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ORIGINAL RESEARCH

Perception of Carbohydrate Availability Augments High-Intensity Intermittent Exercise Capacity Under Sleep-Low, Train-Low Conditions

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The authors tested the hypothesis that perception of carbohydrate (CHO) availability augments exercise capacity in conditions of reduced CHO availability. Nine males completed a sleep-low train model comprising evening glycogen-depleting cycling followed by an exhaustive cycling protocol the next morning in the fasted state (30 min steady state at 95% lactate threshold followed by 1-min intervals at 80% peak power output until exhaustion). After the evening depletion protocol and prior to sleeping, subjects consumed (a) a known CHO intake of 6 g/kg body mass (TRAIN HIGH) or (b) a perceived comparable CHO intake but 0 g/kg body mass (PERCEPTION) or a known train-low condition of 0 g/kg body mass (TRAIN LOW). The TRAIN HIGH and PERCEPTION trials were conducted double blind. During steady state, average blood glucose and CHO oxidation were significantly higher in TRAIN HIGH (4.01 ± 0.56 mmol/L; 2.17 ± 0.70 g/min) versus both PERCEPTION (3.30 ± 0.57 mmol/L; 1.69 ± 0.64 g/min, $p < .05$) and TRAIN LOW (3.41 ± 0.74 mmol/L; 1.61 ± 0.59 g/min, $p < .05$). Exercise capacity was significantly different between all pairwise comparisons ($p < .05$), where TRAIN LOW (8 ± 8 min) < PERCEPTION (12 ± 6 min) < TRAIN HIGH (22 ± 9 min). Data demonstrate that perception of CHO availability augments high-intensity intermittent exercise capacity under sleep-low, train-low conditions, though this perception does not restore exercise capacity to that of CHO consumption. Such data have methodological implications for future research designs and may also have practical applications for athletes who deliberately practice elements of training in CHO-restricted states.

***Keywords**:* placebo, glycogen, CHO restriction, fatigue

In addition to its well-documented role as an energy source, it is now recognized that the glycogen granule exerts regulatory roles in modulating skeletal muscle cell signaling and transcriptional responses to acute exercise sessions (Bartlett et al., 2015; Hearris et al., 2018). Accordingly, deliberately commencing and/or recovering from training sessions with reduced carbohydrate (CHO) availability (the so-called train-low paradigm) increases markers of mitochondrial biogenesis (Hansen et al., 2005; Morton et al., 2009; Yeo et al., 2008) and both whole-body and intramuscular lipid oxidation (Hulston et al., 2010; Yeo et al., 2008). In some instances, both exercise capacity (Hansen et al., 2005) and exercise performance (Cochran et al., 2015; Marquet et al., 2016a, 2016b) have also been augmented with short-term (i.e., 3–10 weeks) train-low approaches, though it is acknowledged that this is not a consistent finding among chronic training studies. On this basis, it has therefore been suggested that CHO should be adjusted day by day and meal by meal in accordance with the goals of both maximizing training quality (i.e., ability to sustain the desired workload) and skeletal muscle adaptations (Impey et al., 2018).

Although there are multiple research designs used to practically achieve train-low conditions (i.e., twice per day training protocols, fasted training, and/or withholding CHO in the recovery period from acute exercise), the “sleep-low, train-low” model has been emerged as a particularly potent strategy to prolong the period of CHO restriction (Bartlett et al., 2013; Lane et al., 2015). In this approach, participants perform an evening training session, restrict CHO during overnight recovery, and then complete a fasted training session the following morning. The accumulative time with reduced muscle glycogen could therefore extend to 12–14 hr depending on the timing and duration of the training sessions and sleep period. When performed chronically, Marquet et al. (2016a, 2016b) observed that 1–3 weeks of sleep-low training in elite triathletes and cyclists improves cycling efficiency (3.1%), 20-km cycling time-trial performance (3.2%), and 10-km running performance (2.9%) compared with traditional train-high approaches.

Despite the aforementioned findings, an obvious limitation of the sleep-low, train-low model is that exercise capacity is likely to be significantly impaired during the morning training session. Indeed, we recently observed that stepwise reductions in preexercise muscle glycogen concentration ~100 mmol/kg of dry weight (as achieved by the sleep-low model) impaired morning exercise capacity at 80% peak power output (PPO) by ~20–50% (Hearris et al., 2019). Nonetheless, we acknowledged that lack of blinding between conditions (subjects were aware of CHO availability given that whole foods were consumed) may have influenced subjects’ perception of their ability to complete high-intensity workloads. Indeed, placebo effects of CHO availability have been reported in conditions of CHO feeding before (Mears et al., 2018) and during (Clark et al., 2000) exercise. To the authors’ knowledge, however, the potential placebo effect of CHO availability has not yet been examined under conditions where exercise is commenced with suboptimal muscle glycogen concentration.

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With this in mind, the aim of the present study was to test the hypothesis that perception of CHO availability augments exercise capacity. To this end, we adopted a sleep-low, train-low model of CHO restriction where recreationally active males commenced an exhaustive morning training session under conditions corresponding to a known prior CHO intake of 6 g/kg body mass (TRAIN HIGH), a perceived comparable CHO intake (PERCEPTION), or a known train-low condition during which no CHO was consumed prior to sleeping (TRAIN LOW). We specifically hypothesized that perception of CHO availability would improve morning exercise capacity compared with known train-low conditions but that perception would not restore exercise capacity to that of true train-high conditions.

