 5, 35, and 50 (9 submaximal epochs total).



Figure 1. Measurement epochs on a common timeline, with the three sampling windows per block (min 5, 35, 50) and the four time trials marked.

Respiratory measurements

Respiratory data were collected with a heated pneumotachograph and amplifier (Series 1110, Hans Rudolph) routed through a mixing chamber (MLA246, ADInstruments) of an open-circuit metabolic cart (ML206 gas analyzer, ADInstruments). Signals were digitized in LabChart (ADInstruments) and measurement windows were marked by operator comments. Since the expired air passed a mixing chamber, gas fractions are chamber-averaged; hence, the raw pneumotach data was analyzed to produce breath-by-breath values. A per-participant scale factor `k` was derived from the mixing chamber data to scale V_T for subsequent analyses. Mixing chamber oxygen consumption ($\dot{V}O_2$), carbon dioxide production ($\dot{V}CO_2$), respiratory exchange ratio (RER), substrate oxidation, and energy cost were reported previously (Jaen-Carrillo, Bruce, Gobbo, et al., 2026; Jaen-Carrillo, Bruce, Lawley, et al., 2026) and are summarized in the discussion for context. $\dot{V}_E/\dot{V}CO_2$ was extracted from the mixing-chamber data for each sampling window (3-min averages).

External load

The Stryd footpod (Next Gen, Stryd Inc., Boulder, CO, USA) was used continuously throughout the test to record running power and cadence; power was used only as the external-load covariate. These data were time-aligned to the LabChart data; quantization error and drift made phase-resolved LRC impossible but was considered inconsequential for 30 s bins.

Signal processing

All analyses were performed in MATLAB 2026a (The Mathworks, Natick, USA), and all code used in these analyses is available at DOI:10.5281/zenodo.23349161.

Breath-by-breath segmentation was performed using hysteresis thresholding of the rectified inspiratory flow. Inspirations with a mid-inspiratory notch were merged when their inter-breath interval fell below 40% of a 10-breath moving median. Variables extracted include per-breath f_R, V_T, $\dot{V}_E$, and duty cycle (inhale time/breath time). Breaths failing amplitude or duration plausibility were discarded. Median per-participant rejection was 0.07%, and quality control sheets for each participant are available in the supplementary material. A total of 75,415 breaths were analyzed, and breaths were subsequently aggregated to 30-s bins (3,484 bins).

Locomotor–respiratory coupling

Coupling was quantified with an open-source algorithm (calc_LRC v2.0.0, DOI:10.5281/zenodo.23341377.). The Stryd cadence stream and the detected breath onsets were combined to produce instantaneous step:breath ratio, and LRC "attachment" was identified when a runner expressed ≥5 consecutive breaths holding a whole or half-integer ratio for ≥30 s. The percent of breaths attached and the dominant ratio are both reported. Attachment uses the frequency criterion only (phase gate R_min = 0, because phase is not recoverable from Stryd cadence), so % attached is an upper bound to the true value.

Statistical analysis

f_R, V_T, $\dot{V}_E$, $\dot{V}_E/\dot{V}CO_2$ and HR were natural-log transformed before statistical analysis, as recommended by Curran-Everett (2018). This step was performed to stabilize variance and makes the effects more interpretable as percentages (Hopkins et al., 2009; Nevill & Atkinson, 1997). Since $\dot{V}_E = f_R \times V_T$, log $\dot{V}_E$ = log f_R + log V_T exactly; furthermore, any noise in the calculated scale factor `k` is absorbed by per-participant random intercepts. Locomotor-respiratory coupling was averaged at the epoch level on a logit scale (since % attached is bounded from 0-100%), with the same fixed structure and per-participant random intercepts. Coefficients were back-transformed and reported as percentage differences with 95% confidence intervals.

Since 41/197 submaximal epochs (21%) had 0% LRC attached (all TT epochs > 0%), they were bounded at 1%; which this pulled the fitted % lower (e.g., block 1 fitted 19.0% vs raw 32.6%).

For the comparison within and between submaximal blocks linear mixed-effect models (MATLAB package fitlme) was performed with the model:

$$y \sim minC + block + (1 + minC \mid participant) + (1 \mid epoch)$$

where *minC* = (minute mark − 35)/45 min and *block* is a 3-level factor. Random intercepts and random slopes per minute are assigned per-participant; a random intercept for each epoch accounts for the correlation among the 30-s bins within a measurement window. Because speed was fixed, *minC* captures

within-block changes while the block term captures between-block differences. *minC* was centered at min 35 and scaled by the 45-min span from the first to the last window (min 5 to 50) so its coefficient is the estimated change across the whole sampled part of a block.

For the time trials modeling was performed with the formula:

$$y \sim trial + minC + (1 + minC \mid participant) + (1 \mid epoch)$$

Time trial performance (durability) was quantified as distance covered in 12 min, as in the parent study (Jaen-Carrillo, Bruce, Gobbo, et al., 2026), and modeled as:

$$log(distance) \sim trial + (1 \mid participant)$$ (one value per trial)

Similarly, running power was used to evaluate a model at matched external load:

$$y \sim trial + minC + log(power \cdot kg^{-1})_p + (1 + minC \mid participant) + (1 \mid epoch)$$

where $log(power)_p$ is centered within participant. Centering within participant accounts for between-trial pace decline, so the trial coefficient captures ventilatory differences at matched external load (decoupling).

As the min-35 and min-50 samples within the submaximal blocks were 15 min apart at an identical speed, they were considered near-replicates. Typical error (TE) and minimal detectable change (MDC = $1.96 \cdot TE \cdot \sqrt{2}$) were computed from these 66 pairs on the log scale.

Each RPE and HR value were paired with the gas/breathing epoch preceding it: i.e., min 20 RPE – min 5 breathing, 40 – 35, and 60 – 50. Then HR and RPE were modeled for submaximal blocks:

$$y \sim minR + block + (1 \mid participant)$$

where *minR* = (minute − 40)/40, which reflects the change from minute 20 to minute 60 within a block. Time trials were modeled as:

$$y \sim trial + (1 \mid participant)$$

and also with matched load, as described above.

Breathing pattern and RPE associations were assessed within-participant using repeated-measures correlation r_{rm} (Bakdash & Marusich, 2017) of block-mean f_R, V_T, $\dot{V}_E$, HR and $\dot{V}_E/\dot{V}CO_2$ (log scale) and block-mean RPE. r_{rm} was also evaluated for each matched epoch (i.e., RPE – f_R as described above) across the entire run. Within-block r_{rm} were included to isolate within-block covariation, and between-participant Pearson correlations compared block 3 to block 1 (% change vs. RPE points).

Biological sex differences were included as an exploratory analysis. Sex × block and sex × trial interactions were added to each model and tested by likelihood ratio. As a sensitivity check, sex was added as a main-effect covariate to every model.

Results

Data overview

Among the 23 participants 290/299 epochs and 75,415 breaths were analyzed. Eight epochs had mid-trial interruptions (e.g., mouthpiece fell out) or other data loss; these were excluded. One participant's TT3 was excluded as the trial was not completed; all other epochs of this runner were retained. Descriptive data for the entire running test are in Table 1. Gas exchange ($\dot{V}O_2$, $\dot{V}CO_2$, RER, $\dot{V}_E/\dot{V}CO_2$) is in Table S4.

