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Review

Training for intense exercise performance: high-intensity or high-volume training?

P. B. Laursen[1,2,3]

[1]*New Zealand Academy of Sport, Auckland, New Zealand,* [2]*Sport Performance Research Institute New Zealand (SPRINZ), School of Sport and Recreation, Auckland University of Technology, Auckland, New Zealand,* [3]*School of Exercise, Biomedical and Health Sciences, Edith Cowan University, Joondalup, Western Australia, Australia*
Corresponding author: Paul B. Laursen, New Zealand Academy of Sport North Island, PO Box 18444, Glen Innes, Auckland 1743, New Zealand. Tel: +64 9 477 5427, Fax: +64 9 479 1486, E-mail: paull@nzasni.org.nz

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Performance in intense exercise events, such as Olympic rowing, swimming, kayak, track running and track cycling events, involves energy contribution from aerobic and anaerobic sources. As aerobic energy supply dominates the total energy requirements after ~75 s of near maximal effort, and has the greatest potential for improvement with training, the majority of training for these events is generally aimed at increasing aerobic metabolic capacity. A short-term period (six to eight sessions over 2–4 weeks) of high-intensity interval training (consisting of repeated exercise bouts performed close to or well above the maximal oxygen uptake intensity, interspersed with low-intensity exercise or complete rest) can elicit increases in intense exercise performance of 2–4% in well-trained athletes. The influence of high-volume training is less discussed, but its importance should not be downplayed, as high-volume training also induces important metabolic adaptations. While the metabolic adaptations that occur with high-volume training and high-intensity training show considerable overlap, the molecular events that signal for these adaptations may be different. A polarized approach to training, whereby ~75% of total training volume is performed at low intensities, and 10–15% is performed at very high intensities, has been suggested as an optimal training intensity distribution for elite athletes who perform intense exercise events.

Both high-intensity (short-duration) training and low-intensity (high-volume) training are important components of training programs for athletes who compete successfully in intense exercise events. In the context of this review, an intense exercise event is considered to be one lasting between 1 and 8 min, where there is a mix of adenosine triphosphate (ATP)-derived energy from both aerobic and anaerobic energy systems. Examples of such intense exercise events include individual sports such as Olympic rowing, kayak and canoe events, most swimming races, running events up to 3000 m and track cycling events.

Exercise training, in a variety of forms, is known to improve the energy status of working muscle, subsequently resulting in the ability to maintain higher muscle force outputs for longer periods of time. While both high-volume training and high-intensity training are important components of an athlete's training program, it is still unclear how to best manipulate these components in order to achieve optimal intense exercise performance in well-trained athletes. While a short-term period of high-intensity training is known to improve performance in these athletes (Laursen & Jenkins, 2002), a high training volume may also be important (Fiskerstrand & Seiler, 2004). More recent work by exercise scientists is revealing how the combination of these distinctly different forms of training may work to optimize the development of the aerobic muscle phenotype and enhance intense exercise performance.

The purpose of this discourse is to: (i) review the energy system contribution to intense exercise performance, (ii) examine the effect of high-intensity training and high-volume training on performance and physiological factors, (iii) assess some of the molecular events that have been implicated in signaling for these important metabolic adaptations and (iv) make recommendations, based on this information, for the structuring of training programs to improve intense exercise performance.

Energy system contribution to intense exercise performance – what is it we are trying to enhance?

Intense exercise events involve a near maximal energy delivery for a sustained period of time. These near maximal efforts require a mix of anaerobic and aerobic energy provision. To illustrate this, Duffield et al. (2004, 2005a, b) examined the aerobic and anaerobic energy system contributions to 100, 200, 400, 800, 1500 and 3000 m track running in well-trained runners. The data from the male runners in these studies are plotted in Fig. 1, revealing that the energy contribution to an intense exercise event arises from a mix of aerobic and anaerobic sources. The crossover point, where aerobic and anaerobic energy contributes equally, occurs approximately at 600 m of near maximal running. This compares well with an earlier crossover estimate made by Gastin (2001) of about 75 s of near maximal exercise. Thus, for an intense exercise event that lasts beyond 75 s, total energy output is mostly aerobically driven. This is a convenient situation for the exercise conditioner, because the aerobic energy system appears to be a more malleable system to adjust. Indeed, both high-intensity training and high-volume training can elicit improvements in aerobic power and capacity.

