

PROMOTING ENDURANCE TRAINING ADAPTATIONS WITH NUTRITIONAL INTERVENTIONS: THE POTENTIAL BENEFITS OF 'LOW CARBOHYDRATE' TRAINING

Barry Drust and James P. Morton

*Research Institute for Sport and Exercise Sciences,
Liverpool John Moores University, Liverpool, United Kingdom*

Review

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Abstract:

Skeletal muscle responds to endurance exercise via increased transcription of metabolic and stress-related genes ultimately to yield increased steady-state levels of specific proteins. These changes in transcriptional activity are highly dependent on the mode, duration, intensity and frequency of the contractile stimulus. One of the major challenges for exercise physiologists over the coming decades is to identify the exercise 'signal(s)' that are responsible for initiating the adaptive response and the precise signal transduction pathways which mediate the adaptive processes. In this regard, it is now becoming apparent that cellular energy status may have an important role to play in this process. For example, many stress-and metabolic-related genes are enhanced when the exercise is commenced under reduced pre-exercise muscle glycogen levels and attenuated when glucose is ingested during exercise. Taken together, such findings suggest that training under conditions of reduced carbohydrate availability from both endogenous and exogenous sources may provide an enhanced stimulus for inducing beneficial adaptations of skeletal muscle. This hypothesis is in marked contrast to the widely held belief that intense training periods should be supported by a high carbohydrate diet in order to maintain training intensity and replenish energy stores for future training sessions. This paper will outline the current thinking regarding the potential for carbohydrate availability to modulate the adaptations typically observed following periods of endurance training. Relevant data from the literature and our own laboratory is presented with a view to providing some potential advantages and disadvantages of training with reduced carbohydrate availability for both athletes and coaches.

Key words: *muscular endurance, endurance training, carbohydrate diet, cellular function, adaptive response, performance improvement*

Introduction

Endurance training is a generic term for any repeated bouts of physical activity that aim at improving the ability of an individual to sustain exercise performance for prolonged periods of time. This type of training is traditionally important in sports such as athletics and cycling as they predominantly rely on the aerobic energy system for the regeneration of ATP. Such training is also important for invasive field sports such as soccer, rugby and hockey as these intermittent activities, in which the exercise pattern includes frequent supra-maximal high-intensity efforts, also require a significant contribution from aerobic metabolism to support their energy requirements.

The acute bouts of exercise that are traditionally incorporated in endurance training programmes

are prolonged and sub-maximal in nature. It is now clear from research undertaken over the last few decades that endurance training programmes should include a mixture of different exercise intensities (from sub-maximal to maximal) and different volumes. Such variation in training stimulus is the only way to ensure that exercise performance can be optimized for both the elite performer and the recreational athlete. This is a direct consequence of the relationship between the training stress and the body's subsequent physiological, structural and biochemical adaptations (specificity) in response to an exercise challenge. An appropriate exercise prescription over time therefore leads to a variety of changes that improve the delivery and utilization of oxygen and hence the potential for aerobic metabolism and performance. These changes include

alterations in the structure and function of the cardiovascular, respiratory and musco-skeletal systems (Kubukeli, Noakes, & Dennis, 2002).

Skeletal muscle is the largest organ in the human body and possesses a tremendous capacity to adapt to the demands of endurance training via various structural, functional and biochemical adaptations (Booth & Baldwin, 1996). The adaptations that the muscle makes to endurance training include mitochondrial biogenesis (Holloszy & Coyle, 1984), fast to slow muscle-fibre transformations (Taylor & Buchman, 1999), changes in substrate metabolism (Henrikssen, 1977) and an up-regulation of cellular defence systems (Morton, et al., 2008). These adaptive responses lead to improvements in cellular function that serves to maintain balance between the demands placed on the system and the capacity to support these requirements (Basel-Duby & Olson, 2006), thereby leading to performance improvements. Subtle alterations in the intensity and duration of exercise lead to variations in a range of primary and secondary messengers that are associated with exercise stress. These include (but are not limited to) increases in intracellular calcium (Chin, 2005), reactive oxygen species (Pattwell & Jackson, 2004), hypoxia (Fluck, 2003), mechanical stretch (Hornberger, Armstrong, Koh, Burkholder, & Esser, 2005) and substrate availability (Hawley, Gibala, & Bermon, 2008). These 'signals' (acting alone or likely in combination with each other) can activate a multitude of signal transduction pathways (Wackerhage, 2006) and initiate the replication of a single gene or sets of genes that enable the transcription and translation of this genetic code into a series of amino acids to create new proteins (Coffey & Hawley, 2007). The cumulative effect of each acute exercise bout leads to a change in the steady-state level of these specific proteins and hence a new functional threshold (Mahoney, Parise, Melov, Safdar, & Tarnopolsky, 2005). It is these repeated and transient changes in gene expression which are thought to form the molecular basis for training adaptation.