Methods

Subjects

Nine recreationally active males who regularly engaged in exercise training (running, cycling, and intermittent sport) between three and six times per week volunteered to participate in the study (mean ± *SD*: age, 25 ± 8 years; body mass, 71.6 ± 8.5 kg; height, 1.78 ± 0.06 m; peak oxygen uptake [VO_2peak], 55.3 ± 8.3 ml·kg^{-1}·min^{-1}; PPO, 331 ± 41 W). All subjects gave written and informed consent after details of the study procedures were explained. No subject had a history of smoking, cardiovascular, or metabolically related disease, and none were under pharmacological treatment during the study. All subjects refrained from strenuous exercise and alcohol for at least 24 hr before each trial. The study was approved by the ethics committee of Liverpool John Moores University.

Experimental Design

In a randomized, repeated-measures design (and after appropriate baseline testing and familiarization [FAM]), subjects performed three experimental trials consisting of a glycogen-depleting protocol in the afternoon prior to the main experimental trial the subsequent morning. At the cessation of the glycogen-depleting protocol, subjects consumed (a) a known CHO intake of 6 g/kg body mass (TRAIN HIGH) or (b) a perceived comparable CHO intake but 0 g/kg body mass (PERCEPTION) or a known train-low condition of 0 g/kg body mass (TRAIN LOW). The TRAIN HIGH and PERCEPTION trials were double blind, where blinding of these two solutions was performed by the corresponding author, who was not present for any of the exhaustive exercise sessions on Day 2 (with the exception of the familiarization trials). The following morning subjects arrived at the laboratory in a fasted state, where they then performed a steady-state (SS; 30 min at 95% of lactate threshold, LT) cycling exercise protocol followed by a high-intensity intermittent (HIT) cycling protocol to exhaustion (1-min bouts at 80% PPO interspersed with 1-min bouts at 40% PPO). The primary outcome was exercise capacity during the HIT protocol. Respiratory gas exchange, heart rate (HR), rate of perceived exertion (RPE), and fingertip capillary blood samples were also obtained at regular intervals during the SS exercise protocol and immediately following the HIT protocol to assess for physiological, metabolic, and perceptual responses to exercise. An overview of the experimental design is shown in Figure 1. The participants were informed that the aim of the study was to compare the effects of two CHO drinks (that differed in composition but not quantity of CHO) on overnight recovery and subsequent morning exercise capacity versus a known noncaloric sugar-free drink. Upon completion of the study, all subjects performed an exit interview where they were informed they had been deceived in the PERCEPTION trial. While no formal questionnaires were administered, no subject reported that the drinks tasted differently, though three subjects did report that they felt hungrier in the both the TRAIN LOW and PERCEPTION trials.

Assessment of LT, Lactate Turn Point, VO_2peak, and PPO

At least 5–7 days prior to the FAM trial, subjects performed a submaximal incremental cycling protocol to determine LT, lactate turn point, VO_2peak, and PPO on an electronically braked cycling ergometer (Excalibur Sport; Lode, Groningen, The Netherlands). Following a 5-min warm-up at 75 W at a self-selected cadence, the submaximal test commenced at 125 W with 25 W increase every 4 min. In a Biosen capillary tube (EKF Diagnostics, Barleben, Germany), 20 μl of fingertip capillary blood samples were collected at the end of each 4-min stage. LT (defined as 1 mmol/L above resting levels) and lactate turn point (defined as the second inflection point on the lactate curve) were plotted live during the test using a Biosen C-Line lactate analyzer (EKF Diagnostics). HR (F10; Polar, Kempele, Finland) was monitored continuously and recorded during the final 10 s of each stage, along with RPE (Borg, 1973). Respiratory gas exchange was recorded during the final 2 min of each stage using an online gas analysis system (CPX Ultima; Medgraphics, St. Paul, MN). The submaximal test ended once lactate turn point had been confirmed. Following a 5-min recovery period, VO_2peak and PPO were assessed. The test to assess VO_2peak and PPO commenced at 25 W below each subject's individual LT and consisted of 1-min stages with 25 W increments until volitional exhaustion. HR was monitored throughout the test. VO_2peak referred to the peak value attained in any 10-s period during the last 60 s of data collection and was supported by verification by two or all the following end point criteria: (a) HR with 10 beats/min of age-predicted maximum, (b) respiratory exchange ratio > 1.1, and (c) plateau of oxygen consumption despite increasing workload.

Day 1: Glycogen Depletion Protocol

On the afternoon of Day 1, subjects arrived at the laboratory (~1500 hr) to perform an intermittent bout of cycling to volitional fatigue. Subjects were asked to record and replicate their energy intake in the 24-hr period prior to commencing the glycogen depletion protocol. Following a 5-min warm-up at a self-selected intensity, subjects cycled for 2 min at 90% PPO, immediately followed by 2 min at 50% PPO. Once subjects could no longer maintain >60 rpm, the interval was decreased to 90 s and then to 1 min at 90% PPO. Subjects repeated this work to rest ratio at 80% PPO, 70% PPO, and 60% PPO, and the exercise protocol was terminated once subjects could no longer maintain >60 rpm at 60% PPO for 1 min. This protocol has been used previously in our laboratory (Bartlett et al., 2013; Impey et al., 2016; Taylor et al., 2013) and is a modification of that of Kuipers et al. (1987) that induces glycogen depletion in both Type I and Type II fibers. Immediately following the cessation of glycogen-depleting exercise (~1700 hr), subjects consumed 30 g of whey protein isolate (Advanced Whey Isolate; Science in Sport, Nelson, United Kingdom) mixed with 250 ml water (in accordance with practical recommendations to promote recovery from endurance exercise) before adhering to one of three dietary protocols. In the