Effect of training on physiological variables and intense exercise performance

The purpose of exercise training is to alter physiological systems in such a way that physical work capacity is enhanced through an improved capacity to deviate from resting homeostasis during subsequent exercise sessions (Hawley et al., 1997). Manipulation of the intensity and duration of work and rest intervals changes the relative demands on particular metabolic pathways within muscle cells, as well as oxygen delivery to muscle (Holloszy & Coyle, 1984). In response, changes occur in both central and peripheral systems, including improved cardiovascular dynamics (Buchheit et al., 2009), neural recruitment patterns (Enoka & Duchateau, 2008), muscle bioenergetics (Hawley, 2002), as well as enhanced morphological (Zierath & Hawley, 2004), metabolic substrate (Hawley, 2002) and skeletal muscle acid–base status (Hawley & Stepto, 2001). The rate at which these adaptations occur is variable (Vollaard et al., 2009) and appears to depend on the volume, intensity and frequency of the training. Importantly, development of the physiological capacities witnessed in elite athletes does not occur quickly, and may take many years of high training loads before peak levels are reached.

Training can be structured in an infinite number of ways, but in general, coaches tend to prescribe periods of prolonged submaximal exercise, moderate periods of training at "threshold" or shorter high-intensity exercise sessions (Hawley et al., 1997). In the context of this review, low-intensity training generally refers to exercise performed below the first ventilatory threshold, "threshold" intensity refers to exercise performed between the first and second ventilatory thresholds and high-intensity training refers to exercise performed above the second ventilatory threshold (Seiler & Kjerland, 2006). Submaximal low-intensity endurance training performed for long durations involves predominantly slow twitch motor unit recruitment, while higher intensity training (usually completed as high intensity interval training) will recruit additional fast twitch motor units for relatively short durations (Enoka & Duch-

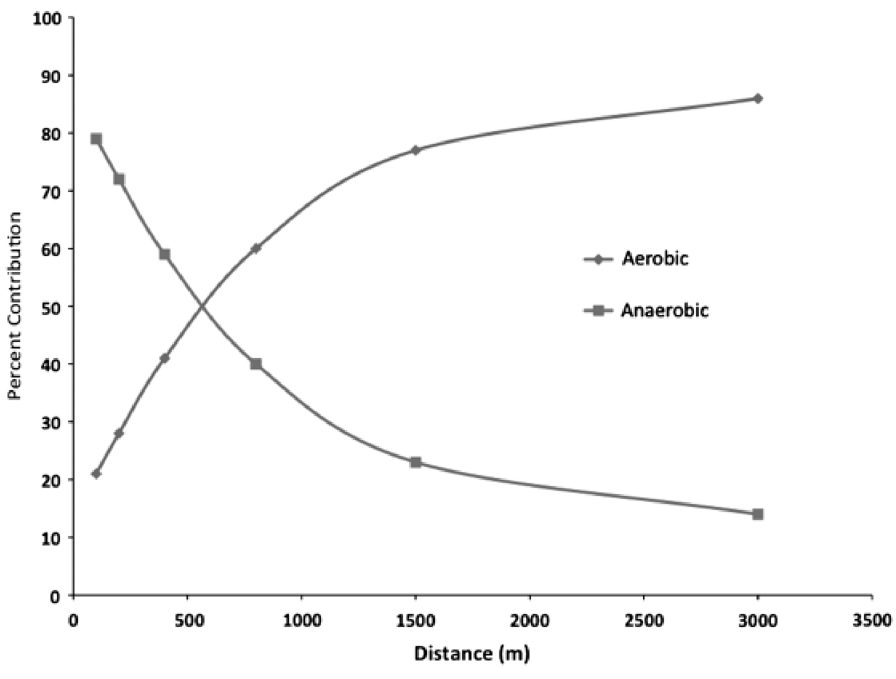

Fig. 1. Percent aerobic and anaerobic energy system contributions to near maximal running over distances ranging from 100 to 3000 m. Figure derived based on the male data obtained from the studies of Duffield et al. (2004, 2005a, b).

ateau, 2008). Both forms of training are important for enhancing the aforementioned physiological systems and intense exercise performance, but the degree and rate at which these variables change in the short term appear to be affected more acutely by high-intensity training (Londeree, 1997).