Table 1. Descriptive Statistics for All 13 Epochs in Protocol Order

Epoch	f_R (breaths·min^{-1})	V_T (L)	$\dot{V}_E$ (L/min)	LRC (% attached)	Speed (km/h)	HR (bpm)	RPE (6–20)
TT0	47.6 [44.0, 51.1]	2.19 [2.00, 2.39]	106.3 [92.1, 120.6]	52.3 [43.6, 60.9]	9.31 [8.76, 9.86]	178 [174, 182]	18.6 [18.1, 19.1]
S1_min5	36.4 [33.5, 39.4]	1.74 [1.56, 1.93]	64.6 [56.4, 72.8]	41.0 [29.9, 52.1]	11.2 [10.6, 11.8]	133 [128, 138]	9.5 [8.9, 10.2]
S1_min35	35.4 [32.6, 38.2]	1.75 [1.55, 1.95]	61.9 [55.1, 68.8]	29.7 [16.8, 42.5]	11.2 [10.6, 11.8]	135 [131, 140]	10.1 [9.5, 10.8]
S1_min50	37.2 [33.8, 40.5]	1.71 [1.51, 1.92]	64.2 [56.7, 71.6]	27.7 [15.1, 40.2]	11.2 [10.6, 11.8]	138 [133, 143]	10.2 [9.6, 10.9]
TT1	49.0 [45.6, 52.5]	2.20 [2.01, 2.39]	108.5 [95.7, 121.3]	58.4 [50.5, 66.3]	9.05 [8.55, 9.54]	178 [174, 182]	17.9 [17.4, 18.5]
S2_min5	42.3 [39.4, 45.2]	1.56 [1.43, 1.69]	66.9 [60.8, 73.0]	40.0 [26.5, 53.4]	11.2 [10.6, 11.8]	142 [137, 146]	11.1 [10.4, 11.8]
S2_min35	41.1 [37.9, 44.3]	1.63 [1.49, 1.77]	67.4 [61.5, 73.4]	49.1 [35.5, 62.8]	11.2 [10.6, 11.8]	141 [137, 146]	11.3 [10.6, 12.0]
S2_min50	41.6 [38.7, 44.6]	1.60 [1.47, 1.73]	66.9 [61.1, 72.8]	37.9 [22.6, 53.1]	11.2 [10.6, 11.8]	143 [138, 147]	11.5 [10.6, 12.3]
TT2	50.1 [47.0, 53.3]	2.15 [1.99, 2.31]	107.5 [98.6, 116.5]	53.4 [45.0, 61.9]	9.01 [8.56, 9.46]	179 [175, 182]	18.6 [18.1, 19.1]
S3_min5	44.4 [41.6, 47.1]	1.57 [1.43, 1.71]	70.3 [63.7, 76.9]	42.7 [28.3, 57.0]	11.2 [10.6, 11.8]	147 [142, 152]	12.3 [11.5, 13.2]
S3_min35	42.3 [39.2, 45.4]	1.55 [1.41, 1.70]	67.0 [59.8, 74.1]	47.9 [34.9, 60.8]	11.2 [10.6, 11.8]	147 [143, 151]	12.7 [11.6, 13.7]
S3_min50	43.4 [40.0, 46.8]	1.56 [1.41, 1.71]	68.1 [61.3, 74.9]	51.5 [35.0, 67.9]	11.2 [10.6, 11.8]	148 [144, 153]	13.0 [12.0, 14.0]
TT3	52.5 [48.9, 56.1]	2.04 [1.88, 2.20]	108.4 [98.0, 118.8]	63.5 [55.1, 71.9]	8.82 [8.36, 9.27] (n = 22)	178 [174, 181]	19.3 [18.9, 19.6]

Notes. Values are mean [95% CI]. TT, time trial; S1–S3, submaximal blocks 1–3 at sampling minute 5, 35 and 50; f_R, respiratory frequency; V_T, tidal volume; $\dot{V}_E$, minute ventilation; HR, heart rate; RPE, rating of perceived exertion (HR and RPE were recorded at minutes 20, 40 and 60 of each block and are shown on the row of the preceding sampling window; one value after each time trial); LRC, locomotor–respiratory coupling. V_T and $\dot{V}_E$ are adjusted using a derived scale factor (see Methods); within-participant contrasts are unaffected. Steady-state speed was fixed per participant (85% of the speed at LT + 0.5 mmol·L^{-1}, 1% gradient); time trials at 12% gradient.

Reliability

Bias between the 35- and 50-min data were ≤1.8% for every outcome, supporting their use as replicates (Table 2). Between-block effects exceeded the MDC for f_R, while the time-trial effects did not.

Table 2. Summary of Within-Trial Variability of Ventilatory Variables

Outcome	n pairs	Bias, %	TE, %	MDC, %	SE (group mean), %
f_R	66	1.76	5.21	14.45	1.09
V_T	66	−0.93	6.14	17.01	1.28
$\dot{V}_E$	66	0.93	4.12	11.42	0.86

Notes. TE, typical error; MDC, minimal detectable change; SE, standard error; f_R, respiratory frequency; V_T, tidal volume; $\dot{V}_E$, ventilation.

Submaximal blocks

Breathing pattern did not change within the submaximal blocks (f_R −1.9% [−4.0, +0.3], p = .098; V_T +1.4% [−2.4, +5.3], p = .47; $\dot{V}_E$ −0.8% [−4.0, +2.6], p = .66) (Figure 2). However, between blocks large differences were observed: compared to block 1, f_R increased +14.7% [12.4, 17.1] in block 2 (p < .001) and +19.3% [16.8, 21.9] in block 3 (p < .001). V_T decreased (block 2: −5.3% [−8.1, −2.5], p < .001; block 3: −7.2% [−10.0, −4.4], p < .001), while overall $\dot{V}_E$ increased (block 2: +9.2% [6.2, 12.2], p < .001; block 3: +10.9% [7.8, 14.1], p < .001) (Table 3). $\dot{V}_E/\dot{V}CO_2$ did not change within blocks (−1.0% [−2.1, 0.2], p = .091) but increased between blocks: block 2 +8.1% [6.9, 9.4], block 3 +10.1% [8.8, 11.4] (both p < .001) (Tables 1, 3). Running power was unchanged (3.26 ± 0.36 W·kg^{-1}).

Unlike f_R, RPE and HR increased within blocks: from minute 20 to 60, RPE +0.6 points [0.3, 0.9] and HR +1.6% [0.7, 2.4] (both p < .001). Between blocks RPE increased by +1.3 points [1.1, 1.6] (block 2) and +2.7 points [2.5, 3.0] (block 3) vs block 1 (both p < .001) (Tables 1, 3). HR also increased between blocks (135.5, 142.0 and 147.4 bpm): block 2 +4.8% [3.5, 6.2], block 3 +8.9% [7.5, 10.4] vs block 1 (both p < .001) (Table 3).