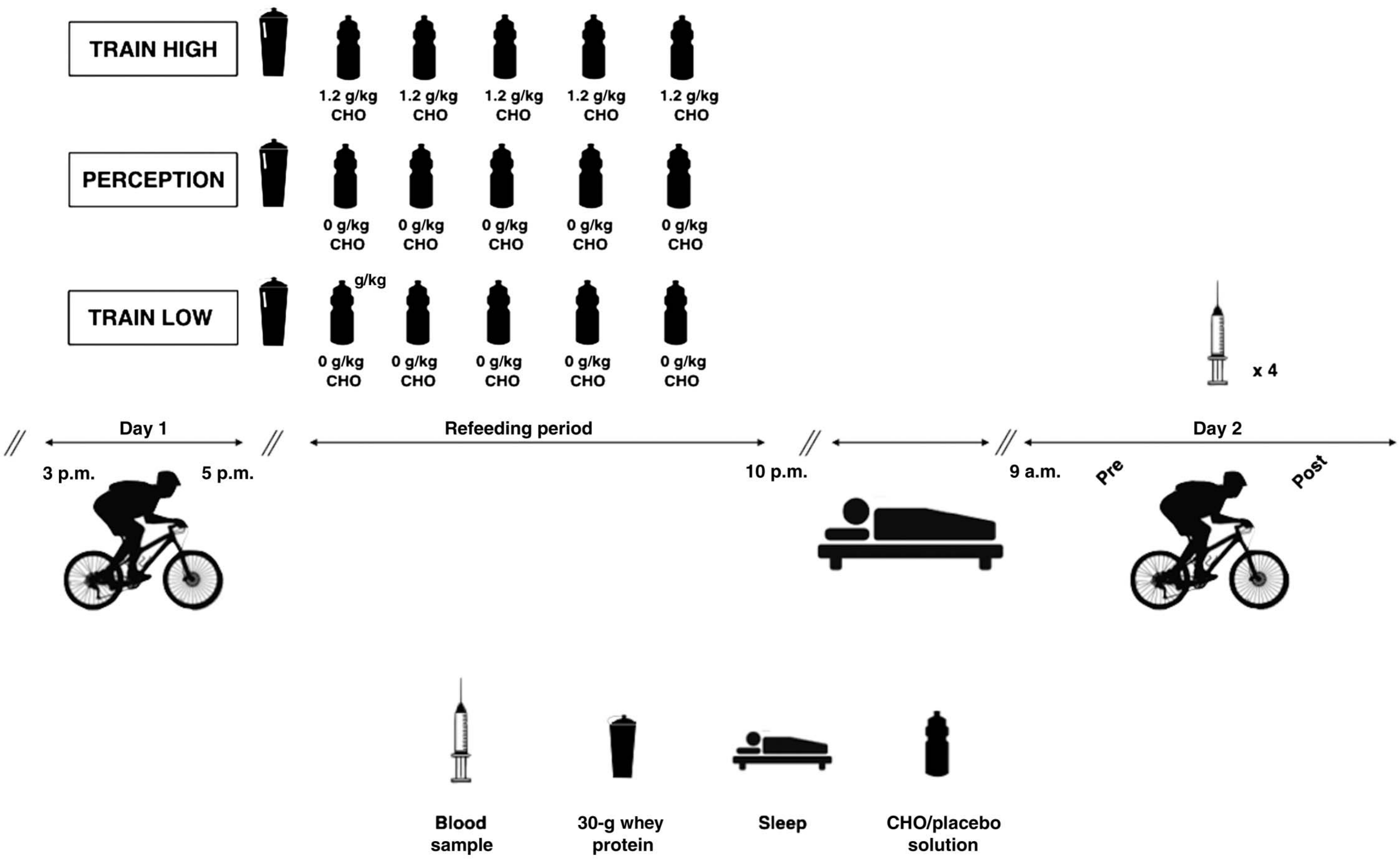

Figure 1 — Overview of the experimental design. CHO = carbohydrate.

TRAIN HIGH trial, subjects consumed 1.2 g/kg maltodextrin (Dry Maltodextrin; Cargill, Manchester, United Kingdom) mixed with 500 ml of water and sugar-free squash (Tesco, Hertfordshire, United Kingdom) per hour for 5 hr. In the PERCEPTION trial, subjects adhered to an identical feeding frequency and volume protocol but consumed a taste-matched placebo solution, where they were told it contained an identical amount of CHO as that consumed (or to be consumed) in the TRAIN HIGH trial (sugar-free squash; Tesco). In the TRAIN LOW trial, subjects consumed the same placebo solution as the PERCEPTION trial but were told the solution contained no CHO. All drinks were administered in visually opaque bottles, and 2.75 L of fluid was consumed over the 5-hr recovery period in each trial. Subjects remained in the laboratory to complete the first 3 hr of the recovery protocol before returning to their homes to complete the last 2 hr of recovery (subjects were provided with the additional 2 × 500 ml solutions to take home). Subjects also slept in their own homes.