Nutritional status as a mediator of the cellular and molecular adaptive responses to 'acute' exercise

The obvious way in which an individual's nutritional intake could theoretically influence the adaptive responses to training is by affecting the ability of an athlete to complete the prescribed training load. It has traditionally been accepted that a diet high in carbohydrate is beneficial for endurance training as it is fundamental in supporting periods of highly intense activity (Karlsson & Saltin, 1971). High carbohydrate diets will support intense periods of training by better maintaining both muscle and liver glycogen stores and ensuring high rates

of carbohydrate oxidation during exercise (Hawley, Tipton, & Millard-Stafford, 2006). This will ensure that athletes are able to perform at the required intensity for the desired time, thereby maximizing their ability to maintain the 'optimal' physiological stimulus required for performance improvements.

However, in recent years the role of glycogen has evolved beyond that of a simple energy store advancing to a regulatory role which also recognizes glycogen as a mediator of cell signalling processes that are associated with mediating the adaptive responses to exercise and training (Hawley, et al., 2006). Altering substrate availability through changes in dietary intake will also alter the concentration of blood-borne nutrients and hormonal responses to exercise (Hawley, et al., 2006). This will in-turn not only affect the storage profile within muscle but more importantly the regulatory processes underlying gene expression (Jump & Clarke, 1999). Several data sets demonstrate that conditions of reduced carbohydrate availability may provide an enhanced stimulus for exercise-induced adaptations of skeletal muscle. For example, genes encoding heat shock protein 72 (Febbraio, et al., 2002), IL-6 (Keller, et al., 2001), hexokinase and PDK4 (Pilegaard, et al., 2002) are expressed to a greater extent when exercise is performed in a glycogen depleted state compared with normal muscle glycogen stores. The proposed 'energy sensor' of the cell, AMPK, also displays higher activity both at rest and following exercise when glycogen is low (Wojtaszewski, et al., 2003). Ingestion of glucose during exercise also blunts expression of metabolic genes such as PDK4, UCP3, PGC1 α , CD36, CPT1 and AMPK α 2 (Cluberton, McGee, Murphy, & Hargreaves, 2005), the exercise-induced increase in AMPK α 2 activity (Akerstrom, et al., 2006) and the release of IL-6 from contracting skeletal muscle (Febbraio, et al., 2003). Taken together, these findings indicate that substrate availability and utilization from both endogenous and exogenous sources, especially in relation to carbohydrate, are an important factor in influencing the adaptive responses of skeletal muscle to exercise. Such data therefore suggest that carefully scheduled periods of training under conditions of low carbohydrate availability may be beneficial for inducing skeletal muscle adaptations and improving subsequent performance (Baar & McGhee, 2008).

Can 'training' with reduced carbohydrate availability enhance the training stimulus and improve performance?

Despite the theoretical rationale provided from those 'acute' studies documented above, few researchers have attempted to manipulate 'chronically' carbohydrate availability during training and examine the subsequent physiological, metabolic and performance adaptations that occur. Hansen,

et al. (2005) provided the initial research in this area and showed that training under conditions of low muscle glycogen concentration enhances both biochemical and performance adaptations. These authors employed a one-legged training model in which one limb was trained twice every second day whereas the contra-lateral limb was trained once daily. In this way, both limbs performed the same amount of work throughout training, yet the limb that trained twice per day performed every second training session under conditions of low initial muscle glycogen levels. The limb that trained with reduced muscle glycogen levels displayed significantly greater increases in citrate synthase activity and also performed better on a "time to exhaustion" test. Whilst these data provide some useful insights into the potential for glycogen to modulate training adaptations, the specific nature of the training protocol (i.e. one-legged knee extensor exercise) and the applicability of the findings have been questioned in terms of their ecological validity (Hawley, et al., 2008). Furthermore, this study solely focused on the effects of low 'muscle' carbohydrate availability and did not examine any potential interactive effects between muscle and circulating substrate on adaptive responses.

