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Review

The elite cross-country skier provides unique insights into human exercise physiology

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Successful cross-country skiing, one of the most demanding of endurance sports, involves considerable physiological challenges posed by the combined upper- and lower-body effort of varying intensity and duration, on hilly terrain, often at moderate altitude and in a cold environment. Over the years, this unique sport has helped physiologists gain novel insights into the limits of human performance and regulatory capacity. There is a long-standing tradition of researchers in this field working together with coaches and athletes to improve training routines, monitor progress, and refine skiing techniques. This review summarizes research on elite cross-country skiers, with special emphasis on the studies initiated by Professor Bengt Saltin. He often employed exercise as a means to learn more about the human body, successfully engaging elite endurance athletes to improve our understanding of the demands, characteristics, and specific effects associated with different types of exercise.

The skier and research

Over the years, Scandinavian researchers in exercise physiology have worked with elite athletes to gain new insights into the mechanisms and limitations of human performance, including physiological adaptation and regulation. Answering questions concerning ultimate physiological limitations requires subjects who routinely perform at or near their maximal capacity, i.e., well-trained athletes (Fig. 1).

One such question posed by Prof. Bengt Saltin and his colleagues is whether the human body is really well adapted for whole-body locomotion such as swimming, rowing, and cross-country skiing? In terms of motor control, the answer is obviously yes, as most people can easily learn how to perform these activities. However, how well are the metabolic demands of working muscles met and can supporting organs (e.g., the lungs and cardiovascular system) supply all of these muscles optimally with blood and oxygen while maintaining blood pressure and the homeostasis of the muscle milieu?

Thus, during his career Saltin focused, among other things, on cardiovascular responses to whole-body exercise. In most seminal studies in this area, the subjects were semi-recumbent or, at best, upright on a cycle ergometer. Accordingly, until recently almost no data concerning the hemodynamic responses of well-trained athletes to whole-body exercise in an upright position have been available.

This latter problem was overcome by studying elite athletes, e.g., cross-country skiers. For this purpose, Saltin and his colleagues designed complex experiments using invasive state-of-the-art procedures to assess oxygen transport and hemodynamics in cross-country skiers during the routine performance of different techniques (Fig. 2). Cross-country skiing, one of the most demanding endurance sports, involves combined upper and lower body effort of varying intensity and duration, on hilly terrain, often at moderate altitude and in a cold environment. Therefore, cross-country skiers demonstrate a very high VO2max and upper and lower bodies that are nearly equally well trained, allowing investigation of potential differences between arm and leg muscles. Moreover, elite skiers skillfully combine their arms and legs during skiing, can work at high intensities with either the upper body or legs alone and are also able to perform submaximal exercise at a relatively high metabolic rate, i.e., with cardiac outputs similar to or higher than those of untrained individuals exercising maximally.

With steep uphill and downhill terrain and repeated changes between techniques, cross-country skiing is technically challenging. Accordingly, this sport places considerable demands on a variety of capabilities, including aerobic and anaerobic power, strength, speed and endurance, as well as technical and tactical expertise. This uniqueness attracts athletes who enjoy the challenge and variation and want...
to improve their skills, as well as researchers who strive to elucidate the demands involved and factors which determine performance.

Performance

Cross-country skiing has been an Olympic event since the very first winter games in Chamonix, France in 1924. Since the 1980s, this sport has been revolutionized – beginning with the introduction of skating techniques and followed by new events such as pursuit, mass-start and sprint races. Today, competitions at the World Championships and Olympic Games involve distances ranging from 1.2 to 50 km, with corresponding times ranging from as little as 2.5 min to more than 2 h. Remarkably, 8 of the 12 events at the 2014 Olympics in Sochi either did not exist or have been significantly altered in format since the Lillehammer games in 1994.

Concurrently, racing velocities have nearly doubled (Sandbakk & Holmberg, 2014), e.g., a 50-km race that took approximately 4 h six decades ago takes only 2 h today, primarily because of better track preparation and ski equipment. These faster speeds are most evident in freestyle events, where the athletes employ multiple skating techniques with skis specially designed for maximal glide, together with longer and stiffer poles. Although aerobic capacities have improved only marginally over the years, the strength and muscular endurance of the upper body of cross-country skiers have become dramatically better (Saltin, 1997; Hoff et al., 1999; Terzis et al., 2006; Stöggl et al., 2011; Sandbakk & Holmberg, 2014).

