NEUROMUSCULAR ADAPTATIONS IN RUNNING

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Introduction

Run training, as with all forms of physical exercise training, stimulates the development of adaptations that should benefit the performance of the task. In the case of distance running, these adaptations often result in improved economy of transport (i.e. lower energy cost to maintain a fixed running speed). Mechanisms behind training-related improvements in running economy fall primarily into two broad categories: metabolic adaptation and neuromuscular adaptation. The focus of this chapter will be on factors that may contribute to neuromuscular adaptations and improvements in running economy primarily in distance runners. In conjunction with this, common training practices will be explored, including: (1) incorporation of resistance training as a means of supporting the performance of running; (2) adaptations that result from chiefly ‘run-only’ training; and (3) possible influences of barefoot running versus shod running on neuromuscular adaptations that develop from running. The chapter begins with a general exploration of the relationship between endurance run training and neuromuscular factors.

Neuromuscular influences of endurance run training

The specificity of training principle would suggest that slow, continuous aerobic exercise, which is commonly performed by distance runners, will compromise high-velocity force production and power. Endurance-only training also impedes gains in strength and can cause reductions in power due to shifting of fibre-type characteristics towards Type I fibre-type and disuse atrophy effects on Type IIa and IIx muscle fibre (Thayer et al., 2000). In addition, functional adaptations that result from endurance training may be limited to metabolic outcomes (Cohen et al., 2010). As a result, distance runners often incorporate interval-type training and/or strength training as methods for supporting the power-based needs that are often important for success in their sport. Plyometric training has also shown positive benefits for use in distance runners by supporting improvements in running economy (Markovic and Mikulic, 2010; Saunders et al., 2006; Turner et al., 2003). Neuromuscular adaptations that result from these types of training interventions may positively influence motor unit activation and recruitment patterns and alter more commonly assessed factors such as stride length and frequency. Bonacci et al. (2009) compiled a comprehensive review of neuromuscular adaptations related to various types of training to which the reader is referred. However, the focus of this chapter will remain on running adaptations.
The quality of running economy may be related to existing (or changes to) elastic properties of the leg muscles in addition to metabolic adaptation. For example, it has been shown that the oxygen cost of running is inversely related to lower limb flexibility in elite marathon runners (Jones, 2002). Those with greater leg stiffness (poorer flexibility) were found to be more economical. Craib et al. (1996) made similar observations in a group of sub-elite runners, hypothesizing that greater leg stiffness might confer an economy advantage by improving storage and return of elastic energy generated during the eccentric phase of the stretch-shortening cycle. These findings are also corroborated by Dalleau et al. (1998), who found better RE in those runners who possessed greater leg stiffness. The investigators hypothesized that increased leg stiffness develops as a neuromuscular adaptive response to endurance run training. However, stiffness can be acutely affected as well. Stiffness may be increased transiently, leading to a lower energy cost, by avoiding over-flexing the knees during running or by running on a less compliant surface (Dalleau et al., 1998). An adaptive response to running that results in increased leg stiffness may seem counterintuitive, however, as a more rigid muscle might be expected to be more prone to injury resulting from repetitive impact.

Heise et al. (2008) found that muscle coactivation of biarticular muscles (rectus femoris and gastrocnemius) during the stance phase leads to increased joint stiffness, which may allow for more efficient use of stored elastic energy. They theorized that coactivation of these muscles may be an adaptive response found in more economical runners. In a group of 16 female runners, muscle coactivation duration was able to explain 45 per cent of the inter-individual variability in running economy; an inverse relationship between running economy and duration of muscle coactivation was noted (Heise et al., 2008). It was also theorized that EMG-based biofeedback might be useful for educating runners about the coactivation process and, thereby, driving higher economy that may result in performance gains.