Performance and physiological effects of increased training intensity

The marked influence of high-intensity training on performance and physiological factors is well known (Laursen & Jenkins, 2002), but an athlete's ability to perform this type of training is limited (Billat et al., 1999). One successful method of performing higher volumes of high-intensity training is termed high-intensity interval training. High-intensity interval training, also called transition training, is defined as repeated bouts of high-intensity exercise (i.e. from maximal lactate steady state or second ventilatory threshold to "all-out" supramaximal exercise intensities), interspersed with recovery periods of low-intensity exercise or complete rest (Hawley et al., 1997).

In already well-trained athletes, the effect of supplementing high-intensity training on top of an already high training volume appears to be extremely effective. In well-trained cyclists, for instance, high-intensity interval training (six to eight sessions), completed at a variety of intensities (i.e. 80–150% VO_{2max} power output) for 2–4 weeks, has been shown to have a significant influence (i.e. +2–4%) on measures of intense exercise performance (i.e. time-to-fatigue at 150% of peak power output; 60.5 ± 9.3 vs 72.5 ± 7.6 s; $P<0.01$), peak power output and 40 km time trial performance (Lindsay et al., 1996; Westgarth-Taylor et al., 1997; Weston et al., 1997; Stepto et al., 1998). In well-trained middle distance runners, Smith et al. (1999, 2003) found improvements in 3000 m running performance when runners performed high-intensity interval training ($8 \times \sim 2$–3 min at VO_{2max} running speed, 2:1 work-to-rest ratio) twice a week for 4 weeks. In a retrospective study performed on elite swimmers, Mujika et al. (1995) found that mean training intensity over a season was the key factor explaining performance improvements ($r = 0.69$, $P<0.01$), but not training volume or frequency. Clearly, a short-term period of high-intensity interval training supplemented into the already high training volumes of well-trained athletes can elicit improvements in both intense and prolonged exercise performance (Laursen & Jenkins, 2002).

While the potent influence that a short-term dose of high-intensity interval training has on intense and prolonged endurance performance is well known, the mechanisms responsible for these performance changes with well-trained individuals are not clear. For example, Weston et al. (1997) had six highly trained cyclists perform six high-intensity interval training sessions (8×5 min at 80% peak power output, 60-s recovery) over 3 weeks, and showed significant improvements in intense exercise performance (time-to-fatigue at 150% peak power output) and 40 km time trial performance, without changes in skeletal muscle glycolytic or oxidative enzyme activities. Thus, despite the likely high rates of carbohydrate oxidation (340 μmol/kg/min) required by these efforts (Stepto et al., 2001), this acute perturbation in energy status of working muscle did not appear to increase metabolic enzyme function in the skeletal muscle of these six cyclists (Weston et al., 1997), as would be predicted based on findings made in less-trained subjects (Gibala & McGee, 2008). Instead, an increase in skeletal muscle buffering capacity was reported (Weston et al., 1997). Other physiological factors that have been shown to increase in parallel with improvements in performance following the addition of high-intensity interval training to the already high training volume of the well-trained athlete include improvements in the ventilatory (Acevedo & Goldfarb, 1989; Hoogeveen, 2000) and lactate thresholds (Edge et al., 2005; Esfarjani & Laursen, 2007; Driller et al., 2009), an increased ability to engage a greater volume of muscle mass (Lucia et al., 2000; Creer et al., 2004) and an increased ability to oxidize fat relative to carbohydrate (Westgarth-Taylor et al., 1997; Yeo et al., 2008).

In a recent study, Iaia et al. (2008, 2009) asked runners who were training 45 km/week to lower their training volume to only 15 km/week for 4 weeks, and instead perform speed endurance training (8–12×30 s sprints; three to five times per week). After this distinct change in training, runners in the speed endurance training groups had maintained their 10 km run performance, VO_{2max}, skeletal muscle oxidative enzyme activities and capillarization compared with the 45 km/week control group (Iaia et al., 2009). However, 30-s sprint (+7%), Yo-Yo intermittent recovery test (+19%) and supramaximal running (+19–27%) performances had increased in the speed endurance training group (Iaia et al., 2008). This study indicates that 4 weeks of low-volume high-intensity interval training can maintain an athlete's endurance performance and muscle oxidative potential (Iaia et al., 2009), and additionally increase intense exercise performance (Iaia et al., 2008).