Cross-country ski race courses are approximately one-third uphill, one-third flat, and one-third downhill, but more than 50% of the total time is spent skiing uphill and performance here is the major determinant of success (Bergh & Forsberg, 1992; Sandbakk & Holmberg, 2014). The varying terrain (with inclines between $+20$ and $-20\%$) and a wide range of speeds (5–70 km/h) require frequent changes between the nine main sub-techniques of classical skiing and skating. Thus, during a 1.5-km sprint race, the skiers change between these sub-techniques approximately 30 times (Andersson et al., 2010), whereas longer distances involve several hundred transitions, in unique contrast to other Olympic sports (e.g., only three transitions in the swimming medley relay and two during a triathlon).

This technical complexity motivates skiers to strive for maximally efficient generation of power and

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**Fig. 1.** The elite cross-country skier – a unique producer of energy and power.

**Fig. 2.** Photographs illustrating the complexity of the experimental procedures in the first comprehensive assessment of central and peripheral hemodynamics in subjects performing quadripedal exercise in the upright position. This cross-country skier roller skied on a treadmill with catheters in his femoral artery, both femoral veins, and subclavian vein. One of the catheters in the femoral vein was advanced into the heart for assessment of cardiac output by the Fick procedure. The other catheter in the femoral vein and the one in the subclavian vein allowed the blood flow in the arms and legs to be determined by thermodilution. An additional catheter in the corresponding vein of the contralateral arm allowed infusion of stable isotopes for monitoring fat and carbohydrate oxidation (Van Hall et al., 2003). A detailed description of these procedures can be found elsewhere (Van Hall et al., 2003; Calbet et al., 2004, 2005; Holmberg & Calbet, 2007).
speed from metabolic energy, particularly at high speeds (Sandbakk et al., 2010). Faster speeds require greater propulsive forces and the best cross-country skiers generate peak poling forces as high as 430 N (about half of their body weight) with each arm within as little as 0.05 s, with leg push-off forces of 1600 N (twice body weight) (Stöggel et al., 2011). With each technique, elite skiers must generate very large forces rapidly and skillfully, which has led to more focus on biomechanics in this context. Several teams of investigators have successfully integrated physiological and biomechanical approaches to provide novel insights that have improved cross-country skiing performance and helped develop this sport in other ways as well (Holmberg et al., 1998; Holmberg et al., 2006; Zory et al., 2006; Andersson et al., 2010; Björklund et al., 2010; Bøjesen-Moller et al., 2010; Mikkola et al., 2013; Pellegrini et al., 2013; Bucher Sandbakk et al., 2014; Kehler et al., 2014; Rud et al., 2014).

The lungs

Pulmonary function, both at rest and during exercise, has been examined extensively (Dempsey, 1986; Dempsey & Johnson, 1992) and the prevailing view is that endurance training by healthy humans does not result in structural changes in the lungs (Wetter & Dempsey, 1992; Wagner, 2005). Although elite cross-country skiers exhibit 5–20% higher static and dynamic lung volumes and flow rates than untrained individuals (Holmberg et al., 2007), this is probably more due to other factors, such as selection for appropriate genetic endowment.

The primary goal of pulmonary gas exchange during exercise is to maintain arterial O₂ saturation and the pH homeostasis. While this is achieved by most exercising humans at sea level, with certain highly trained endurance athletes, such as rowers, arterial O₂ saturation can fall below 90% during exhaustive exercise (Nielsen et al., 1999). On the other hand, at sea level at least, elite cross-country skiers maintain arterial saturation relatively well, as demonstrated both by direct arterial blood sampling (Calbet et al., 2005; Holmberg & Calbet, 2007) and pulse oximetry (Holmberg et al., 2007), during submaximal as well as exhaustive exercise and when using various skiing techniques (Holmberg & Calbet, 2007; Holmberg et al., 2007).

Interestingly, with the double-poling cross-country skiing technique, pulmonary gas exchange and arterial saturation are remarkably better than during the diagonal skiing, as indicated by the smaller difference between alveolar and arterial O₂ pressures (Holmberg & Calbet, 2007). One possible explanation is that while double-poling the skier bends the torso from an upright to a nearly horizontal position, allowing better overall ventilation/perfusion matching in the lungs. In addition, during double-poling, locomotor and respiratory movements are closely coupled (Holmberg et al., 2007; Lindinger & Holmberg, 2011), with exhalation being assisted by the forceful contraction of the abdominal muscles which flex the trunk and inhalation enhanced by the extension of the trunk (Boggs, 2002).