Day 2: SS and HIT Exercise Capacity Test

Subjects arrived at the laboratory between 0800 and 0830 hr the following morning after an overnight fast. Body mass (seca, Hamburg, Germany), motivation to train (using a visual analog scale; McCormack et al., 1988), and resting blood lactate and blood glucose were initially measured. Subjects then completed 30-min SS cycling at 95% of LT. Breath-by-breath gas analysis (CPX Ultima; Medgraphics) was measured for 2 min during 8–10, 18–20, and 28–30 min, and substrate utilization was assessed according to Jeukendrup and Wallis (2005). Blood glucose and blood lactate samples were obtained at 15 and 30 min. Measurements of HR (F10; Polar) and RPE (Borg, 1973) were recorded at 10-min intervals during the SS exercise. Following the completion of SS exercise, subjects were provided with 3-min active recovery at 50 W and subsequently commenced the HIT exercise capacity test consisting of 1-min bouts at 80% PPO interspersed with 1-min bouts at 40% PPO until volitional exhaustion. A final capillary blood sample was collected at the termination of the HIT protocol.

Familiarization

Eight subjects completed the full experimental protocol described above while adhering to a water-only (i.e., no flavoring) FAM condition at least 7 days prior to their first experimental trial (one of the nine subjects withdrew from FAM after several minutes of the SS exercise protocol having reported feelings of muscle soreness). Upon completion of all three experimental trials, we compared each subject's exercise capacity during the FAM trial and the TRAIN LOW trial and observed no significant difference, as evidenced by a t test for paired samples (FAM = 5 ± 5 min, PLA = 7 ± 6 min, $p = .25$).

Blood Analyses

Blood samples were obtained via finger prick capillary sampling using a 1.8-mm sterile safety lancet (SARSTEDT AG & Co, Nümbrecht, Germany) after sterilization using a preinjection medical swab (Medlock Medical Ltd., Oldham, United Kingdom). A 20-µl blood sample was collected in a Biosen capillary tube (EKF Diagnostics) and analyzed using Biosen C-Line for blood glucose and lactate concentrations (EKF Diagnostics).

Statistical Analysis

Data were analyzed using one- or two-way repeated-measures general linear model where the within factors were time and condition (TRAIN LOW, PERCEPTION, and TRAIN HIGH). Where significant main effects were found, paired sample *t* tests with Bonferroni adjustment for multiple comparisons were performed to identify differences. In relation to our primary outcome variable of exercise capacity, we also report uncertainty of outcomes as 95% confidence intervals (95% CIs) and make probabilistic magnitude-based inferences about the true (large sample) values of outcomes by qualifying the likelihood that the true effect represents a substantial change, according to Batterham and Hopkins (2006). All data in text, tables, and figures are expressed as mean ± *SD* with $p < .05$ indicating statistical significance. Statistical analyses were performed using Statistics Package for the Social Sciences (SPSS) for Windows (version 24; SPSS Inc., Chicago, IL).

Results

Glycogen Depletion Protocol

There was no difference ($p = .71$) in time to exhaustion during the glycogen depletion protocol between the TRAIN HIGH (79 ± 20 min), PERCEPTION (75 ± 16 min), and TRAIN LOW (79 ± 22 min) trials.

Physiological and Perceptual Responses During SS Exercise

There was no difference ($p = .258$) in subjects' motivation to exercise prior to commencing the SS protocol (TRAIN HIGH: 6.7 ± 2.7 cm; PERCEPTION: 6.4 ± 1.7 cm; TRAIN LOW: 5.1 ± 2.1 cm). Subjects' HR ($p = .006$) and RPE ($p < .001$) increased during SS, though no difference was apparent between conditions ($p = .299$ and .273, respectively; see Table 1).

Table 1 HR, VO_2 (as % of VO_2peak), and RPE During the SS Exercise Protocol (as Completed on the Morning of Day 2) in the TRAIN LOW, PERCEPTION, and TRAIN HIGH Trials

	Time (min)		
Measure	**10**	**20**	**30**
HR (beats/min)			
TRAIN LOW	145 ± 16	147 ± 17	150 ± 19*,**
PERCEPTION	146 ± 11	149 ± 11	151 ± 14*,**
TRAIN HIGH	142 ± 14	143 ± 14	146 ± 15*,**
%VO_2peak			
TRAIN LOW	61 ± 9	63 ± 7	61 ± 6
PERCEPTION	63 ± 8	64 ± 7	62 ± 6
TRAIN HIGH	64 ± 9	61 ± 9	63 ± 6
RPE (AU)			
TRAIN LOW	12 ± 2	14 ± 2	16 ± 3*,**
PERCEPTION	12 ± 2	13 ± 3	15 ± 3*,**
TRAIN HIGH	12 ± 2	14 ± 2	15 ± 3*,**

Note. HR = heart rate; RPE = rate of perceived exertion; SS = steady state; VO_2 = oxygen uptake; VO_2peak = peak oxygen uptake.
*Significant difference from 10. **Significant difference from 20. Both *p*s < .05.

Metabolic Responses During SS Exercise and HIT Capacity Test

During SS, respiratory exchange ratio ($p < .001$) and CHO oxidation rate ($p < .001$) decreased while fat oxidation increased ($p < .001$). Average CHO oxidation was higher throughout SS in TRAIN HIGH than both PERCEPTION ($p = .019$) and TRAIN LOW ($p = .012$), while fat oxidation was lower ($p = .016$ and .023, respectively). Blood glucose was higher throughout SS and HIT in TRAIN HIGH than in PERCEPTION ($p = .002$) and TRAIN LOW ($p = .021$) and also decreased during exercise ($p < .001$). Blood lactate rose throughout SS and was significantly increased in TRAIN HIGH compared with both PERCEPTION ($p = .016$) and TRAIN LOW ($p = .023$) after HIT (see Figure 2).