Based on this evidence, there seems to be a clear need to complete 'whole-body' externally valid training protocols that can simultaneously examine the role of both endogenous and exogenous carbohydrate availability on skeletal muscle adaptations to exercise training. Recent work in our laboratory has attempted to bridge this gap in the literature by completing an experimental study to examine the influence of both endogenous and exogenous carbohydrate availability in modulating training-induced improvements in exercise performance and mitochondrial related adaptations of human skeletal muscle. Three groups of subjects completed 6 weeks of high-intensity intermittent running occurring four times per week. Group 1 and 2 trained twice per day, two days per week (once in the morning and once in the afternoon where training sessions were interspersed with a 3-4 h rest period) whereas Group 3 trained once per day four days per week. In this way, each group performed the same amount of work throughout the training period, yet groups 1 and 2 performed every second training session with reduced pre-exercise muscle glycogen levels. In order to allow us also to examine the effects of exogenous glucose supplementation on influencing training adaptations, the subjects in Group 1 (LOW+GLU) consumed a carbohydrate beverage (6.4%) immediately prior to and at designated intervals throughout every second (i.e. afternoon) training session, whereas the subjects in Group 2 (LOW+PLA) consumed an identical amount of a taste, consistency and odour matched placebo solution at identical times immediately pri-

or to and throughout the exercise protocol. In contrast, subjects in Group 3 (NORM) commenced every training session with normal glycogen stores and consumed no beverages during any of their training sessions. Resting muscle biopsies were obtained from the *vastus lateralis* and *gastrocnemius* muscles immediately before the first training session and at 72 h after completion of the training programme. The subjects were also assessed for maximal oxygen uptake and intermittent running performance (Yo-Yo Intermittent Recovery test 2) before and after training interventions.

Post-training biopsy samples from both muscles revealed significantly greater increases in SDH activity in subjects training in the LOW+PLA condition compared with the other two conditions. These data therefore confirm and extend those findings of Hansen and colleagues by also demonstrating that carbohydrate availability (from both endogenous and exogenous sources) appears to be an important modulator of the mitochondrial enzyme adaptations induced during brief periods of endurance training. Interestingly, we also observed that the magnitude of the training-induced increase in total protein content of PGC1 α was similar between groups, thus suggesting that the transcriptional co-activator PGC1 α protein (at least that of total protein) did not provide a mechanistic explanation for our findings. Finally, we also observed similar improvements in performance between groups suggesting that although carbohydrate availability may have the potential to modulate subtle cellular alterations, they may not translate into whole body performance adaptations.

Potential advantages and disadvantages associated with training with low carbohydrate training

The data discussed in the present review may be of importance for athletic populations in that it provides initial evidence that carefully scheduled periods of 'low-carbohydrate' training may be beneficial for inducing oxidative adaptations of skeletal muscle. Exercising in conditions of reduced carbohydrate availability likely increases the potential signalling pathways (although these remain to be elucidated precisely) associated with modulating these adaptations, which may ultimately lead to improved metabolic control.

However, the limited availability of supporting data in the literature, along with some uncertainty regarding the applicability of data to other populations, currently prevents conclusive support for this training approach. For example, the participants discussed in the preceding studies were recreationally active and thus it remains to be determined whether such observations are also apparent in other populations such as highly trained individuals. Whilst it is possible that such nutritional interventions may

promote similar adaptations in these populations, a reduced carbohydrate availability may compromise the completion of the required volume and intensity of training that is necessary to provide an overload stimulus in already highly conditioned muscle (Barr & McGee, 2008). Furthermore, exercising in carbohydrate depleted states will increase circulating stress hormones, accentuate gluconeogenesis and may thereby compromise muscle mass, a response

that is not advantageous for individuals who require explosive or powerful movements for performance. Gleeson, Lancaster and Bishop (2001) also suggests that training in conditions of reduced carbohydrate availability may impair mood and increase the risk of infection thereby limiting training effectiveness in other ways. Additional research projects in the area are clearly needed before the implications of such issues can be clearly determined.