Although, as mentioned above, oxygenation of the pulmonary blood is maintained relatively well in elite cross-country skiers at sea level, the degree of desaturation during maximal exertion varies between individuals and modes of exercise (e.g., running vs diagonal stride or double-poling cross-country skiing). Most ski-research laboratories are at sea level or low altitude and maintained at room temperature (+20°C). Accordingly, little is yet known about the effects of moderate/high altitude (Olympic competitions being held as high as 1800 m above sea level) and cold temperature (as low as −20°C) on the aerobic capacity of cross-country skiers. Our unpublished observations, made in connection with an earlier study (Holmberg et al., 2007), indicate that although at sea level arterial saturation in cross-country skiers is not reduced to the same extent as in rowers, this saturation in elite skiers decreases significantly at moderate altitude, where approximately one third of World Cup skiing competitions take place.

Oxygen uptake

Elite cross-country skiers exhibit exceptionally high aerobic power, both absolute (L/min) and relative (mL/kg/min) and, indeed, few male skiers have won medals in a major championship with VO₂max values of less than 6 L/min or ~80–90 mL/kg/min (Bergh & Forsberg, 1992; Saltin, 1997; Holmberg et al., 2007; Sandbakk & Holmberg, 2014; Tønnessen et al., 2014). Female skiers demonstrate ~10% lower values, some reaching ~75 mL/kg/min (Saltin, 1997; Rusko, 2003; Sandbakk et al., 2014). There is a distinction between the VO₂max and VO₂peak in cross-country skiing. Because of the technical complexity of cross-country skiing, with different sub-techniques that activate upper and lower body muscles to different extents, both of these parameters are important for performance. VO₂max is consistently attained when using the diagonal skiing sub-technique (Stromme et al., 1977; Holmberg et al., 2007) and usually with the uphill skating techniques (G2 and G3 skating), but the VO₂peak of elite skiers employing other sub-techniques is 5–15% lower (Holmberg et al., 2007; Sandbakk et al., 2014). In an earlier investigation on elite international skiers (Holmberg et al., 2007), the highest VO₂ values were reached during diagonal skiing, with 4% and 14% lower values when running uphill.
or double-poling. This somewhat greater oxygen uptake during combined arm and leg exercise has been ascribed to more complete extraction of oxygen in the periphery (Stenberg et al., 1967).

In contrast to cycling and running, the multiple sub-techniques involved in cross-country skiing offer unique opportunities to distinguish between VO$_{2\text{max}}$ and VO$_{2\text{peak}}$, especially with newly developed skiing-specific treadmills and ergometers. As in the case of kayaking and canoeing, upper body aerobic power and performance during cross-country skiing are closely related (Bilodeau et al., 1995; Gaskill et al., 1999; Mahood et al., 2001). Novel physiological insights have motivated elite skiers to attempt to enhance their VO$_{2\text{peak}}$ to $\geq95\%$ of VO$_{2\text{max}}$ with all of the sub-skiing techniques, particularly those that involve the smallest amount of muscle (e.g., double-poling) and/or are associated with the lowest VO$_{2\text{peak}}$/VO$_{2\text{max}}$ ratios.

**Cardiac output, blood flow, and oxygen extraction**

Oxygen uptake by skeletal muscles is directly related to the capacity of the cardiovascular system (Saltin & Calbet, 2006), with cardiac output being considered the most important determinant of oxygen delivery and a close relationship between delivery and utilization of oxygen over a wide range of metabolic demands (Andersen & Saltin, 1985; Segal & Kurjiaka, 1995). Cardiac outputs in excess of 40 L/min and stroke volumes greater than 200 mL have been observed in elite cross-country skiers (Ekblom & Hermansen, 1968). Maximal heart rate is unchanged or slightly reduced by training and the higher maximal cardiac output in well-trained individuals is explained primarily by a larger stroke volume (Ekblom et al., 1968) due to increased left ventricular diameter and mass (Finkellhor et al., 1986; Levy et al., 1993; Hoogsteen et al., 2003), more rapid diastolic filling (Levine, 2008), a larger end-diastolic volume (Starling, 1918; Frank, 1895), and enhanced compliance (Levine, 2008).