Few studies have been conducted to explore neuromuscular adaptations that result specifically from endurance training. However, Cohen et al. (2010) sought to assess whether such adaptations might be observed in endurance trained adult males and boys. Different aged populations were assessed to gauge whether age-related effects on neuromuscular adaptations could be identified. Trained and untrained subjects from the two age cohorts were assessed for isometric strength of elbow and knee extensors and flexors and EMG activity of the associated agonist and antagonist muscle groups. While age-related and training-related effects were noted for some measures (i.e. higher rate of muscle activation and rate of torque development in adults), there was no clear evidence of neuromuscular adaptation when comparing trained to untrained cohorts. As a result, the authors concluded that endurance training elicits chiefly metabolic adaptations (Cohen et al., 2010).

Indices of neuromuscular adaptation in runners have been reported by other investigators. For example, Paavolainen et al. (1999c) showed that 5 km race time was related to neuromuscular characteristics in a homogenous group of elite male orienteers. Specifically, the ability of runners to generate force rapidly during maximal and submaximal running was related to race performance. Similarly, ground contact time was shorter in those with the better race performance. Spending less time during ground contact, especially during the braking phase of contact would, presumably, conserve energy. In support of this, shorter ground contact time was also related to better RE (Paavolainen et al., 1999c). This tends to support the theory proposed by Kram and Taylor (1990) that suggests the energy cost of running is a function of mass and ground contact time. They noted an inverse relationship between the rate at which energy is used during running and the amount of time the foot generates force against the ground. Thus, those runners with better economy tend to also have shorter ground contact time.
Acute neuromuscular effects

Neuromuscular control appears to be modified during the course of sustained running. Paavolainen et al. (1999b) found that braking and propulsion components of ground contact times were longer immediately following completion of a 10 km time trial. In addition to these changes, peak and vertical ground reaction forces were significantly reduced and there was a reduction in muscle activation during a 20 m maximal sprint performed after the time trial. The investigators hypothesized that repetitive stretch–shortening cycles reduced the ability of the neuromuscular system to maintain force production and to tolerate impact forces. It was suggested that a decline in muscle stiffness, coupled with a longer transition time between braking and propulsion, led to less conservation of elastic energy. These effects were corroborated by a reduction in IEMG activity during the maximal 20 m runs (Paavolainen et al., 1999b). Thus, acute and high-repetition SSCs have been shown to transiently influence neuromuscular control properties and force production, both of which are important factors in RE. Those runners who were able to better maintain running performance under fatiguing conditions were also found to have higher relative pre-activation and lower relative agonist IEMG-activity during the propulsion phase than the lower caliber runners. This supplies further evidence for the importance of neuromuscular control and conservation of elastic energy via maintenance of muscle stiffness during distance running.

Neuromuscular characteristics were also attributed to success in 5 km race performance (Paavolainen et al., 1999c). Specifically, the ability to produce force quickly was an important factor in maximal and submaximal running. The faster runners tended to demonstrate shorter ground contact time, braking phase time and propulsion phase time than their slower, matched counterparts.

Running economy

Running economy (RE) is a term used to reflect steady-state oxygen uptake under specified conditions (i.e. fixed submaximal treadmill speed at zero grade, controlled environment) (McCann and Higginson, 2008). It has also been defined as the energy demand for a given submaximal velocity (Saunders et al., 2004a). More economical runners will maintain steady-state running at a lower oxygen uptake. Further, when RE is improved through training, the effect is evidenced by a reduction in the oxygen uptake needed to sustain a fixed submaximal running speed. Thus, an increase in RE is reflected by a reduction in total energy cost. Numerous factors have been reported to influence RE. Saunders et al. (2004b) provided a schematic that identifies 17 different variables that may impact RE. These variables can be broken into five subsets that include: training, environment, physiology, biomechanics and anthropometry. Much attention has been given to many of these subsets, but teasing apart specific effects and the magnitude of such effects is a complex process. While scientists may be keenly interested in specific slices of the overall outcome and strive to characterize mechanisms for adaptation, trainers and the athletes themselves are more likely to view the big picture outcomes that training provides (i.e. improved performance, better pace maintenance, quality of training). Since RE has been reported to be a better predictor of race performance than aerobic power among elite runners (Costill et al., 1973), it has garnered a great deal of attention from the scientific community. In the following sections, consideration will be given to a variety of training interventions that have been investigated as a means of improving RE and, in some instances, endurance run performance.
Run training-imposed changes in economy