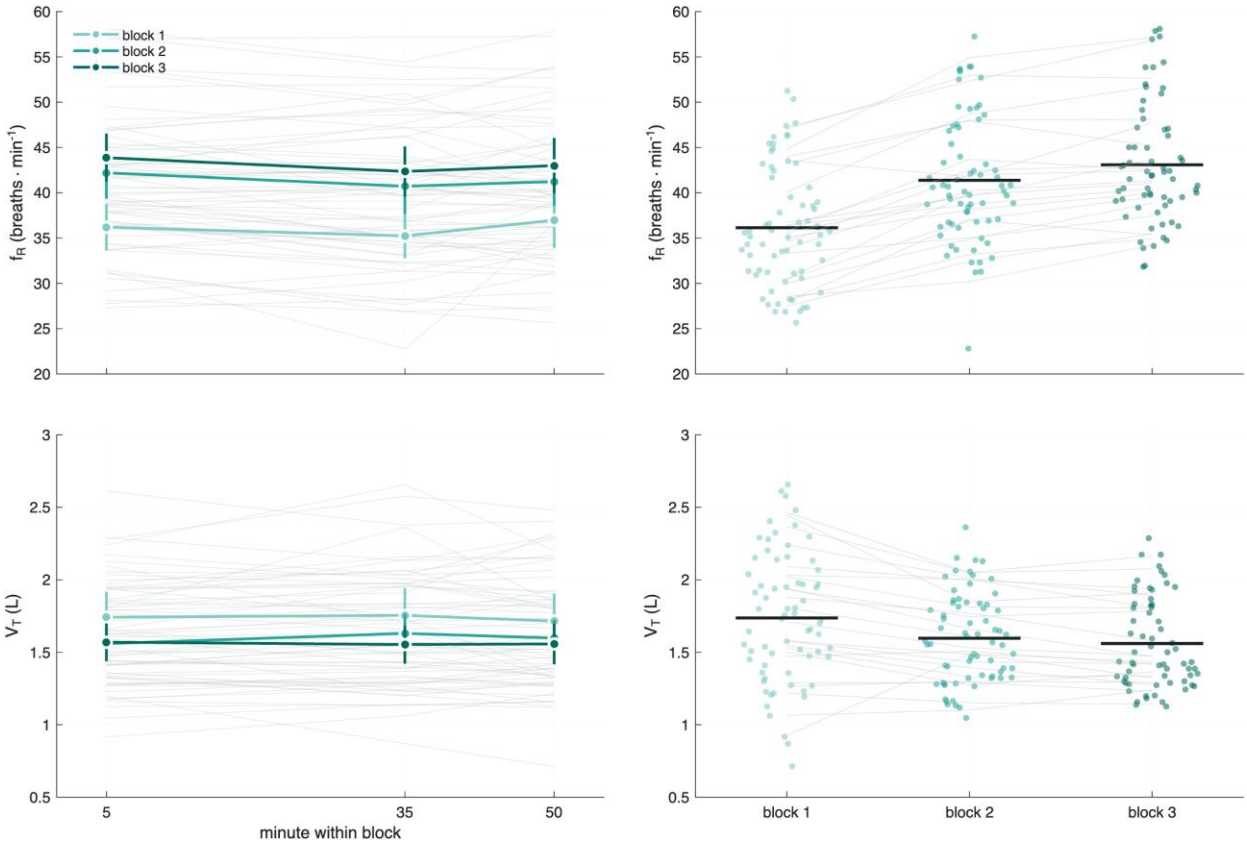


Figure 2. Left column: f_R and V_T against minute within block, one line per participant in gray with the group mean ± 95% CI over the three sampling minutes, colored by block. Right column: swarm charts by block with participant connectors and group-mean bars. f_R, respiratory frequency; V_T, tidal volume.

Table 3. Submaximal model coefficients

Outcome	Term	% difference	95% CI	p
f_R	Within block	−1.9	[−4.0, 0.3]	.098
	Block 2 vs 1	14.7	[12.4, 17.1]	< .001
	Block 3 vs 1	19.3	[16.8, 21.9]	< .001
V_T	Within block	1.4	[−2.4, 5.3]	.474
	Block 2 vs 1	−5.3	[−8.1, −2.5]	< .001
	Block 3 vs 1	−7.2	[−10.0, −4.4]	< .001
$\dot{V}_E$	Within block	−0.8	[−4.0, 2.6]	.656
	Block 2 vs 1	9.2	[6.2, 12.2]	< .001
	Block 3 vs 1	10.9	[7.8, 14.1]	< .001
$\dot{V}_E/\dot{V}CO_2$	Within block	−1.0	[−2.1, 0.2]	.091
	Block 2 vs 1	8.1	[6.9, 9.4]	< .001
	Block 3 vs 1	10.1	[8.8, 11.4]	< .001
HR	Within block	1.6	[0.7, 2.4]	< .001
	Block 2 vs 1	4.9	[4.0, 5.7]	< .001
	Block 3 vs 1	8.9	[8.0, 9.8]	< .001
RPE	Within block	0.6 (points)	[0.3, 0.9]	< .001
	Block 2 vs 1	1.3	[1.1, 1.6]	< .001
	Block 3 vs 1	2.7	[2.5, 3.0]	< .001

Notes. Log-transformed outcomes back-transformed to % difference. f_R, V_T, $\dot{V}_E$: 30-s bins, $\dot{V}_E/\dot{V}CO_2$: one value per epoch; HR and RPE: one value per rating (minutes 20, 40, 60). RPE is modeled on the Borg scale and reported in points. Within

263 block = change from minute 5 to 50 or from minute 20 to 60 (HR, RPE). f_R, respiratory frequency; V_T, tidal volume; $\dot{V}_E$,
264 minute ventilation; $\dot{V}_E/\dot{V}CO_2$, ventilatory equivalent for carbon dioxide; HR, heart rate; RPE, rating of perceived exertion

265

266 **Time trials**

267 During the self-paced time trials, distance covered (i.e., average speed) decreased progressively (TT1
268 −2.8% [−4.7, −0.8], p = .006; TT2 −3.3% [−5.3, −1.4], p = .001; TT3 −5.1% [−7.0, −3.1], p < .001 vs
269 TT0), while running power declined less (TT3 −4.0% [−5.8, −2.1], p < .001). Unadjusted, breathing
270 pattern showed substantial changes: for TT3 vs TT0, f_R was +12.5% (p < .001), V_T −7.1% (p < .001),
271 and $\dot{V}_E$ showed a statistically negligible increase (+4.3%, p = .086) (Figure 3). At matched external load
272 these differences held (f_R +13.4% [9.5, 17.5], p < .001; V_T −6.6% [−9.8, −3.2], p < .001; $\dot{V}_E$ +5.6% [0.9,
273 10.6], p = .019) (Figure 4). Coefficients for both models are contained in Table 4. The changes were
274 graded across time trials: for example, f_R increased +3.6% (p = .046), +7.3% (p < .001), and +13.4% (p
275 < .001) in TT1-TT3 respectively. f_R was not associated with external load within participants (r_{rm} = 0.03
276 [−0.01, 0.07], p = .170) while V_T was (r_{rm} = 0.20 [0.15, 0.24], p < .001).

277 $\dot{V}_E/\dot{V}CO_2$ increased consistently between trials (TT1 +4.2% [2.4, 6.1], TT2 +7.8% [5.9, 9.8], TT3
278 +10.7% [8.7, 12.7] vs TT0; all p < .001) and load was not associated with $\dot{V}_E/\dot{V}CO_2$ (p = .662) (Table
279 4). HR was near-maximal and similar in every trial (178.0 bpm at TT0; 177.8, 178.5 and 177.5 bpm in
280 TT1–TT3; all p ≥ .617 vs TT0).

281 The association between f_R and external load was weak but significant within time trials (r_{rm} = 0.05
282 [0.01, 0.09], p = .017), but not between trials (r_{rm} = −0.01 [−0.25, 0.22], p = .904). f_R increased +2.6%
283 per trial minute (r_{rm} = 0.67), whereas external load did not (r_{rm} = 0.00). The V_T–load association was
284 stronger between trials (r_{rm} = 0.38 [0.16, 0.57]) than within trials (0.08 [0.04, 0.12]).

285 RPE was near maximal in every trial (18.6, 17.9, 18.6, 19.3); vs TT0, TT1 −0.7 points [−1.1, −0.3] (p =
286 .002), TT2 +0.0 points [−0.4, 0.4], TT3 +0.7 points [0.3, 1.1] (p = .002). Thus at TT3, f_R was +13.4%
287 higher at matched load with RPE <1 point and HR <1% different from TT0 (Tables 1, 4).