Exercise Capacity During the HIT Test

High-intensity intermittent exercise capacity was different between conditions ($p < .001$), whereby TRAIN HIGH (22 ± 9 min; $p = .005$: 95% CI for differences = 3–16 min, *almost certainly beneficial*) was greater than both PERCEPTION (12 ± 6 min) and TRAIN LOW (8 ± 8 min; $p = .001$: 95% CI for differences = 7–20 min, *almost certainly beneficial*). Exercise capacity was also greater in PERCEPTION compared with TRAIN LOW ($p = .025$: 95% CI for differences = 1–8 min, *very likely beneficial*; see Figure 3a). Seven subjects completed more intervals in PERCEPTION than TRAIN LOW, while all nine subjects completed more intervals in TRAIN HIGH compared with both non-CHO trials (see Figure 3b). There was no trial order effect ($p = .849$).

Discussion

Confirming our hypotheses, we provide novel data by demonstrating that perception of CHO availability augments HIT exercise capacity under sleep-low, train-low conditions, though perception of CHO availability does not near improve exercise capacity to that of CHO consumption. We therefore consider our data to have methodological implications for future sleep-low, train-low research designs by clearly highlighting the requirement for placebo-controlled trials. Furthermore, when considering that perception of CHO availability can improve exercise capacity, our data may also have practical applications for those athletes who deliberately practice CHO periodization strategies in an attempt to strategically enhance oxidative adaptations of skeletal muscle.

To achieve our sleep-low, train-low model of CHO restriction, we employed a similar glycogen depletion and resynthesis protocol to that recently studied in our laboratory (Hearris et al., 2019). While we acknowledge that we did not directly assess muscle glycogen, evaluations of substrate utilization during the SS exercise protocol are consistent with differences in CHO availability between the TRAIN HIGH trial and the non-CHO trials. On the basis of the fitness levels of the present subjects (i.e., VO_2peak, 55.3 ± 8.3 $ml \cdot kg^{-1} \cdot min^{-1}$) and absolute CHO intake (i.e., 6 g/kg), we estimate from our previous data (Hearris et al., 2019) and a recent meta-analysis (Areta & Hopkins, 2018) that muscle