Beyond neuromuscular and metabolic adaptations that result from run training, tissue-specific changes have been reported as well. For example, Fletcher et al. (2010) sought to investigate whether run training coupled with isometric training leads to increased triceps-surae tendon stiffness, which is associated with improved running economy. These investigators imposed isometric plantarflexion exercise (working at 80 per cent of MVC) 3 days per week for 8 weeks. Stiffness of the triceps-surae and MVC were assessed every 2 weeks, with RE measured at baseline and upon completion of the 8-week intervention. The group of highly trained middle- and long-distance runners maintained their run training throughout the study. A non-intervention control group of runners was used for comparison. While the training intervention failed to significantly affect tendon stiffness and RE, a significant inverse relationship was found between RE and stiffness of the triceps-surae tendon. This relationship occurred irrespective of group assignment. The investigators observed that acute changes in tendon stiffness and RE can occur and that these changes may happen in tandem. They suggest that less compliant muscle would lower the energy transfer to the tendon, resulting in a lower cost of the muscle activity. Conversely, a more compliant tendon would lead to more muscle fibre shortening and/or an increased velocity of shortening for a given joint movement, which would raise the cost of muscle activity. Whether an increase in tendon stiffness is a function of chronic adaptation or acute high-intensity training is not evident. It is possible that isometric training would be more likely to elicit positive effects on tendon stiffness in moderately trained runners who are not as well adapted as the runners used in this study.

Brisswalter and Legros (1995) applied training overload (300 per cent volume increase over 2 weeks) on well-trained middle-distance runners to gauge impact on running economy and running pattern. Two trends were found to develop: improved economy (~9 per cent) was observed only at the running speed that corresponded with the volume overload (which occurred at 80 per cent intensity); the change in economy was associated with individual stride-rate adaptation although stride length was not altered. The improvement in economy was attributed to an adaptation in foot pattern, as well as an improvement in foot stability at the training pace.

Other differences have been reported in mechanical factors that are important to run performance and economy based on sex and training emphasis (i.e. middle distance versus long distance) (Chapman et al., 2012). Chapman et al. (2012) found that elite female runners showed significantly shorter ground contact times when running at the same speeds as males. They also had greater stride frequency and shorter stride length compared to male counterparts. However, these differences appeared to be a function of height as when the data were normalized for height, the differences disappeared. The only exception to this was with stride frequency, which remained higher in women across all running speeds. When comparing middle-distance to long-distance trained males, the rate of change in ground contact time differed significantly as the running speed was increased. The long-distance runners showed a significantly larger decline in contact time as running speed increased compared to the middle-distance runners. This effect translated into a 31.1 per cent increase in metabolic cost for the LD runners versus a 25.4 per cent increase for the MD runners when moving from 5 to 7 m.s⁻¹. Based on these findings, the authors suggest that gait differences between distance specialists may be a function of preferred and/or competition speeds and that the preferred speed among LD runners could be driven by economy factors. For information related to neural adaptations and sprint training, the reader is referred to a review by Ross et al. (2001). For a more applied review of power training and sport, readers are referred to Young (2006).
Resistance training: effects on run economy

Despite seemingly divergent outcomes based on the principle of specificity, resistance exercise training is a commonly accepted practice among distance runners. Numerous benefits of resistance training for runners have been identified, including better maintenance of form and economy, improved leg power and speed (Paavolainen et al., 1999a), improved sprint ability (Mikkola et al., 2011), attenuation of cardiovascular drift (Hayes et al., 2004), enhanced neuromuscular characteristics (Mikkola et al., 2011) and reduced injury risk. Muscular strength endurance has been linked to better fatigue resistance during distance running as well (Hayes et al., 2011). It has also been suggested that development of power could be impeded as a result of continuous focus on aerobic training in some athletes, which may adversely affect neuromuscular adaptation as well as heighten the risk of overtraining (Elliott et al., 2007).