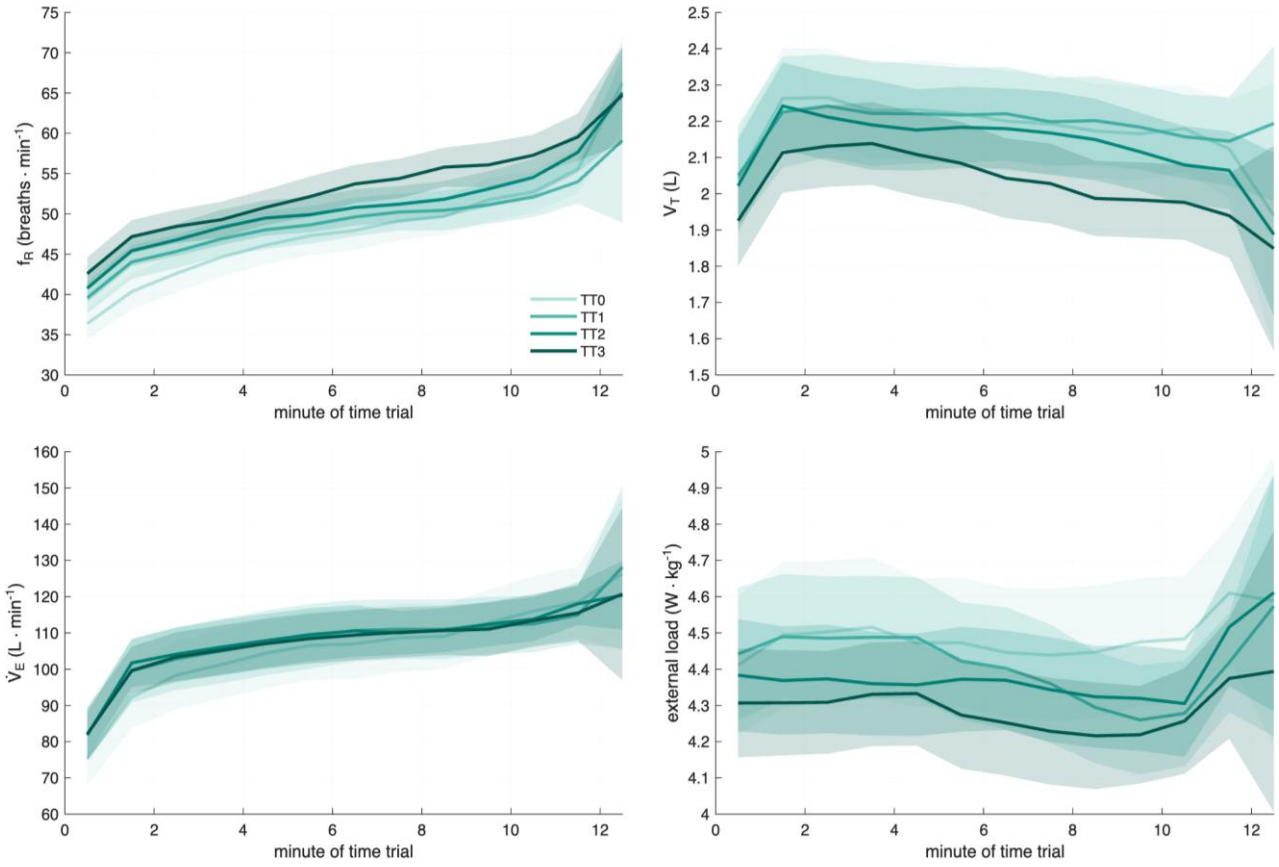


Figure 3. Within-trial time courses (f_R, V_T, $\dot{V}_E$, external load) against minute of trial. Lines represent the group mean with 95% CI ribbon with one color per trial. f_R, respiratory frequency; V_T, tidal volume; $\dot{V}_E$, minute ventilation.

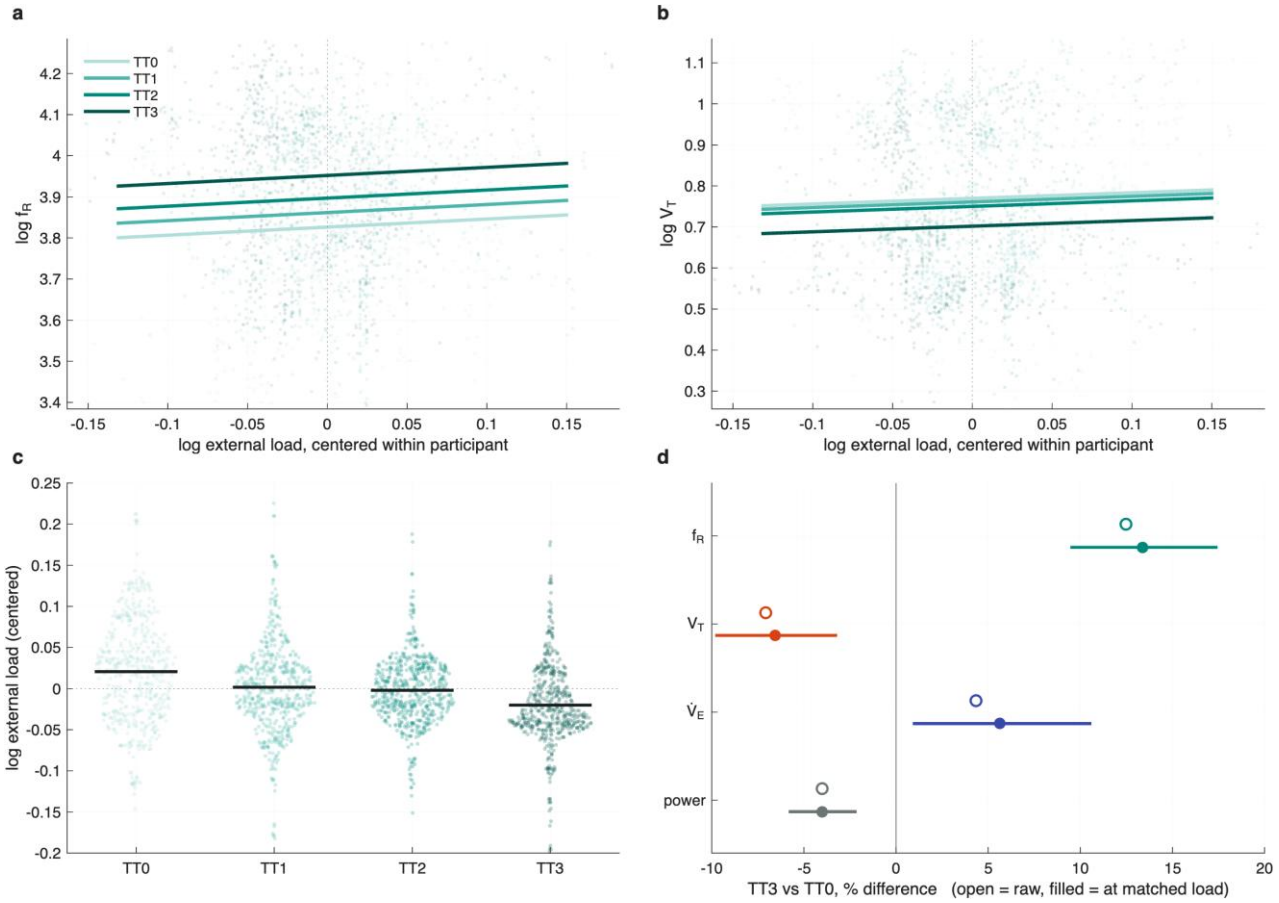


Figure 4. Matched-load comparison in four panels: (a) f_R and (b) V_T against external load with fitted lines per trial, (c) the distribution of centered load per trial, and (d) raw vs matched-load TT3−TT0 differences. f_R, respiratory frequency; V_T, tidal volume; $\dot{V}_E$, minute ventilation.