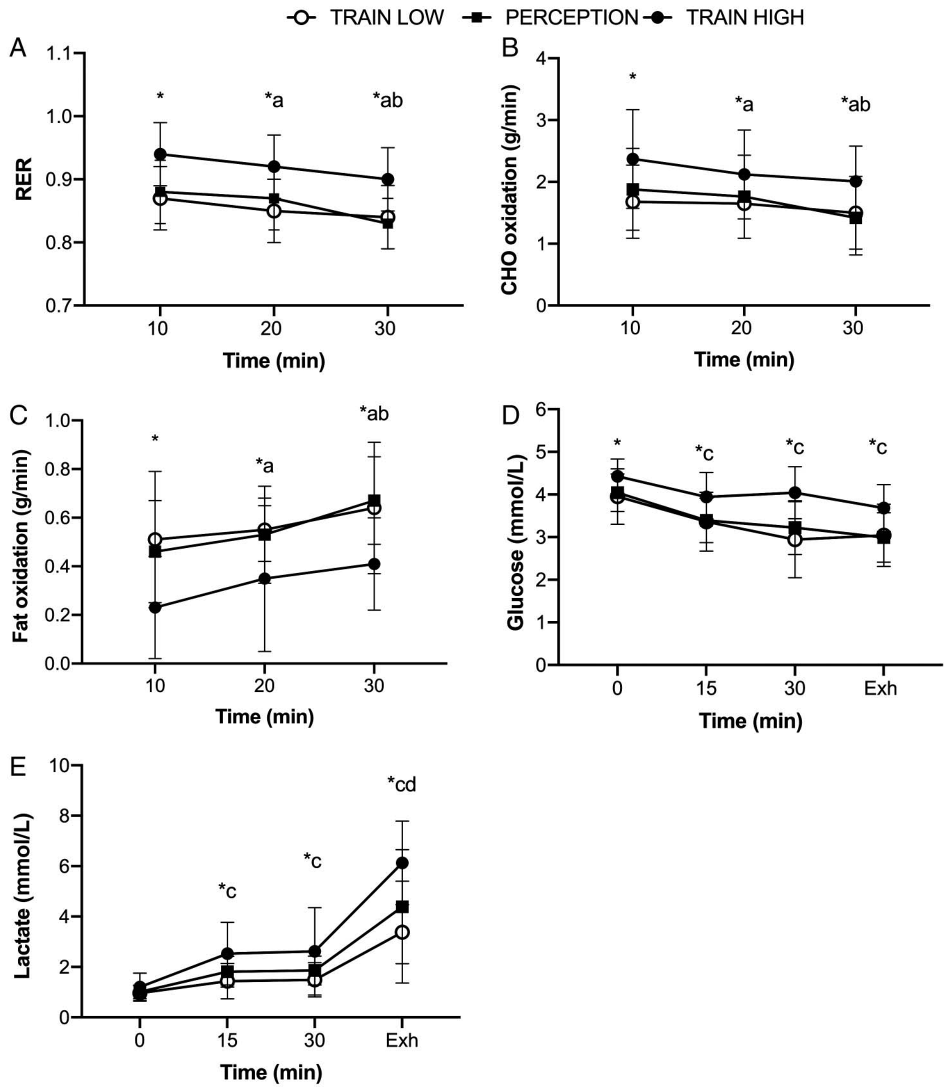

Figure 2 — (a) Respiratory exchange ratio, (b) CHO oxidation, (c) lipid oxidation, (d) blood glucose, and (e) blood lactate concentration during the SS exercise protocol (as completed on the morning of Day 2). CHO = carbohydrate; Exh = exhaustion; SS = steady state. *Significant difference between TRAIN HIGH, PERCEPTION, and TRAIN LOW trials, $p < .05$. [a]Significant difference from 10. [b]Significant difference from 20. [c]Significant difference from 0. [d]Significant difference from 15 and 30. All $ps < .05$.

glycogen concentration in TRAIN HIGH was in the region of 300–350 mmol/kg of dry weight, as opposed to 100–150 mmol/kg of dry weight in the PERCEPTION and TRAIN LOW trials.

Consistent with the well-documented effect of muscle glycogen availability on exercise capacity (Bergström et al., 1967; Hawley et al., 1997; Hearris et al., 2019; Impey et al., 2016), it is unsurprising that all nine subjects were able to exercise for significantly longer during the TRAIN HIGH trial compared with the non-CHO trials. The magnitude of improvement observed here (i.e., ~15 min) agrees favorably with our recent data (Hearris et al., 2019) where we observed that small differences in preexercise muscle glycogen concentration (~100 mmol/kg of dry weight) improves HIT exercise capacity at 80% PPO between ~20% and 50% (8–18 min). In our previous study, however, we acknowledged that lack of blinding between trials may have influenced subjects' motivation and perceived ability to complete high-intensity workloads (Hearris et al., 2019). To overcome the issue of subjects being visually aware of the quantity of CHO-rich foods consumed (Mears et al., 2018), we deliberately chose to blind CHO availability in the present study by using taste-matched beverages delivered in opaque bottles.

It is noteworthy that when comparing subjects' exercise capacity between the TRAIN LOW and water-only FAM trials, no significant differences in exercise capacity were observed. Such data highlight that when subjects were aware that no prior CHO had been consumed (despite differences in taste between the TRAIN LOW and FAM trials), exercise capacity was not affected. However, when subjects perceived they had consumed CHO before sleeping in the PERCEPTION trial, seven of the nine subjects performed significantly more work compared with the known TRAIN LOW trial, despite reporting no significant differences in their motivation to exercise. A placebo effect of CHO availability has been documented previously (in conditions of normal preexercise muscle glycogen concentration) where CHO has been fed before (Mears et al., 2018) and during (Clark et al., 2000) cycling time trials equating to durations of approximately 20 and 60 min, respectively. In contrast, no placebo effect of CHO feeding is evident when the exercise duration extends beyond 3 hr,

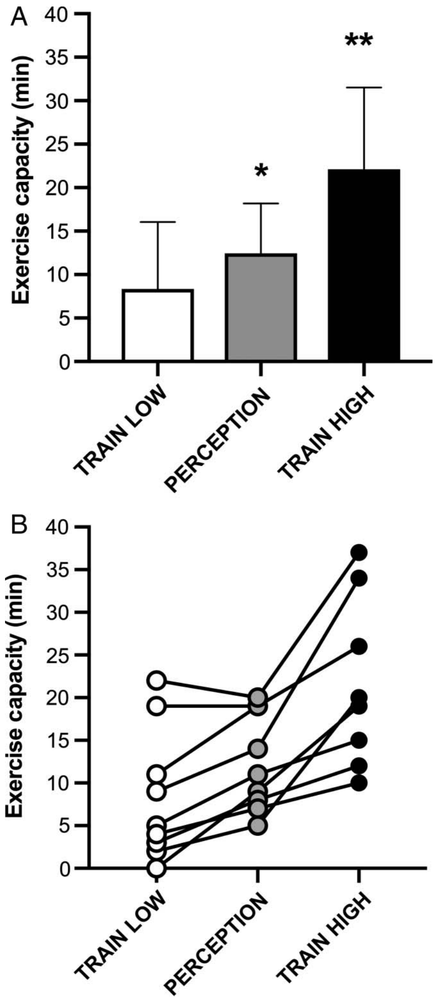

Figure 3 — (a) Exercise capacity (means ± *SDs*) and (b) individual subject's exercise capacity during the TRAIN LOW, PERCEPTION, and TRAIN HIGH trials. *Significant difference from TRAIN LOW. **Significant difference from both TRAIN LOW and PERCEPTION. Both $ps < .05$.

likely due to near glycogen depletion and that the metabolic requirement for CHO dominates over the central drive (Hulston & Jeukendrup, 2009). Nonetheless, the present data demonstrate that a placebo effect of prior CHO ingestion may also manifest in those conditions where short-term HIT exercise is commenced with considerably reduced preexercise muscle glycogen concentration.