Tanaka and Swensen (1998) hypothesized that resistance trained distance runners may be better able to sustain performance at fixed submaximal running speeds by either enabling force contribution from each myofibre to be reduced or by requiring fewer myofibres to sustain the work. It was further suggested that resistance training leads to a lesser need for contributions from lower efficiency Type II fibres (Tanaka and Swensen, 1998). These benefits would be achieved by improved quality of the Type I fibre content that may accompany resistance training.

Taipale et al. (2010) examined the effects of differing strength training interventions on measures related to distance running performance, including running economy and VO₂max velocity (vVO₂max). Strength training was performed concurrently with normal run training over a 28-week period in a population of recreational runners. They found that explosive strength training and maximal strength training were more effective than circuit weight training for improving RE and vVO₂max. These benefits were associated with greater strength gains and neuromuscular adaptations (measured via EMG activity of the vastus lateralis and medialis) in the two groups.

Ferrauti et al. (2010) failed to identify improvements in RE or muscle coordination in response to 8 weeks of concurrent run and resistance training in recreational marathon runners despite significant gains in leg strength. Strength training was performed twice weekly and focused on the trunk (for muscular endurance) and lower extremity (high intensity). The high-intensity strength training of the leg muscles was designed to promote motor unit recruitment pattern improvements while minimizing hypertrophic gain in an effort to improve RE. Ground contact time revealed a significant interaction when compared to a run endurance group such that contact time tended to increase in the concurrently trained group while tending to decrease in the run-only group. Despite this interaction, RE remained the same. Stride length and stride frequency, indices of muscle coordination, were unaffected by concurrent training. However, stride length was significantly decreased in the run-only group. Thus, some of the alterations may have been a function of changes to run volume or intensity that occurred in the subjects as they were building towards a marathon competition. The investigators hypothesized that a larger subject pool or longer study duration may have revealed more profound effects (Ferrauti et al., 2010).

Paavolainen et al. (1999b) introduced a 9-week explosive strength training regimen on top of normal endurance training in elite distance runners to study the effects on 5 km race performance. Explosive training included plyometric-type jumping exercises, leg press and leg extension/flexion exercises with low loads and maximal velocity repetitions, and sprint sets. Lifting loads fell below 40 per cent of 1 RM. Significant improvements in 5 km race time (3.1 per cent faster) and in RE were associated with reduced ground contact time during
constant velocity running in the strength-trained group. This occurred despite no significant effects on stride rate, stride length or ground reaction force during constant velocity running. Strength training was associated with significant gains in maximal isometric force production of the leg extensors and maximal anaerobic run test velocity (V_MART). The improvement in RE (8.1 per cent lower oxygen cost) correlated with the improvement in V_MART. VO2_max was not affected by the training intervention. Thus, the gains in performance were attributed to improved neuromuscular function that led to gains in muscle power and a lower cost of steady state transport (Paavolainen et al., 1999b).

**Plyometric training and running economy**

Plyometric training has been widely used to support and enhance performance in a variety of sport activities (Markovic and Mikulic, 2010). Commonly, this type of training has been advocated for sport tasks that incorporate jumping, agility and explosive power generation. The training technique revolves around the stretch-shortening cycle (SSC) of muscle activation. By challenging the neural and musculotendinous systems that are involved via repeated SSCs, it is believed that more force can be generated over less time, allowing for an increase in power production by the muscle. Thus, plyometric training would theoretically stimulate neuromuscular adaptations that could have application for many types of movement tasks, including distance running. One of the draws for endurance athletes is that plyometric-type training has been reported to induce positive neural adaptations and mechanical advantages with an attenuated hypertrophic response that is commonly associated with heavy resistance training (Häkkinen et al., 1985; Saunders et al., 2006). Plyometric training has also been found to stimulate neuromuscular adaptations (better maintained muscle recruitment pattern) that support the bike-to-run transition in triathletes (Bonacci et al., 2011). However, the neuromuscular adaptations that developed did not translate into improved economy upon completion of the bicycling phase (Bonacci et al., 2011).