The extensive cardiac output required to achieve and maintain VO$_{2\text{max}}$ probably requires large blood volumes. Indeed, elite cross-country skiers demonstrate relatively high total levels of hemoglobin (Lundgren et al., 2015), a surrogate for blood volume. These skiers can perform maximal combined arm and leg exercise with relatively low afterload (as indicated by a mean arterial pressure close to 95 mmHg) (Calbet et al., 2004), thereby reducing cardiac work and O$_2$ consumption. However, vascular tone must be appropriate, as excessive vasodilation will reduce the perfusion pressure.

For this reason, when skiing with both the legs and arms, vasodilation must be restricted to a certain extent. In fact, Secher et al. (1977) demonstrated that adding arm exercise to ongoing cross-country skiing reduces blood flow to the legs. This response may be even more crucial in the case of elite cross-country skiers, as Calbet et al. (2004) showed that in these athletes the maximal vascular conductances of the arms and legs together exceed the pumping capacity of the heart and without restriction of vasodilatory signals to the active muscles of all four limbs, the mean blood pressure will fall to 75–77 mmHg. (see also Calbet et al., 2015).

A unique characteristic of cross-country skiers is their ability to achieve high VO$_{2\text{peak}}$/VO$_{2\text{max}}$ ratios even when employing sub-techniques that involve less muscle mass than classical diagonal skiing. Moreover, research indicates this ability has been improved by recent developments in training. A high VO$_{2\text{peak}}$ requires rapid delivery of O$_2$ to the active muscles in combination with extensive O$_2$ extraction and rapid O$_2$ delivery to a small muscle mass requires high perfusion pressure accompanied by commensurate vascular conductance.

The mechanisms by which skiers maintain elevated perfusion pressures during exercise with only a small mass of muscle appear to involve fine-tuned regulation of regional vascular conductances (Calbet & Joyner, 2010). The report by Volianitis et al. (2004) indicates that such autonomic neural regulation during arm cranking and certain skiing sub-techniques involving a smaller amount of muscle can be mediated by resetting of the carotic baroreflex to a higher blood pressure. But what about vascular conductance, is this also an important determinant of performance during exercise involving less muscle, such as intense double-poling? Most experimental evidence to date indicates that it is (for a review see, Calbet & Lundby, 2012).

Vascular conductance depends on vascular tone and structural factors, but at present, very little is known about the effects of training on such factors. As both the endothelium-dependent and -independent vasodilatory responses of elite athletes are similar to those of less well-trained athletes (Jendzowsky & DeLorey, 2012; Green et al., 2013), vascular conductance in elite athletes is unlikely to be limited by insufficient vasodilation or inappropriate vasoconstriction. Thus, structural factors are probably limiting (Rowley et al., 2011) and, indeed, cross-country skiers have wide conduit arteries in their upper arms, similar in size to those of kayakers (Lundgren et al., 2015), which explains why the former can reach almost twice as high perfusion of their arms as other physically active individuals (Volianitis & Secher, 2002; Volianitis et al., 2003; Calbet, 2015).

Is the distribution of blood flow to different parts of the body an important factor in connection with performance? Cross-country skiing presents challenges concerning not only how much blood is dis-
tributed to various active muscles but also how rapidly re-distribution occurs during the repeated transitions between upper-, lower-, and whole-body movements (Andersson et al., 2010). Rådegran and Saltin (1998) demonstrated that maximal perfusion of skeletal muscle is attained within 30–45 s after the onset of exercise. Although this time is probably much shorter for muscles submitted to intermittent activation, this question has yet to be definitively addressed. New technologies will be needed to determine how rapidly regional circulation adapts to the rapid changes in technique observed in actual competitions. Although relevant information can be provided by near-infrared spectroscopy, assessment of blood flow simultaneously in several regions of the body continues to present a major challenge.

Once the skier manages to supply active muscles with sufficient O₂, this oxygen must be extracted, i.e., taken up and utilized by the mitochondria. Both the leg and arm muscles of most elite cross-country skiers extract O₂ to a remarkable extent (Calbet et al., 2005), i.e., 93–95% by the leg muscles, and only 10–12% less by the arms. This difference between the two sets of limbs has been attributed to the more pronounced heterogeneity in the distribution of blood flow between muscles (or functional portions of the same muscle), lower mean transit time, lower diffusion area, and longer diffusion distance in the arms (Calbet et al., 2005).