In summary, it is clear that when a period of high-intensity interval training is supplemented into the already high training volumes of well-trained endurance athletes, further enhancements in both intense and prolonged endurance performance are possible. As well, lower volume high-intensity interval training can maintain endurance performance ability in already well-trained endurance athletes. While high-intensity training can have the aforementioned profound effects acutely on various aspects of intense exercise performance, the importance of a high-training-volume background should not be overlooked (Fiskerstrand & Seiler, 2004; Esteve-Lanao et al., 2005, 2007; Seiler & Kjerland, 2006).

Performance and physiological effects of additional training volume

When individuals are untrained, and commence a period of training characterized by long duration, low-intensity sessions, profound adaptations to skeletal muscle and supporting systems are witnessed, including increases in the mitochondrial content and respiratory capacity of muscle fibers (Holloszy & Coyle, 1984). As a consequence of the increase in mitochondria, exercise of the same intensity results in a disturbance in homeostasis that is smaller in trained than in untrained muscles, leaving some authors to suggest that the influence of prolonged training in already trained muscle may be limited (Laursen & Jenkins, 2002). Costill and colleagues (1991) do well to summarize an outsider's viewpoint on the issue, stating that, "it is difficult to understand how training at speeds that are markedly slower than competitive pace for 3–4 h/day will prepare (an athlete) for the supramaximal efforts of competition." Nevertheless, athletes commonly perform a large number of long-duration, low-intensity training sessions per week, which combine to form an athlete's high weekly training volume. Indeed, it has been estimated that well-trained (including world-elite) athletes perform $\sim 75\%$ of their training at intensities below the first ventilatory threshold, despite competing at much higher intensities (Seiler & Kjerland, 2006). This type of training likely contributes to their high skeletal muscle energy status (Yeo et al., 2008), their ability to sustain high muscular power outputs for long durations (Coyle et al., 1988) and their ability to recover from high-intensity exercise (Seiler et al., 2007).

Relative to the number of studies showing enhancements in intense exercise performance with high-intensity interval training (Laursen & Jenkins, 2002), there are relatively few studies documenting improvements in performance with step increases in training volume (Costill et al., 1991). This may be due to the fact that the time course for performance improvement with increases in training volume may not occur as rapidly (Costill et al., 1991) compared with acute increases in high-intensity training (Weston et al., 1997; Laursen et al., 2002), making investigation into its influence more challenging for researchers. In one study that managed to achieve this, Costill et al. (1991) divided collegiate swimmers into groups that trained either once or twice a day for 6 weeks. As a result, one group performed twice the volume of training of the other (4950 vs 9435 m/day) at similar high-training intensities (estimated by the authors to be 95 vs 93.5% VO_{2max} per interval). Despite higher levels of citrate synthase activity from the deltoid muscle shown in the group that doubled their training volume, performance times following a taper over distances ranging from 43.2 to 2743 m were not different between the groups. While this study demonstrates that a relatively acute period of high-volume training (with similar high training intensities) does not appear to enhance performance, there may be subtle positive effects of low-intensity high training volumes (Fiskerstrand & Seiler, 2004; Esteve-Lanao et al., 2005, 2007; Seiler & Kjerland, 2006).