Table 4. Time-Trial Model Coefficients

Outcome	Term	Raw, %	95% CI	p	Matched, %	95% CI	p
f_R	TT1 vs TT0	3.2	[−0.4, 7.0]	.085	3.6	[0.1, 7.2]	.046
	TT2 vs TT0	6.8	[3.0, 10.7]	< .001	7.3	[3.7, 11.1]	< .001
	TT3 vs TT0	12.5	[8.4, 16.7]	< .001	13.4	[9.5, 17.5]	< .001
	Minute of trial (per min)	2.6	[2.2, 3.0]	< .001	2.6	[2.2, 3.0]	< .001
	External load (per +10%)	—	—	—	1.9	[1.2, 2.6]	< .001
V_T	TT1 vs TT0	−1.1	[−4.6, 2.4]	.529	−0.9	[−4.3, 2.6]	.623
	TT2 vs TT0	−2.3	[−5.7, 1.3]	.204	−1.9	[−5.3, 1.5]	.269
	TT3 vs TT0	−7.1	[−10.4, −3.7]	< .001	−6.6	[−9.8, −3.2]	< .001
	Minute of trial (per min)	−0.2	[−0.4, 0.0]	.065	−0.2	[−0.4, 0.0]	.072
	External load (per +10%)	—	—	—	1.3	[0.7, 2.0]	< .001
$\dot{V}_E$	TT1 vs TT0	2.0	[−2.8, 7.0]	.420	2.6	[−1.9, 7.3]	.269
	TT2 vs TT0	4.3	[−0.5, 9.4]	.081	5.1	[0.5, 9.9]	.031
	TT3 vs TT0	4.3	[−0.6, 9.5]	.086	5.6	[0.9, 10.6]	.019

Outcome	Term	Raw, %	95% CI	p	Matched, %	95% CI	p
	Minute of trial (per min)	2.4	[2.0, 2.8]	< .001	2.4	[2.0, 2.8]	< .001
	External load (per +10%)	—	—	—	2.9	[2.0, 3.8]	< .001
$\dot{V}_E/\dot{V}CO_2$	TT1 vs TT0	4.2	[2.4, 6.1]	< .001	4.6	[2.7, 6.6]	< .001
	TT2 vs TT0	7.8	[5.9, 9.8]	< .001	8.3	[6.3, 10.3]	< .001
	TT3 vs TT0	10.7	[8.7, 12.7]	< .001	11.2	[9.1, 13.4]	< .001
	External load (per +10%)	—	—	—	0.4	[−1.5, 2.4]	.662
HR	TT1 vs TT0	−0.1	[−1.3, 1.1]	.844	0.3	[−0.9, 1.5]	.605
	TT2 vs TT0	0.3	[−0.9, 1.6]	.617	0.8	[−0.4, 2.0]	.179
	TT3 vs TT0	−0.2	[−1.5, 1.0]	.703	0.7	[−0.5, 2.0]	.262
	External load (per +10%)	—	—	—	2.5	[1.2, 3.8]	< .001
RPE (points)	TT1 vs TT0	−0.7	[−1.1, −0.3]	.002	−0.6	[−1.0, −0.2]	.008
	TT2 vs TT0	0.0	[−0.4, 0.4]	> .999	0.1	[−0.3, 0.6]	.542
	TT3 vs TT0	0.7	[0.3, 1.1]	.002	1.0	[0.5, 1.4]	< .001
	External load (per +10%)	—	—	—	0.7	[0.2, 1.2]	.003
Distance (mean speed)	TT1 vs TT0	−2.8	[−4.7, −0.8]	.006	—	—	—
	TT2 vs TT0	−3.3	[−5.3, −1.4]	.001	—	—	—
	TT3 vs TT0	−5.1	[−7.0, −3.1]	< .001	—	—	—

Notes. Log-transformed outcomes back-transformed to % difference (RPE in Borg points). f_R, respiratory frequency; V_T, tidal volume; $\dot{V}_E$, minute ventilation; $\dot{V}_E/\dot{V}CO_2$, ventilatory equivalent for carbon dioxide; HR, heart rate; RPE, rating of perceived exertion

Perceived exertion and breathing pattern

f_R was associated with RPE both at the block (r_{rm} = 0.79 [0.65, 0.88]) and epoch-level (r_{rm} = 0.66) for the submaximal blocks (Table 5). Within blocks there was no association (p = .760), despite a weak association between $\dot{V}_E$ and RPE (−0.20, p = .021). The change in RPE from block 1 to 3 was not substantially associated with any variables here.

Table 5. Breathing pattern, HR and perceived exertion (RPE) across submaximal blocks

Variable	r_{rm}, block means	p	r_{rm}, within blocks	p	Δ block 3 vs 1, %	r (Δ vs ΔRPE)	p
f_R	0.79 [0.65, 0.88]	< .001	−0.03 [−0.20, 0.14]	.760	+19.7	0.33 [−0.11, 0.66]	.136
V_T	−0.42 [−0.64, −0.15]	.003	−0.14 [−0.31, 0.03]	.099	−7.3	0.00 [−0.42, 0.42]	.989
$\dot{V}_E$	0.47 [0.21, 0.67]	< .001	−0.20 [−0.36, −0.03]	.021	+10.0	0.11 [−0.33, 0.51]	.626
HR	0.76 [0.60, 0.86]	< .001	0.17 [0.00, 0.33]	.051	+9.0	0.00 [−0.41, 0.41]	.989

Variable	r_{rm}, block means	p	r_{rm}, within blocks	p	Δ block 3 vs 1, %	r (Δ vs ΔRPE)	p
$\dot{V}_E/\dot{V}CO_2$	0.76 [0.61, 0.86]	< .001	—	—	+10.2	0.26 [−0.17, 0.61]	.235

Notes. Values are r [95% CI]. r_{rm}, block means: repeated-measures correlation of block means with block-mean RPE (3 per participant; df = 44). r_{rm}, within blocks: each breathing epoch (min 5, 35, 50) paired with the following rating (min 20, 40, 60), grouped by participant × block (df = 131); $\dot{V}_E/\dot{V}CO_2$ was not available at the epoch level for all participants. r (Δ vs ΔRPE): Pearson correlation across participants of the block 1 to 3 change in each variable with the change in RPE (mean ΔRPE = +2.7 points; n = 22–23).

Locomotor–respiratory coupling

LRC was higher during the time trials (56.9%) than during submaximal running (40.6%) (Figure 5). Between submaximal blocks LRC increased (block 2 vs 1 β = 0.74 [0.08, 1.39], p = .029; block 3 vs 1 β = 1.14 [0.48, 1.80], p < .001), but there was no change within blocks (p = .123). LRC was higher in TT3 vs. TT0 (β = 0.56 [0.10, 1.02], p = .019) but not in TT1 or TT2 (p = .241 and .803, respectively). Preferred LRC ratio changed between submaximal blocks: it was most commonly 5:1 in block 1 (38% of epochs), and 4:1 in blocks 2 and 3 (45% and 64%). During the time trials it was most commonly 3:1 (39–50%).

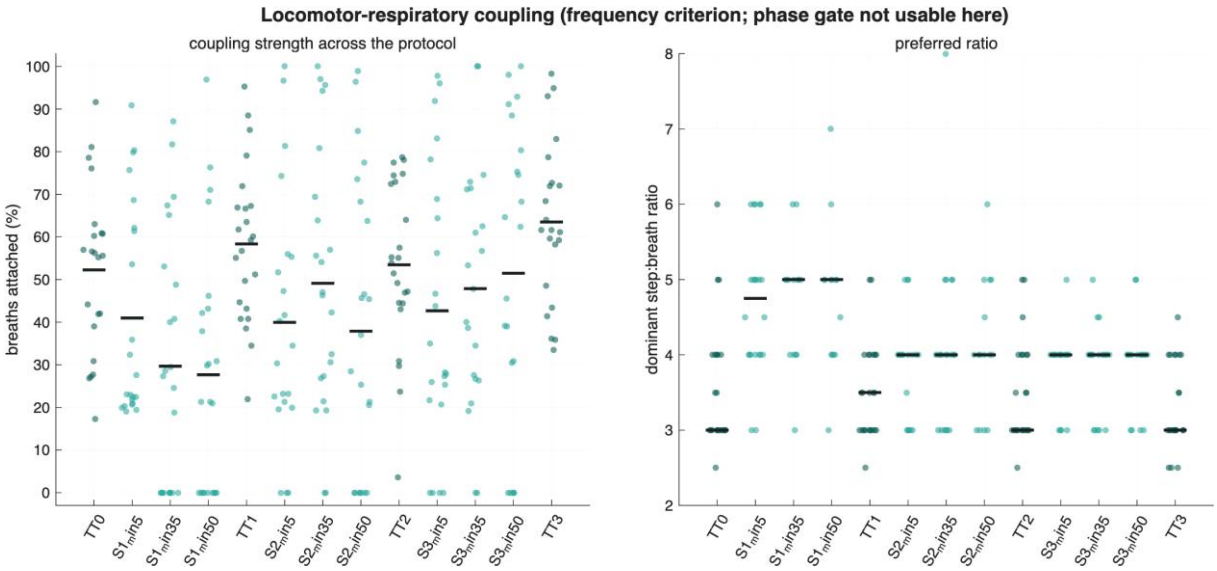


Figure 5. Locomotor-respiratory coupling strength (% breaths attached) and dominant step:breath ratio across all 13 epochs.