SSC training involving plyometrics has focused primarily on the lower body musculature. Saunders et al. (2006) examined the effects of 9 weeks of plyometric training on running economy in a population of highly trained distance runners. Plyometric exercises employed fast concentric/eccentric movement patterns and included activities such as straight-leg jumps, squat jumps for height, fast feet drills (where minimum ground contact time and high force production were emphasized), bounding, and high-skipping among others. Running economy (fixed speeds of 14, 16 and 18 km.h⁻¹) was assessed prior to and after 5 and 9 weeks of plyometric training. RE was unchanged at the lower running speeds for any time-point. However, a significant improvement in economy was noted after 9 weeks of plyometric training at the highest running speed (18 km.h⁻¹). The oxygen requirement for this speed was reduced by 4.1 per cent in the plyometric group, while no change was found in the control group. No other cardiorespiratory variables were affected by the training intervention during RE testing. Likewise, no changes in max were found. However, there was a trend for the VO₂ versus running speed slope to be lower in the plyometric group after 9 weeks of training. The plyometric group also tended to show improvement (14.7 per cent) in average power production for a five-jump plyometric test (p = 0.11) at 9 weeks. Improved RE was attributed, in part, to improved locomotor muscle metabolism (i.e. improved efficiency of ATP use) and improved recovery of elastic energy (Saunders et al., 2006). It was also speculated that an improvement in whole-body mechanics occurred only with the fastest speed under evaluation, which was deemed more representative of normal training and competition running speed. Finally, since cardiorespiratory substrate use measures were largely unaffected, the improved...
RE at the fastest speed was primarily attributed to gains in muscular power and conservation of elastic energy and/or from better gait coordination and technique that accompanied plyometric training (Saunders et al., 2006). While mechanics and changes in gait patterns can be evaluated and quantified, methods for quantifying changes in elastic energy remain elusive (Saunders et al., 2004b). Notably, it has been theorized that those most likely to benefit from interventions designed to boost economy will be the lesser-trained runners (McCann and Higginson, 2008). Thus, plyometric training may be found to elicit more profound and possibly multifaceted effects in less well-trained runners.

For a comprehensive review on plyometric training and performance adaptations, see Markovic and Mikulic (2010).

**Barefoot running and neuromuscular adaptation**

Barefoot running has gained considerable attention in the past several years. A recent PubMed search using ‘barefoot running’ revealed that 28 publications have been produced since January 2011 in this general area. Despite the recent heightened attention, a number of sports medicine investigations were conducted in the early to mid 1980s involving barefoot running (Burkett et al., 1985; Robbins and Hanna, 1987; Rodgers and Leveau, 1982). Early investigators explored factors including the potential for barefoot running to help prevent running-related injury (Robbins and Hanna, 1987), and effects of barefoot running on limb kinematics (Burkett et al., 1985). Robbins and Hanna (1987) proposed that running shoes impede sensory input and induce more foot rigidity. These effects of shod running could be associated with a greater injury frequency.