The efficacy of low-intensity long-duration training sessions has been shown in at least three studies. In one of the first studies to show the importance of low-intensity high-volume training, Fiskerstrand and Seiler (2004) retrospectively investigated changes in training volume, intensity and performance in 21 international medal-winning Norwegian rowers from 1970 to 2001. From the 1970s to the 1990s, VO_{2max} increased by 12% (5.8–6.5 L/min) while 6-min rowing ergometer performance increased by 10%. Coinciding with these performance changes was an increase in low-intensity training (i.e. blood lactate <2 mM; 30–50 h/month), or high training volume, coupled with reductions in race pace and supramaximal intensity training (blood lactate 8–14 mM; 23–7 h/month). As a result, training volume increased by 20% over this period of time (924–1128 h/year), as did intense exercise performance results (Fiskerstrand & Seiler, 2004). In another longitudinal study conducted over a 6-month period, Esteve-Lanao et al. (2005) compared the influence of different amounts of intensity and volume training on running performance in eight sub-elite endurance runners ($VO_{2max} = 70.0 \pm 7.3$ mL/kg/min). The authors found strong relationships between time spent training at intensities below the first ventilatory threshold and both 4 km ($r = -0.79$; $P = 0.06$) and 10 km ($r = -0.97$; $P = 0.008$) run performance (Esteve-Lanao et al., 2005). In an another recent study, Ingham et al. (2008) divided elite British rowers into groups that performed either 12 weeks of low-intensity (100% of training performed below the lactate threshold) or mixed-intensity training (30% above, 70% below lactate threshold). While both groups improved similarly in terms of their performance, the low-intensity training group improved their speed at lactate threshold to a greater extent than the mixed training group (Ingham et al., 2008). Clearly, important adaptations appear to occur with low-intensity continuous training that are not observed with mixed or high-intensity training.

While the immediate effect of low-intensity high-volume training on intense exercise performance can be difficult to assess, it would appear that the insertion of these low-intensity training sessions has a positive impact on performance, despite being performed at an intensity that is markedly less than that which is specifically performed at during intense exercise competition. It is often purported that these periods of relatively low-intensity, high training volumes may provide the aerobic platform needed to facilitate the specific adaptations that occur in response to the high-intensity or specific workouts. Others feel that a high training volume may be important for achieving optimal body composition and engraining the neuromuscular blueprint needed to optimize performance. While the author is unaware of any research to back these claims, it would appear that intense exercise athletes do tend to organize their training into periods of both high-intensity and prolonged low-intensity phases (Fiskerstrand & Seiler, 2004; Esteve-Lanao et al., 2005, 2007; Seiler & Kjerland, 2006; Ingham et al., 2008). The disconnect between the scientific literature and the practices of elite intense exercise athletes highlights the urgent need for scientific research into the effects of high-volume training in high-level athletes, including the time course of adaptations as well as the long-term effects (i.e. detraining effects).

The important interplay between high-intensity training and high-volume training

The review of studies that manipulate training intensity and volume over a short-term period reveals that successful training programs may benefit from both forms of training at particular periods within an athlete's training program. When training does not have an appropriate blend of both high-intensity training and high-volume training inserted into the program, performance ability can stagnate. For example, Iaia et al. (2008, 2009) examined the influence of marked changes in intensity and volume training on performance and metabolic enzyme activity in endurance-trained runners. In this study, runners training 45 km/week lowered their training volume to only 15 km/week for 4 weeks, but instead performed speed endurance training (8–12 × 30 s sprints; 3–5 times/week). While markers of sprint performance were improved, 10 km run performance was only maintained, and not enhanced (Iaia et al., 2008, 2009). In a study on competitive swimmers, Faude et al. (2008) used a randomized cross-over design where swimmers performed two different 4-week training periods, each followed by an identical taper week. One training period was characterized by a high training volume, while the other involved high-intensity training; neither program involved aspects of both. The authors found no difference between the training periods for 100 and 400 m swim performance times, or individual anaerobic thresholds (Faude et al., 2008). Clearly, a mix of both high-intensity training and high-volume training is important, but predominance of one form of training or the other does not appear to be as beneficial. In a study demonstrating the importance of having equal amounts of distinctly different training, Esteve-Lanao et al. (2007) divided 12 sub-elite runners into two separate groups that performed equal amounts of high-intensity training (~ 8.4% of training above respiratory compensation point). The difference between the groups in terms of their training, however, was the amount of low- vs moderate-intensity training they performed. In one group, more low-intensity training (below the first ventilatory threshold; 81 vs 12%) was performed. In the other group, more moderate-intensity training (above first ventilatory threshold but below the second ventilatory threshold; 67 vs 25%) was performed. While intense exercise performance was not assessed, it is interesting to note that the magnitude of the improvement in 10.4 km running performance 5 months following the intervention was significantly greater ($P = 0.03$) in the group that performed more low-intensity training (-157 ± 13 vs -122 ± 7 s). Admittedly, the 10.4 km test used to assess running performance falls outside of the intense exercise spectrum, but does suggest that the aerobic power and capacity of these runners were enhanced by this training scheme; a capacity identified previously in this article as critical to intense exercise performance success beyond ~75 s of all-out near maximal activity.