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Correspondence to:

Barry Drust

Research Institute for Sport and Exercise Sciences

Liverpool John Moores University

Henry Cotton Campus

Webster Street

Liverpool

L3 2ET

UK

E-mail: B.Drust@ljmu.ac.uk

Phone: + 44 151 231 4027

Fax: + 44 151 231 4353

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POBOLJŠAVANJE ADAPTACIJE NA TRENING IZDRŽLJIVOSTI NUTRICIONISTIČKIM INTERVENCIJAMA: POTENCIJALNE KORISTI OD “NISKOUGLJIKOHIDRATNOG” TRENINGA

Sažetak

Trening izdržljivosti opći je naziv za bilo koju ponavljaju fizičku aktivnost kojoj je cilj usavršavanje sposobnosti organizma da zadrži intenzitet rada tijekom dužeg perioda. Dugotrajne vježbe dovest će do mnogobrojnih promjena koje poboljšavaju dopremanje i iskoristivost kisika te na taj način dolazi do povećanja potencijala aerobnog metabolizma i poboljšanja izvedbe u aerobnim uvjetima rada. Navedene promjene uključuju izmjene u strukturi i funkciji srčano-žilnog, dišnog i mišično-skeletnog sustava. Skeletni mišići odgovaraju na vježbe izdržljivosti povećanjem transkripcije metaboličkih gena i gena povezanih sa stresom da bi, naposljetku, izazvali povećano stabilno stanje specifičnih proteina. Ti adaptacijski odgovori dovode do poboljšanja stanične funkcije koja služi za održavanje ravnoteže između energetske zahtjeva na sustav i kapaciteta koji zadovoljavaju te potrebe te na taj način dovode do poboljšanja u sportskoj izvedbi. Način prehrane je moćan modulator adaptacije skeletnih mišića, izazvane vježbama izdržljivosti. Nekoliko istraživanja pokazalo je da smanjena uporaba ugljikohidrata može pojačano potaknuti adaptacije skeletnog mišića izazvane vježbanjem. Ti rezultati upućuju na to kako je dostupnost substrata i njihovo korištenje iz endogenih i egzogenih izvora, osobito onih povezanih s ugljikohidratima, vrlo važan faktor utjecaja na adaptacijske reakcije skeletnog mišića na vježbanje. Takvi podaci sugeriraju da pažljivo raspoređeni periodi treninga u uvjetima niskog unosa ugljikohidrata mogu biti korisni za poticanje adaptacija skeletnog mišića te poboljšanje kasnije izvedbe. Posljednji podaci iz našeg laboratorija ispitali su utjecaj šestotjednog visokointenziv-

nog intervalnog programa treninga, koji se provodio u uvjetima niske koncentracije mišićnog glikogena, s egzogenom suplementacijom ugljikohidratima i bez nje, na adaptaciju skeletnog mišića čovjeka i izvedbu vježbi. Uzorci mišićne biopsije, koja se provodila nakon treninga, otkrila je znatnije povećanje aktivnosti sucino dehidrogenaze (SDH) u ispitanika koji su trenirali s niskom razinom glikogena i bez suplementacije ugljikohidratima u usporedbi s ispitanicima koji su trenirali u drugačijim uvjetima (više zalihe glikogena i suplementacija ugljikohidratima). Slična poboljšanja zabilježena su između grupa i tijekom izvedaba vježbe, što sugerira da, iako dostupnost ugljikohidrata može potencijalno utjecati na prilagođavanje suptilne stanične promjene, taj se potencijal ne može prenijeti i na adaptaciju izvedbe cijelog tijela. Podaci o kojima se raspravlja u ovom članku mogu biti važni za sportsku populaciju budući da dokazuju kako pažljivo raspoređeni periodi treninga u uvjetima niskog unosa ugljikohidrata mogu biti korisni za poticanje oksidativne adaptacije skeletnog mišića. Vježbanje tijekom kojega se unosi manje ugljikohidrata vjerojatno dovodi do povećanja potencijalnih važnih putova (iako to još nije precizno razjašnjeno) povezanih s prilagođavanjem tih adaptacija, koje mogu u konačnici dovesti do poboljšane metaboličke kontrole. Bilo kako bilo, ograničena dostupnost potkrepljujućih podataka u literaturi, zajedno s nekim nedoumicama vezanima uz primjenjivost tih podataka na drugim populacijama, za sada priječe konačnu potvrdu korisnosti takvog trenažnog pristupa. Sve navedeno upućuje na to da su potrebna dodatna istraživanja prije nego se sa sigurnošću može zaključiti o primjerenosti ove trenažne metode.