While we acknowledge that the magnitude of effect with perception was less than that of actual CHO consumption (~5 vs. 15 min at 80% PPO), the present data are of practical relevance for reasons related to both research design and practical application with athletic populations. Indeed, when considering that previous studies reporting decrements in power output or exercise capacity during acute train-low training sessions (using the twice per day or sleep-low models) have not blinded subjects to the "low CHO availability" condition (Hansen et al., 2005; Hearris et al., 2019; Hulston et al., 2010; Yeo et al., 2008, 2010), it is possible that such impairments in performance may also be due, in part, to psychological reasons as opposed to physiological factors per se. Similarly, given that Marquet et al. (2016b) observed that just 1 week of a sleep-low training intervention (incorporating only three train-low sessions) improved 20-km cycling time-trial performance by 3.2%, it is possible that such improvements were simply due to subjects' belief that the sleep-low protocol would lead to superior improvements in performance, as opposed to physiological or metabolic adaptations. In relation to practical application, the placebo effect of prior CHO intake may also extend the effects of caffeine (Lane et al., 2013) and CHO mouth rinse (Kasper et al., 2016) as potential tools to increase exercise capacity for those athletes who deliberately practice CHO restriction in an attempt to amplify training adaptations (Impey et al., 2018).

In summary, we provide novel data by demonstrating that perception of CHO availability augments HIT exercise capacity under sleep-low, train-low conditions, though perception does not restore exercise capacity to that of CHO consumption. Such data have implications for future sleep-low, train-low research designs by clearly highlighting the requirement for placebo-controlled trials. In addition, our data may also have practical applications for those athletes who deliberately incorporate periods of CHO restriction into their training programs in an attempt to strategically enhance mitochondrial-related adaptations of skeletal muscle.

Acknowledgments

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References

Areta, J.L., & Hopkins, W.G. (2018). Skeletal muscle glycogen content at rest and during endurance exercise in humans: A meta-analysis. *Sports Medicine, 48*(9), 2091–2102. PubMed ID: 29923148 doi:10.1007/s40279-018-0941-1

Bartlett, J.D., Hawley, J.A., & Morton, J.P. (2015). Carbohydrate availability and exercise training adaptation: Too much of a good thing? *European Journal of Sport Science, 15*(1), 3–12. doi:10.1080/17461391.2014.920926

Bartlett, J.D., Louhelainen, J., Iqbal, Z., Cochran, A.J., Gibala, M.J., Gregson, W., . . . Morton, J.P. (2013). Reduced carbohydrate availability enhances exercise-induced p53 signaling in human skeletal muscle: Implications for mitochondrial biogenesis. *American Journal of Physiology—Regulatory, Integrative and Comparative Physiology, 304*(6), R450–R458. doi:10.1152/ajpregu.00498.2012

Batterham, A.M., & Hopkins, W.G. (2006). Making meaningful inferences about magnitudes. *International Journal of Sports Physiology and Performance, 1*(1), 50–57. PubMed ID: 19114737 doi:10.1123/ijspp.1.1.50

Bergström, J., Hermansen, L., Hultman, E., & Saltin, B. (1967). Diet, muscle glycogen and physical performance. *Acta Physiologica Scandinavica, 71*(2–3), 140–150. doi:10.1111/j.1748-1716.1967.tb03720.x

Borg, G.A. (1973). Perceived exertion: A note on "history" and methods. *Medicine and Science in Sports, 5*(2), 90–93.

Clark, V.R., Hopkins, W.G., Hawley, J.A., & Burke, L.M. (2000). Placebo effect of carbohydrate feedings during a 40-km cycling time trial. *Medicine & Science in Sports & Exercise, 32*(9), 1642–1647. PubMed ID: 10994918 doi:10.1097/00005768-200009000-00019

Cochran, A.J., Myslik, F., MacInnis, M.J., Percival, M.E., Bishop, D., Tarnopolsky, M.A., & Gibala, M.J. (2015). Manipulating carbohydrate availability between twice-daily sessions of high-intensity interval training over 2 weeks improves time-trial performance. *International Journal of Sport Nutrition and Exercise Metabolism, 25*(5), 463–470. doi:10.1123/ijsnem.2014-0263

Hansen, A.K., Fischer, C.P., Plomgaard, P., Andersen, J.L., Saltin, B., & Pedersen, B.K. (2005). Skeletal muscle adaptation: Training twice every second day vs. training once daily. *Journal of Applied Physiology, 98*(1), 93–99. doi:10.1152/japplphysiol.00163.2004

Hawley, J.A., Palmer, G.S., & Noakes, T.D. (1997). Effects of 3 days of carbohydrate supplementation on muscle glycogen content and utilisation during a 1-h cycling performance. *European Journal of Applied Physiology and Occupational Physiology, 75*(5), 407–412. PubMed ID: 9189727 doi:10.1007/s004210050180

Hearris, M.A., Hammond, K.M., Fell, J.M.& Morton, J.P. (2018). Regulation of muscle glycogen metabolism during exercise: Implications for endurance performance and training adaptations. *Nutrients, 10*(3), 298. doi:10.3390/nu10030298

Hearris, M.A., Hammond, K.M., Seaborne, R.A., Stocks, B., Shepherd, S.O., Philp, A., . . . Louis, J.B. (2019). Graded reductions in preexercise muscle glycogen impair exercise capacity but do not augment skeletal muscle cell signaling: Implications for CHO periodization. *Journal of Applied Physiology, 126*(6), 1587–1597. doi:10.1152/japplphysiol.00913.2018

Hulston, C.J., & Jeukendrup, A.E. (2009). No placebo effect from carbohydrate intake during prolonged exercise. *International Journal of Sport Nutrition and Exercise Metabolism, 19*(3), 275–284. doi:10.1123/ijsnem.19.3.275