The synthesis of these studies reveals the importance of combining periods of both high and low-intensity training into the training programs of the intense exercise athlete. Seiler and Kjerland (2006) refer to this training distribution as a polarized model, where approximately 75% of sessions are performed below the first ventilatory threshold, with 15% above the second ventilatory threshold and <10% performed between the first and second ventilatory thresholds. For the exercise scientist, these observations beg the question: why might the mixing of distinct high and low-intensity training sessions be so effective at increasing the energy status of working muscle and subsequent exercise performance? Seiler et al. (2007) offer a plausible hypothesis for why successful elite intense exercise athletes benefit from periods of both high training intensities and volumes. In this study, the authors monitored acute disturbances in autonomic balance using heart rate variability following different types of exercise in highly trained Norwegian orienteers (Seiler et al., 2007). On separate occasions, athletes ran for 60 and 120 min below their first ventilatory threshold, for

30 min between their first and second ventilatory threshold and intermittently for 60 min above their second ventilatory threshold. Irrespective of running for either 1 or 2 h below the first ventilatory threshold, markers of autonomic balance disturbance were not altered to the same degree as compared with either a 30-min session performed between the first and second ventilatory threshold, or a 60-min high-intensity interval training session performed above the second ventilatory threshold. The authors proposed that the first ventilatory threshold may be an important demarcation point identifying the training intensity above which autonomic balance may be altered. However, two recently published manuscripts (Meyer et al., 2004; Faude et al., 2009) suggest that prolonged (i.e. 3 h) low-intensity training (below ventilatory threshold; v-slope method) may not be adequate to induce recovery or regeneration in the 4-day period following a 13-day intensive training phase. Nevertheless, the period of overreaching applied to the athletes in this study could be considered abrupt, where more well-trained, experienced athletes might build gradually into the same relative training load. When phases of high training loads are repeated without adequate recovery, and autonomic balance is continually disturbed, this results in overtraining (Billat et al., 1999). Notwithstanding the limitations of monitoring staleness in athletes using heart rate variability (Bosquet et al., 2008), and that other factors such as hormonal disturbances, psychological stressors, muscle damage, injury and illness may be responsible for prolonged fatigue in athletes (Bosquet et al., 2008), the documented training organization of elite athletes (Seiler & Kjerland, 2006) may serve to maximize performance by optimizing mitochondrial protein synthesis signaling without significantly compromising autonomic balance (Seiler et al., 2007).

How does it happen? Beginning to understand molecular signaling

While the picture is far from complete, scientists have begun to make impressive inroads toward understanding how skeletal muscle adapts to varying exercise stimuli, and for an excellent review on the topic, the reader may refer to the work of Coffey and Hawley (2007). As assessed by these authors (Coffey & Hawley, 2007), there appear to be at least four primary signals (along with a number of secondary messengers, redundancy and cross-talk) that can lead to an increase in mitochondrial mass and glucose transport capacity in skeletal muscle following several forms of exercise training. These include (i) mechanical stretch or muscle tension, (ii) an increase in reactive oxygen species that occurs when oxygen is processed through the respiratory pathways, (iii) an increase in muscle calcium concentration as required for excitation–contraction coupling and (iv) the altered energy status (i.e. lower ATP concentrations) in muscle. These mechanisms and pathways are complex, with many beyond the scope of this review. For the purpose of this discourse, however, the focus will be on the last two of these primary signals, which have received increased attention in recent studies.

The first of these mentioned molecular signals is the prolonged rise in intramuscular calcium, such as that which occurs during prolonged endurance exercise or high exercise training volumes. These high calcium concentrations activate a mitochondrial biogenesis messenger called the calcium–calmodulin kinases (Fig. 2). Second, the altered energy status in muscle associated with small reductions in ATP concentrations, such as that present during high-intensity exercise, elicits a relatively large concomitant rise in adenosine monophosphate (AMP), which activates the AMP-activated protein kinase (AMPK). With these two secondary phenotypic adaptation signals identified, it becomes apparent how different types of endurance training modes might elicit similar adaptive responses (Burgomaster et al., 2008). In support of these distinct pathways, Gibala et al. (2009) showed significant increases in AMPK immediately following four repeated 30-s "all-out" sprints. This was associated 3 h later with a twofold increase in peroxisome proliferator-activated receptor-γ coactivator-1α (PGC-1α) mRNA, a transcriptional coactivator that has been described by some as the "master switch" for mitochondrial biogenesis (Adhihetty et al., 2003) (Fig. 2). Of note, however, is that this occurred without an increase in the calcium–calmodulin kinases (Gibala et al., 2009), which are known to be stimulated during prolonged repeated contractions (Rose et al., 2007).