Sex differences

f_R responses did not differ by sex: in submaximal block 3 vs. 1 females increased +18.4% while males did +20.2% (interaction p = .674). For TT3 vs TT0 at matched load females increased +16.7% while males did +10.1% (interaction p = .126) (Table S6). V_T decreased more in males between blocks (−9.6% vs. females −4.4%, interaction p = .010), while males increased RPE more than females (+3.4 vs. +2.0 points, interaction p < .001). $\dot{V}_E$ trended higher in females (+12.8% vs. males +9.3%, interaction p = .078). No effect of biological sex was found for $\dot{V}_E/\dot{V}CO_2$, HR or the time-trial contrasts (all $p \geq 0.07$). Adding sex as a covariate had statistically negligible effects on both submaximal and time trial comparisons.

Discussion

This study examined acute and long-duration changes in breathing pattern during a prolonged laboratory trail running simulation. Within submaximal bouts most parameters were stable; however, runners increased f_R, $\dot{V}_E$, and decreased V_T between bouts. The magnitude of f_R change exceeded that of V_T, perhaps reflecting the acute effort increase on either side of the time trial. Within and between-time trial responses corroborate this interpretation: not only did absolute performance decrease (lower speed), but f_R increased consistently and out-of-proportion to the V_T decrease. Hence, the time trial triggered distinct adjustments in the breathing pattern that persisted throughout the following submaximal bout, indicating incomplete recovery. Locomotor-respiratory coupling, another component of breathing pattern, showed similar sensitivity to the time trial: it was higher than during submaximal running, and it showed a stepwise change between blocks. Together these findings support an exposure-dependent relationship between trail-running specific demands and breathing pattern responses in line with current ventilatory control theories. Within the framework of Zanini et al. (2025), time-trial performance declined (i.e., reduced durability) while $\dot{V}O_2$ and energy cost were preserved (i.e., high metabolic resilience); the breathing pattern adjustments therefore appear to reflect the fatigue processes that contribute to durability (e.g., central command and effort), rather than a loss of metabolic resilience.

Previous investigations of these data showed the submaximal trials were steady state with consistent within-block $\dot{V}O_2$, energy cost, low blood lactate, and RER (Jaen-Carrillo, Bruce, Gobbo, et al., 2026). The current study showed that breathing pattern was also stable; only HR and RPE increased within blocks (Table 3). Between blocks, all studied variables (f_R, V_T, $\dot{V}_E$, $\dot{V}_E/\dot{V}CO_2$, HR, and LRC ratio) showed marked changes. For example, the 15–19% between-block increase in f_R occurred despite no change in $\dot{V}CO_2$ (−1.0% [−2.9, 1.0]) and only slight increases in $\dot{V}O_2$ (+2.0% [0.1, 3.8]) (Tables S4-S5). The pattern changes reported here (block 3 vs. 1, f_R +19%, V_T −7%) are similar to those reported by Stevenson et al. (2024) (+16% / −16% at VT1 after 2 h cycling) and Lloria-Varella et al. (2026) (+16% / −9%). Furthermore, the increased $\dot{V}_E/\dot{V}CO_2$ (~10% across blocks) was primarily due to increased $\dot{V}_E$,

despite decreased V_T (~5-7%). The decrease in ventilatory efficiency may be explained by the tachypneic pattern and increased dead space ventilation. Decreasing V_T could occur secondary to the increasing f_R, although the increased $\dot{V}_E$ and dissociation of $\dot{V}_E$ and $\dot{V}CO_2$ suggests that f_R changes were out-of-proportion (in excess) to ventilatory demand. This could be a hyperventilatory response secondary to the increased central command drive to breathe, although end-tidal CO_2 could not be resolved in these data to confirm this. Regardless, this change in breathing pattern was likely not due to metabolic demand.

During the time trials performance declined (i.e., reduced durability; distance covered −5.1% [−7.0, −3.1] TT3 vs. TT0; −6.6% in the full cohort of the parent study) despite stable HR, $\dot{V}O_2$, and decreasing $\dot{V}CO_2$ (5–9%, Table S5). RPE was near maximal (18-19) while RER and blood lactate decreased. Since f_R was higher at matched load, the "excess" frequency" is unlikely to be metabolically driven. Most likely the f_R response was due to increased central command and effort, which is known to stimulate f_R particularly at higher intensities (Nicolo et al., 2025). Within each time trial f_R increased while external load was flat (r_{rm} = 0.00). Within participants f_R was associated with RPE (r_{rm} = 0.79) more closely than $\dot{V}_E$ (0.47) or V_T (−0.42). Across runners, bigger RPE changes had a nonsignificant positive association with f_R changes (r = 0.33 [−0.11, 0.66]) but not with V_T or HR (r ≈ 0). In addition, there could be increased contribution from muscle afferent feedback, as maximal voluntary contraction was altered in men specifically in this study (Jaen-Carrillo, Bruce, Lawley, et al., 2026). These observations specifically align with the differential control model as outlined by (Nicolo & Sacchetti, 2023). Other contributors such as respiratory muscle fatigue (Mador & Acevedo, 1991) and thermal load (measured 2.3% body-mass loss, sweat rate ~1.1 $L \cdot h^{-1}$ in Jaen-Carrillo, Bruce, Gobbo, et al. (2026); see also Gonzalez-Alonso et al. (2023)) may contribute to the tachypneic response.

Locomotor-respiratory coupling (LRC) followed a similar exposure-dependent trend like breathing pattern: LRC was higher during the time trials than during submaximal running, increased stepwise between submaximal blocks, and stayed consistent within each block. Because cadence was stable between blocks, the shift in preferred ratio from 5:1 to 4:1 was mainly driven by increasing f_R rather than any changes in stride timing. The combination of increased f_R and higher LRC is counterintuitive, since higher f_R mathematically limits the boundaries of spontaneous coupling: at an average cadence of 170 steps per minute observed in this cohort (Jaen-Carrillo, Bruce, Lawley, et al., 2026), an LRC ratio of 4:1 corresponds to about 43 breaths per minute. Ratios of 5:1 to 8:1 correspond to a f_R between 20-35, which are plausible respiratory frequencies for the submaximal intensity running. A ratio of 3:1 implies f_R = 57, which reflects peak exercise intensity (Neder et al., 2003). Hence, the range of "available" ratios at submaximal intensity is wider than at higher intensities, which suggest that spontaneous coupling is more likely at lower intensities. The current study observed the opposite: the increasing LRC prevalence in blocks 2 and 3 and higher prevalence in the time trials strongly suggests

that LRC is stimulated by intensity and fatigue as suggested previously (Bechbache & Duffin, 1977; Fulton et al., 2018). It is still unknown whether the "step-driven flows" mechanism of LRC contributes to its prevalence or implications such as reduced work of breathing.

The inclusion of repeated-measures correlation to RPE revealed a dissociation between f_R and effort: during the time trials RPE and HR were near-maximal and unchanged, but f_R was +13.4% higher at matched load in TT3. Within-trial f_R also increased ~2.6%·min^{-1} independent of load. During the submaximal blocks RPE increased +0.6 points while f_R did not change (−1.9%), and f_R did not co-vary with RPE within blocks ($r_{rm} = -0.03$). Thus, observed changes in RPE were not associated with observed changes in f_R. Rather, breathing pattern responded in a stepwise fashion after exposure to each time trial effort, while RPE slowly drifted upwards throughout each submaximal block. Since these blocks were at a lower relative intensity, changes in effort and central command may modulate f_R to a lesser degree compared to at higher intensities (Nicolo & Sacchetti, 2023). The higher-intensity time trials stimulated breathing pattern changes to a large degree, but with only one discrete RPE value collected at the end of the time trial, acute changes in the f_R – RPE relationship were not measured. In this context the f_R – RPE association was weaker than previously reported in incremental exercise or shorter time trials (Nicolo et al., 2016).