Hulston, C.J., Venables, M.C., Mann, C.H., Martin, C., Philp, A., Baar, K., & Jeukendrup, A.E. (2010). Training with low muscle glycogen enhances fat metabolism in well-trained cyclists. *Medicine & Science in Sports & Exercise, 42*(11), 2046–2055. PubMed ID: 20351596 doi:10.1249/MSS.0b013e3181dd5070

Impey, S.G., Hammond, K.M., Shepherd, S.O., Sharples, A.P., Stewart, C., Limb, M., . . . Morton, J.P. (2016). Fuel for the work required: A practical approach to amalgamating train-low paradigms for endurance athletes. *Physiological Reports, 4*(10), e12803. doi:10.14814/phy2.12803

Impey, S.G., Hearris, M.A., Hammond, K.M., Bartlett, J.D., Louis, J., Close, G.L., & Morton, J.P. (2018). Fuel for the work required: A theoretical framework for carbohydrate periodization and the glycogen threshold hypothesis. *Sports Medicine, 48*(5), 1031–1048. PubMed ID: 29453741 doi:10.1007/s40279-018-0867-7

Jeukendrup, A.E., & Wallis, G.A. (2005). Measurement of substrate oxidation during exercise by means of gas exchange measurements. *International Journal of Sports Medicine, 26*(Suppl. 1), S28–S37. doi:10.1055/s-2004-830512

Kasper, A.M., Cocking, S., Cockayne, M., Barnard, M., Tench, J., Parker, L., . . . Morton, J.P. (2016). Carbohydrate mouth rinse and caffeine improves high-intensity interval running capacity when carbohydrate restricted. *European Journal of Sport Science, 16*(5), 560–568. PubMed ID: 26035740 doi:10.1080/17461391.2015.1041063

Kuipers, H., Keizer, H.A., Brouns, F., & Saris, W.H. (1987). Carbohydrate feeding and glycogen synthesis during exercise in man. *Pflugers Arch, 410*(6), 652–656.

Lane, S.C., Areta, J.L., Bird, S.R., Coffey, V.G., Burke, L.M., Desbrow, B., . . . Hawley, J.A. (2013). Caffeine ingestion and cycling power output in a low or normal muscle glycogen state. *Medicine & Science in Sports & Exercise, 45*(8), 1577–1584. PubMed ID: 23439421 doi:10.1249/MSS.0b013e31828af183

Lane, S.C., Camera, D.M., Lassiter, D.G., Areta, J.L., Bird, S.R., Yeo, W.K., . . . Hawley, J.A. (2015). Effects of sleeping with reduced carbohydrate availability on acute training responses. *Journal of Applied Physiology, 119*(6), 643–655. doi:10.1152/japplphysiol.00857.2014

Marquet, L.A., Brisswalter, J., Louis, J., Tiollier, E., Burke, L.M., Hawley, J.A., & Hausswirth, C. (2016a). Enhanced endurance performance by periodization of carbohydrate intake: "Sleep low" strategy. *Medicine & Science in Sports & Exercise, 48*(4), 663–672. doi:10.1249/MSS.0000000000000823

Marquet, L.A., Hausswirth, C., Molle, O., Hawley, J.A., Burke, L.M., Tiollier, E., & Brisswalter, J. (2016b). Periodization of carbohydrate intake: Short-term effect on performance. *Nutrients, 8*(12), 755. doi:10.3390/nu8120755

McCormack, H.M., Horne, D.J., & Sheather, S. (1988). Clinical applications of visual analogue scales: A critical review. *Psychological Medicine, 18*(4), 1007–1019. PubMed ID: 3078045 doi:10.1017/S0033291700009934

Mears, S.A., Dickinson, K., Bergin-Taylor, K., Dee, R., Kay, J., & James, L.J. (2018). Perception of breakfast ingestion enhances high-intensity cycling performance. *International Journal of Sports Physiology and Performance, 13*(4), 504–509. PubMed ID: 28952831 doi:10.1123/ijspp.2017-0318

Morton, J.P., Croft, L., Bartlett, J.D., Maclaren, D.P., Reilly, T., Evans, L., . . . Drust, B. (2009). Reduced carbohydrate availability does not modulate training-induced heat shock protein adaptations but does upregulate oxidative enzyme activity in human skeletal muscle. *Journal of Applied Physiology, 106*(5), 1513–1521. doi:10.1152/japplphysiol.00003.2009

Taylor, C., Bartlett, J.D., van de Graaf, C.S., Louhelainen, J., Coyne, V., Iqbal, Z., . . . Morton, J.P. (2013). Protein ingestion does not impair exercise-induced AMPK signalling when in a glycogen-depleted state: Implications for train-low compete-high. *European Journal of Applied Physiology, 113*(6), 1457–1468. PubMed ID: 23263742 doi:10.1007/s00421-012-2574-7

Yeo, W.K., McGee, S.L., Carey, A.L., Paton, C.D., Garnham, A.P., Hargreaves, M., & Hawley, J.A. (2010). Acute signalling responses to intense endurance training commenced with low or normal muscle glycogen. *Experimental Physiology, 95*(2), 351–358. doi:10.1113/expphysiol.2009.049353

Yeo, W.K., Paton, C.D., Garnham, A.P., Burke, L.M., Carey, A.L., & Hawley, J.A. (2008). Skeletal muscle adaptation and performance responses to once a day versus twice every second day endurance training regimens. *Journal of Applied Physiology, 105*(5), 1462–1470. doi:10.1152/japplphysiol.90882.2008