With these results in mind, it becomes clear what has been known by coaches for decades; that is, with respect to prescribing training that improves performance, "there's more than one way to skin a cat." The high mitochondrial oxidative capacity, improved fat oxidation potential, and increased glucose transport capacity in the skeletal muscle of endurance athletes may be achieved through either high volumes of endurance training, high intensities of endurance training or various combinations of both. Higher volumes of exercise training are likely to signal for these adaptations through the calcium–calmodulin kinases (Rose et al., 2007), while higher intensities of endurance training, which lowers ATP concentrations and raises AMP levels, appear more likely to signal for mitochondrial biogenesis through the AMP-activated protein kinase pathway (Gibala et al., 2009). As shown in Fig. 2, these different signaling molecules have similar downstream targets

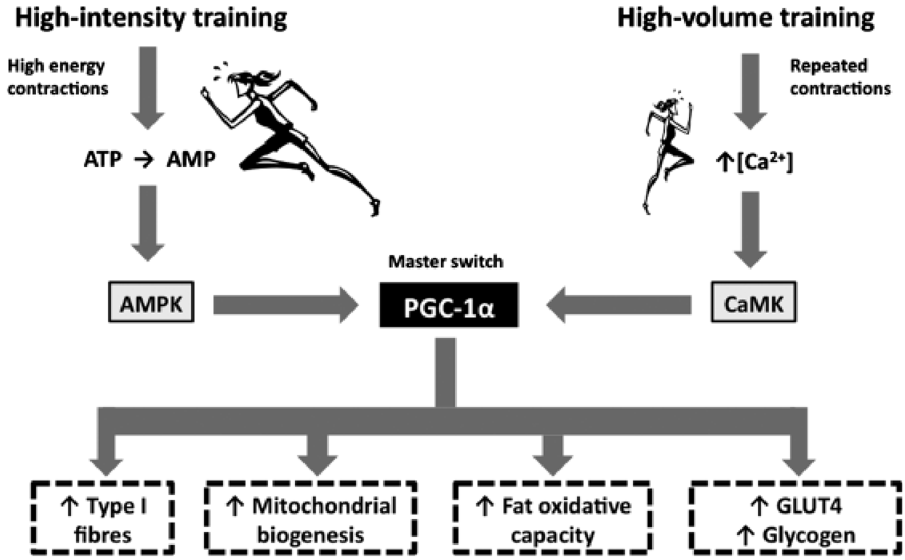

Fig. 2. Simplified model of the adenosine monophosphate kinase (AMPK) and calcium–calmodulin kinase (CaMK) signaling pathways, as well as their similar downstream target, the peroxisome proliferator-activated receptor-γ coactivator-1α (PGC-1α). This "master switch" is thought to be involved in promoting the development of the aerobic muscle phenotype. High-intensity training appears more likely to signal via the AMPK pathway, while high-volume training appears more likely to operate through the CaMK pathway. ATP, adenosine triphosphate; AMP, adenosine monophosphate; GLUT4, glucose transporter 4; [Ca^{2+}], intramuscular calcium concentration.

(Baar, 2006). The result is an increased capacity to generate ATP aerobically. Thus, at the molecular level, it may be the blend of signals induced from combined high-volume training and high-intensity training that elicits either a stronger or more frequent promotion of the aerobic muscle phenotype through PGC-1α mRNA transcription (Fig. 2). As well, the lower intensity higher volume training sessions are likely to promote the development of the aerobic phenotype without disturbing autonomic balance that could lead to overtraining (Seiler et al., 2007). These speculative comments highlight an important area for future research.

How do we optimally structure training programs for high-performing endurance athletes?