Exploratory analyses showed that f_R changes were similar in both sexes (block 3 vs 1 +18.4% vs +20.2%), but male participants showed a larger V_T decrease (−9.6% vs −4.4%) and a larger RPE response (+2.0 vs +3.4 points). This parallels the previous report that showed greater durability and physiological resilience in the female runners (Jaen-Carrillo, Bruce, Lawley, et al., 2026). Other studies have reported that female athletes demonstrate smaller breathing pattern changes (i.e., time on task effects) compared to males at equivalent relative exercise intensities (Archiza et al., 2021; Dominelli & Molgat-Seon, 2022; LoMauro & Aliverti, 2021). As the study was not powered for sex comparisons, these findings should be considered hypothesis-generating.

Limitations

The examination between submaximal blocks is confounded by the study design, since later blocks include not only exercise duration but also interspersed maximal efforts. Regardless, this is an inherent feature of this design as it replicates real-world trail running. While breath-by-breath data was reconstructed from the raw pneumotach data, the calibration data were unrecoverable, so absolute V_T and $\dot{V}_E$ are reported on a scaled axis. Since this analysis compares within-participants, the conclusions are unaffected; however, the values reported in Table 1 may be inaccurate. Mixing chamber values are reported in Table S4. Since HR and RPE data were recorded at different intervals than respiratory epochs, the epoch-level pairing is approximate and might affect reported outcomes. Autocorrelation within time trial epochs was 0.42–0.63 (median), thus every model was refitted on epoch means and

every conclusion remained (Table S1). Since LRC calculations can differ depending on frequency or phase criterion, the frequency-only analysis performed here likely overestimates LRC prevalence; within-participant differences are likely correct while absolute levels are only descriptive. Running power was estimated with a foot-worn sensor, which may underestimate the 12% treadmill gradient; this may explain why power declined less than distance covered across the time trials (TT3 vs TT0 −4.0% vs −5.1%), and could cause the matched-load models to slightly underestimate the true load decline. Footpod speed was likewise unreliable on the incline, so performance was taken from treadmill distance.

Practical applications

This study highlights how breathing pattern monitoring is especially relevant to trail running with interspersed high-intensity efforts. f_R showed the greatest sensitivity to the uphill time trials, while virtually all variables changed in a stepwise fashion after subsequent time trials. Future studies of long-duration exercise might use this information to complement durability and physiological resilience assessments and better understand internal to external workload coupling across interspersed bouts of varying intensity. Including LRC and RPE in scientific studies can help illuminate mechanistic underpinnings of exercise physiology and performance.

Conclusions

In trained trail runners completing a specific treadmill task, respiratory frequency and minute ventilation increased while tidal volume decreased. This response tracked exposure to maximal efforts, rather than continuous time-on-task drift, and was accompanied by a strengthening of locomotor–respiratory coupling. These findings characterize the breathing pattern response to a trail-running specific test as an exposure-dependent, intensity-dependent adjustment rather than a continuous time-on-task drift, and support decomposing $\dot{V}_E$ into f_R and V_T whenever ventilatory responses are used to assess durability and physiological resilience.

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Author Contributions

EH: software, formal analysis, visualization, writing – original draft, writing – review & editing. DJC: conceptualization, methodology, investigation, data curation, project administration, writing – review & editing.

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Data Availability

All analysis code is available as a single MATLAB live script (durability_analysis.mlx) at DOI:10.5281/zenodo.23349161, which reproduces every number and figure reported in this paper.

Supplementary Tables

Table S1. Epoch-level sensitivity refits (one value per epoch; no within-epoch serial correlation)

Model	Term	% difference	95% CI	p
f_R (submaximal)	Within block (min 5 → 50)	−1.8	[−3.9, 0.2]	.083
	Block 2 vs 1	14.7	[12.3, 17.2]	< .001
	Block 3 vs 1	19.4	[16.8, 22.0]	< .001
f_R (time trials, matched load)	TT1 vs TT0	4.8	[1.3, 8.4]	.008
	TT2 vs TT0	8.9	[5.3, 12.7]	< .001
	TT3 vs TT0	15.8	[11.5, 20.2]	< .001
	External load (per +10%)	7.1	[2.9, 11.4]	< .001
V_T (submaximal)	Within block (min 5 → 50)	1.4	[−1.7, 4.5]	.388
	Block 2 vs 1	−5.3	[−8.2, −2.4]	< .001
	Block 3 vs 1	−7.3	[−10.2, −4.3]	< .001
V_T (time trials, matched load)	TT1 vs TT0	−0.3	[−3.9, 3.5]	.892
	TT2 vs TT0	−1.7	[−5.3, 2.0]	.360
	TT3 vs TT0	−5.3	[−9.1, −1.3]	.010
	External load (per +10%)	4.6	[0.1, 9.2]	.044
$\dot{V}_E$ (submaximal)	Within block (min 5 → 50)	−0.8	[−3.5, 2.0]	.573
	Block 2 vs 1	9.2	[6.1, 12.3]	< .001
	Block 3 vs 1	10.8	[7.7, 14.1]	< .001
$\dot{V}_E$ (time trials, matched load)	TT1 vs TT0	4.5	[−0.2, 9.4]	.059
	TT2 vs TT0	7.1	[2.3, 12.1]	.004
	TT3 vs TT0	9.7	[4.3, 15.3]	< .001
	External load (per +10%)	12.2	[6.4, 18.4]	< .001

Notes. Same fixed effects as the main models, fitted to epoch means with a participant random intercept. Matched-load models use epoch-mean log power centered within participant; load expressed per +10% running power.

Table S2. Within-epoch residual lag-1 autocorrelation (time-trial matched-load models)

Outcome	Median lag-1 r	90th percentile
f_R	0.51	0.80
V_T	0.42	0.75
$\dot{V}_E$	0.65	0.84

Notes. Lag-1 autocorrelation of 30-s-bin residuals within each epoch; motivates the epoch-level refits in Table S1.

Table S3. Locomotor–respiratory coupling (percent of breaths attached), logit-scale mixed models

Model	Term	β (logit)	95% CI	Odds ratio	p
Submaximal	Block 2 vs 1	0.74	[0.08, 1.39]	2.09	.029
	Block 3 vs 1	1.14	[0.48, 1.80]	3.14	< .001
	Within block (min 5 → 50)	−0.51	[−1.16, 0.14]	0.60	.123
Time trials	TT1 vs TT0	0.27	[−0.19, 0.73]	1.31	.241
	TT2 vs TT0	−0.06	[−0.51, 0.40]	0.94	.803
	TT3 vs TT0	0.56	[0.10, 1.02]	1.75	.019

Notes. logit(% attached) ~ minC + block + (1 | participant) for submaximal epochs and ~ trial + (1 | participant) for time trials; proportions bounded at 1–99% before the logit. Fitted % attached: blocks 1–3 19.0, 32.8, 42.3; TT0–TT3 54.0, 60.6, 52.5, 67.2

Table S4. Gas exchange from the laboratory summary sheet (3-min mixing-chamber averages)