More contemporary investigators have also investigated kinematic adaptations related to barefoot or minimalist running (Divert et al., 2005b; Lieberman, 2012; Perl et al., 2012). Perl et al. (2012) studied the effects of footwear on running economy and kinematics. It is commonly found that shod runners are more prone to rearfoot strike while barefoot runners are more likely to show forefoot strike patterns. These differences may influence kinematic and economy factors during steady state running. Perl et al. (2012) compared minimalist footwear (Vibram FiveFingers™) to standard running shoes (Asics Gel-Cumulus 10™). Two trials were completed using each style of footwear: forefoot strike (FFS) and rearfoot strike (RFS). Trial order was randomized and expired gases were collected while at steady state (trials were a minimum of 5 minutes). Stride frequency and foot mass were matched between footwear types. Footstrike style (FFS versus RFS) was not found to affect economy within each type of footwear. However, economy was influenced by footwear type within a strike style such that during FFS running, the minimally shod condition was 2.4 per cent more economical. RFS was found to be 3.2 per cent more economical when performed with minimalist footwear. There was wide variability within subjects when minimally shod for economy, ranging from 9.7 per cent more economical to 7.3 per cent less economical; though most subjects were more economical with minimalist footwear. While the mechanisms are yet to be soundly confirmed, economical advantages associated with minimalist footwear were attributed to: (1) greater storage of elastic energy and recoil in the longitudinal arch; (2) less knee flexion during gait (a possible energy conservation adaptation); and (3) increased elastic energy storage in the Achilles tendon (Perl et al., 2012). Further work is needed to investigate each of these proposed mechanisms for enhanced economy in minimalist footwear. Likewise, given the broad variability within subjects under the different conditions, further examination of individual variation is warranted.

Divert et al. (2005a) explored stiffness adaptations under shod and barefoot conditions during treadmill running in male runners. They found that vertical stiffness and leg stiffness decreased
during 4 minutes of running (3.61 m.s\(^{-1}\)) in the shod condition, while in the barefoot condition stiffness was stable. A significant difference between conditions was noted for stride frequency (5 per cent higher in barefoot), while vertical displacement, leg compression and maximal vertical force were significantly lower (15, 5 and 3.5 per cent, respectively) in barefoot running. The lower mean and vertical leg stiffness measures in the shod condition were attributed to the notion that musculotendinous stiffness was not increased adequately to compensate for shoe compliance during the shod running condition (Divert et al., 2005a) Alteration of shoe properties (both acute and chronic) should be considered when examining kinematic and economical measures of runners.

de Koning (1992) suggested that neurologic adaptation may result from barefoot running. He noted significant differences between shod and barefoot running in EMG activity of the tibialis anterior muscle, with higher activity observed during barefoot running. He suggested that this difference may be due to an attempt of the neuromuscular system to attenuate the ground impact force by controlling plantar flexion and/or foot pronation during landing. Barefoot running was also found to elicit a lower landing velocity than shod running. Whether these adaptations are more about protection, comfort or fatigue remains to be answered (de Koning, 1992). Based on early and more contemporary research, it is evident that barefoot

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running will influence gait pattern, lower extremity muscle activation patterns and leg stiffness, economy and potentially injury incidence. However, neuromuscular adaptations that develop from introduction of barefoot running are yet to be clearly established. Further, whether adaptive responses to barefoot running develop as a result of protection from injury (i.e. shock attenuation) or more from an inherent drive for higher economy of transport is unknown. For further information on the evolutionary influences of barefoot running and its medical implications, Lieberman (2012) provides a review of these topics.

Summary

Numerous factors have the potential to alter running patterns. As with any form of physical training, adaptation will occur. The adaptive response to run training appears to generate several positive outcomes: (1) reduced cost of transport; (2) attenuated impact forces as a means of minimizing injury occurrence; and (3) delayed fatigue development. Neuromuscular adaptations that contribute to these advantages appear to be related to developing increased leg stiffness and reducing knee flexion during gait, which both help to conserve elastic energy. Other neuromuscular factors that may contribute to adaptation include increased stiffness of the Achilles tendon and the tendon surae. Further beneficial adaptations may result from incorporation of resistance, plyometric training or barefoot running. As above, neuromuscular adaptations that result from these types of training are also commonly linked to stiffness changes.

Other factors that should be investigated more thoroughly include the effects of eccentric loading of muscle on neuromuscular adaptations, running surface rigidity and gait alterations, and the effects of footwear rigidity on economy, adaptive response and forces applied to the lower extremity. In addition, clothing that has been designed to support run performance (i.e. elastic compression stockings) should also be studied more thoroughly to clearly elucidate their effects on mechanical and energetic factors of locomotion.

References

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