While this manuscript offers a unique discourse describing a binary model by which training is organized into periods characterized by either high training intensities, or high training volumes, the reality of the matter is that athletes often perform sessions where there are mixed amounts of both (e.g. a 6-h group bike training session over hilly terrain). Thus, characterizing all training sessions as being either a prolonged low-intensity, moderate-intensity or high-intensity session can be problematic. Nevertheless, the synthesis of this information reveals a pattern highlighting the importance of applying periods of both high-intensity training and high-volume training at the appropriate time in a training program, in order to elicit an optimal intense exercise performance. Experts in training program design refer to this as the art of periodization (Issurin, 2008). While the high-intensity training stimulus over the lead up period to intense exercise performance appears critical (Londeree, 1997), the submaximal or prolonged training durations (volume of repeated muscular contractions) cannot be downplayed (Fiskerstrand & Seiler, 2004). These high-volume training periods may elicit the molecular signals needed to stimulate mitochondrial protein synthesis without creating undue autonomic disturbance that could lead to overtraining (Seiler et al., 2007). Over time, the progressive result is likely to be an improved efficiency of skeletal muscle and a development of the fatigue-resistant aerobic muscle phenotype. Indeed, development of the successful intense exercise athlete tends to require a number of years exposure to high training volumes and intensities (Schumacher et al., 2006). The art of successful intense exercise coaching, therefore, appears to involve the manipulation of training sessions that combine long duration low-intensity periods with phases of very high-intensity work, appropriate recovery and tapering (Mujika et al., 2000; Issurin, 2008; Pyne et al., 2009).

The paper will finish with two practical examples that demonstrate the effectiveness of this model. The first example is New Zealand's Olympic 800-m running legend, Sir Peter Snell. Snell was a protégé of the late New Zealand athletics coach Arthur Lydiard, who was renowned for organizing the training of middle- and long-distance runners into early phases of high training volumes (up to 160 km/week), before "strength" phases consisting of hill running, followed by high-intensity track sessions in the acute period leading up to a major event. This was innovative at the time because 160 km training weeks were the sort of training only completed by most marathon runners (Snell P, personal communication). The result for Snell was an 800 m world record in 1962 (1:44.3), and winning double Gold in the 800 and 1500 m events at the 1964 Tokyo Olympic Summer Games.

Another report of a high-volume training plan that elicited a winning intense exercise performance was that of the German 4000-m team pursuit cycling world record achieved at the Sydney 2000 Olympic Games (Schumacher & Mueller, 2002). In this paper, Schumacher and Mueller (2002) provide a detailed account of the training performed by the cyclists over the 7-month lead-up to the critical event. In general, training involved extremely high volumes (29 000–35 000 km/year) that included long periods of low-intensity road training ($\sim 50\%$ VO_{2max}) interspersed with stage racing (grand tour) events. While the road racing component of the cyclists' training program would have entailed numerous periods of both high-volume and high-intensity stimuli, it was not until the final 8 days before the Sydney Olympics that a specific high-intensity training taper period on the track was prescribed. Nevertheless, this training design yielded outstanding results, and the model has since been replicated by both the Australian and British cycling teams to break this record repeatedly over the last two Olympic Games (Quod M, Cycling Australia, Australian Institute of Sport, personal communication).

Summary

Our understanding of how best to manipulate the training programs of athletes competing in intense exercise events so that performance is optimized is far from complete. It would appear that a polarized approach to training may be optimal, where periods of both high and low-intensity training but high-volume training are performed. The supplementation of high-intensity training to the high-volume program of the already highly trained athlete can elicit further enhancements in endurance performance, which appears to be largely due to an improved ability of the engaged skeletal muscle to generate ATP aerobically. Prolonged durations of low-intensity or high-volume training are likely to facilitate adaptation by signaling for the aerobic phenotype, yet the intensity may be low enough to promote autonomic balance, recovery and athlete health. Some of the important molecular signals arising from various forms of exercise training include the AMPK and calcium–calmodulin kinases, likely to be activated in response to intense and prolonged exercise, respectively. Both of these signals have similar downstream targets in the skeletal muscle that promote the development of the aerobic muscle phenotype. A further understanding of how best to organize and manipulate the training programs for future intense exercise athletes will require the continued cooperation of sport scientists, coaches and athletes alike.

Key words: interval training, aerobic capacity, energy system, molecular signaling, mitochondrial biogenesis, AMPK, CaMK.

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