Epoch	$\dot{V}O_2$ (mL/kg/min)	$\dot{V}CO_2$ (L/min)	RER	$\dot{V}_E$ (L/min)	$\dot{V}_E/\dot{V}CO_2$
TT0	49.9 [47.1, 52.7]	3.18 [2.81, 3.55]	0.94 [0.91, 0.96]	111.1 [98.2, 124.1]	35.1 [33.6, 36.5]
S1_min5	32.8 [30.3, 35.2]	1.87 [1.63, 2.12]	0.83 [0.82, 0.85]	66.5 [57.8, 75.1]	35.6 [34.2, 37.0]
S1_min35	33.4 [31.2, 35.6]	1.87 [1.65, 2.09]	0.81 [0.79, 0.83]	66.5 [59.4, 73.7]	35.9 [34.5, 37.3]
S1_min50	33.6 [31.4, 35.7]	1.92 [1.71, 2.12]	0.83 [0.81, 0.85]	69.2 [62.4, 76.0]	36.5 [34.8, 38.2]
TT1	48.7 [46.0, 51.4]	3.01 [2.69, 3.33]	0.91 [0.89, 0.92]	110.0 [97.8, 122.3]	36.5 [35.2, 37.9]
S2_min5	33.3 [31.1, 35.5]	1.77 [1.59, 1.96]	0.80 [0.78, 0.81]	69.5 [62.7, 76.3]	39.5 [37.8, 41.2]
S2_min35	33.3 [31.2, 35.5]	1.82 [1.63, 2.01]	0.82 [0.80, 0.84]	69.1 [62.6, 75.7]	38.3 [36.6, 40.0]
S2_min50	33.0 [30.7, 35.3]	1.80 [1.61, 1.99]	0.82 [0.80, 0.84]	68.9 [62.3, 75.6]	38.6 [37.0, 40.1]
TT2	49.1 [46.6, 51.6]	2.95 [2.66, 3.24]	0.89 [0.87, 0.91]	111.1 [100.1, 122.1]	37.8 [36.4, 39.2]
S3_min5	34.4 [32.3, 36.4]	1.84 [1.65, 2.03]	0.79 [0.78, 0.81]	73.4 [66.4, 80.4]	40.3 [38.7, 41.8]
S3_min35	33.7 [31.7, 35.7]	1.82 [1.63, 2.00]	0.80 [0.78, 0.82]	70.3 [63.5, 77.1]	39.0 [37.3, 40.8]
S3_min50	33.7 [31.9, 35.6]	1.83 [1.63, 2.02]	0.80 [0.78, 0.82]	71.1 [64.5, 77.7]	39.3 [37.6, 41.0]
TT3	48.8 [46.1, 51.5]	2.84 [2.57, 3.12]	0.87 [0.86, 0.89]	109.6 [99.5, 119.7]	38.8 [37.3, 40.3]

Notes. Values are mean [95% CI]; n = 21–23 per epoch. $\dot{V}_E$ here is the laboratory summary-sheet value (not the breath-by-breath pneumotach value in Table 1). $\dot{V}O_2$, $\dot{V}CO_2$ and RER were reported previously (Jaén-Carrillo et al., 2026) and are shown for context.

Table S5. Decomposition of $\dot{V}_E/\dot{V}CO_2$: models for summary-sheet $\dot{V}_E$, $\dot{V}CO_2$ and $\dot{V}O_2$

Outcome	Term	%	95% CI	p	Matched, %	95% CI	p
$\dot{V}_E/\dot{V}CO_2$	Within block (min 5 → 50)	−1.0	[−2.1, 0.2]	.091			
	Block 2 vs 1	8.1	[6.9, 9.4]	< .001			
	Block 3 vs 1	10.1	[8.8, 11.4]	< .001			
	TT1 vs TT0	4.2	[2.4, 6.1]	< .001	4.6	[2.7, 6.6]	< .001
	TT2 vs TT0	7.8	[5.9, 9.8]	< .001	8.3	[6.3, 10.3]	< .001
	TT3 vs TT0	10.7	[8.7, 12.7]	< .001	11.2	[9.1, 13.4]	< .001
$\dot{V}_E$ (summary sheet)	Within block (min 5 → 50)	−0.1	[−2.0, 1.8]	.897			
	Block 2 vs 1	6.3	[4.3, 8.4]	< .001			
	Block 3 vs 1	9.0	[7.0, 11.1]	< .001			
	TT1 vs TT0	−0.6	[−4.2, 3.1]	.727	1.8	[−1.3, 5.0]	.258
	TT2 vs TT0	0.9	[−2.7, 4.7]	.622	3.6	[0.4, 6.9]	.026
	TT3 vs TT0	1.2	[−2.5, 5.0]	.532	5.8	[2.3, 9.4]	.001
$\dot{V}CO_2$	Within block (min 5 → 50)	0.9	[−1.0, 2.8]	.370			
	Block 2 vs 1	−1.7	[−3.5, 0.3]	.088			
	Block 3 vs 1	−1.0	[−2.9, 1.0]	.318			
	TT1 vs TT0	−4.7	[−8.2, −1.0]	.013	−2.7	[−5.9, 0.6]	.103
	TT2 vs TT0	−6.4	[−9.8, −2.8]	< .001	−4.3	[−7.5, −1.0]	.011
	TT3 vs TT0	−8.6	[−12.0, −5.1]	< .001	−4.9	[−8.3, −1.4]	.007
$\dot{V}O_2$	Within block (min 5 → 50)	0.0	[−1.8, 1.7]	.971			
	Block 2 vs 1	−0.3	[−2.1, 1.5]	.726			
	Block 3 vs 1	2.0	[0.1, 3.8]	.034			
	TT1 vs TT0	−1.9	[−4.6, 0.8]	.163	−0.6	[−3.2, 2.0]	.645
	TT2 vs TT0	−1.8	[−4.5, 0.9]	.188	−0.4	[−3.0, 2.3]	.773
	TT3 vs TT0	−2.4	[−5.1, 0.4]	.087	0.0	[−2.8, 2.9]	.988

Notes. Epoch-level linear mixed models on log values with a participant random intercept; submaximal: minC + block; time trials: trial, raw and at matched load (log power centered within participant). Because $\log(\dot{V}_E/\dot{V}CO_2) = \log \dot{V}_E - \log \dot{V}CO_2$, the $\dot{V}_E/\dot{V}CO_2$ effect is approximately the $\dot{V}_E$ effect minus the $\dot{V}CO_2$ effect.

Table S6. Exploratory sex comparison: sex-specific contrasts and sex × time interactions

Outcome	Contrast	Females (n = 11)	Males (n = 12)	p (interaction)
f_R	Block 3 vs 1	18.4 [14.9, 22.0]	20.2 [16.7, 23.8]	.674
	TT3 vs TT0 (matched)	16.7 [11.3, 22.3]	10.1 [4.9, 15.5]	.126
V_T	Block 3 vs 1	−4.4 [−8.4, −0.4]	−9.6 [−13.2, −5.8]	.010
	TT3 vs TT0 (matched)	−5.6 [−10.1, −0.9]	−7.5 [−12.0, −2.8]	.519
$\dot{V}_E$	Block 3 vs 1	12.8 [8.4, 17.3]	9.3 [5.2, 13.7]	.078

Outcome	Contrast	Females (n = 11)	Males (n = 12)	p (interaction)
	TT3 vs TT0 (matched)	9.7 [3.1, 16.8]	1.6 [−4.7, 8.2]	.223
$\dot{V}_E/\dot{V}CO_2$	Block 3 vs 1	10.4 [8.6, 12.3]	9.8 [8.0, 11.6]	.741
	TT3 vs TT0	11.9 [9.1, 14.8]	9.5 [6.7, 12.3]	.582
HR	Block 3 vs 1	7.8 [6.6, 9.1]	9.9 [8.7, 11.2]	.074
	TT3 vs TT0	−0.5 [−2.3, 1.3]	0.0 [−1.7, 1.8]	.841
RPE (points)	Block 3 vs 1	2.0 [1.6, 2.3]	3.4 [3.1, 3.8]	< .001
	TT3 vs TT0	1.0 [0.4, 1.6]	0.4 [−0.2, 1.0]	.211

Notes. Sex × block or sex × trial added to each model; p from a likelihood-ratio test of all interaction terms. Values are % differences (RPE in points) with 95% CI. f_R, V_T, $\dot{V}_E$: 30-s-bin models (time trials at matched load); $\dot{V}_E/\dot{V}CO_2$, HR, RPE: epoch-level models.

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