Furthermore, O₂ extraction may play a key role in exercise involving less muscle mass such as double-poling. For example, the increases in arm muscle activity and pole forces associated with elevation of the intensity of double-poling (Stöeggl et al., 2013) or when changing from the diagonal stride to double-poling (Björklund et al., 2015) are accompanied by a reduction in oxygen extraction, possibly due to mechanical hindrance to flow even at higher perfusion pressure. In principle, training designed to improve O₂ extraction in the arms to approach the value observed for the legs should enhance the VO₂peak/VO₂max ratio during double-poling. In practice, it remains to be determined how this could be achieved, although recent studies by Boushel and colleagues (Boushel et al., 2014) indicate that high-volume, low-intensity training may be one such possibility.

In summary, the elite cross-country skier demonstrates exceptional abilities to achieve extremely high cardiac output with relatively low afterload, to distribute the blood available efficiently to active muscles, and to extract and utilize most of the O₂ these muscles receive. Apparently, the VO₂max of these athletes has remained virtually unchanged in recent decades, implying no alteration in cardiac output or systemic O₂ extraction. Nonetheless, performance has improved dramatically, reflecting improvements in equipment, as well as more efficient training of metabolic adaptations and better utilization of potential during competitions. The observation that the VO₂peak/VO₂max ratio when using double-poling or other sub-techniques involving lower muscle mass has also improved indicates that the limits have not yet been reached. The major factors that limit performance need to be identified and training programs designed accordingly.

**Morphology**

**Fiber type**

Most available information on the muscle fibers of cross-country skiers from 1960 to 1990 are based on histochemical analyses and demonstrate a predominance (~70–75%) of type 1 (slow twitch) fibers in the leg, shoulder, and arm muscles (Saltin, 1997).

The composition of fiber types in muscle displays considerable plasticity in animal models, as well as under conditions of extreme perturbation. For example, nerve cross-union alters nearly all functional elements of muscle fibers (Buller et al., 1960) and chronic electrical stimulation induces transformation of fast to slow muscle (Pette & Vrbova, 1992). Although muscle biopsies reveal pronounced differences between the fiber profiles of sprint and endurance athletes, it is not known whether this reflects training and/or genetic factors (Schiaffino & Reggiani, 2011). However, the metabolic, contractile, and/or Ca²⁺-handling properties of muscles can clearly be altered by routine training, with no change in myosin heavy chain composition (Saltin & Gollnick, 1983).

**Fiber size**

The area occupied by muscle fibers is clearly enhanced by training of strength and power and certain types of endurance training may cause hypertrophy (Andersen & Henriksson, 1977b; Fry, 2004). Cross-country skiers exhibit larger areas of muscle fibers than other endurance athletes. Moreover, skiers in the 1990s demonstrated 15–25% larger fiber areas, especially in their arm muscles, than successful skiers of the 1970s (Saltin, 1997), probably due to enhanced emphasis on strength and power training.

**Capillaries**

Depending on the intensity and duration, endurance training leads to marked proliferation of muscle capillaries (Andersen & Henriksson, 1977a; Ingjer, 1978), independent of the types of muscle fibers present. The numbers of capillaries in the leg muscles of competitive cross-country skiers are as large as those
in the leg muscles of cyclists and runners (~5–7 capillaries per fiber) (for refs, see Saltin, 1997), although the density of capillaries in the skiers’ arm and shoulder muscles is lower. Swimmers and kayakers, for whom the upper body obviously plays a dominant role in performance, exhibit numbers of capillaries in their arm and shoulder muscles that are as high as in the legs of cyclists and runners (see Saltin, 1997), indicating that there is still room for improvement by cross-country skiers in this respect, thereby enhancing maximal \( O_2 \) extraction by the arm muscles.

A recent, unpublished study found the same average density of capillaries in the leg and arm muscles of trained skiers (417 ± 14 capillaries/mm\(^2\) or 5.8 ± 0.8 and 6.3 ± 0.3 capillaries per fiber for the legs and arms, respectively). However, the arm muscles contained 14% more capillaries per type MHC2a fiber. Furthermore, although there was no difference in the mean size of the various types of fibers in the leg muscles, in the arms, type MHC2a were larger than type MHC1 fibers. Thus, more capillaries per type MHC2a fiber in arm muscles is associated with the larger size of these fibers.

**Mitochondria**

The current consensus is that enhanced muscle oxidative capacity exerts only a minor impact on VO\(_{2}\)\(\text{max}\) during whole-body exercise (Henriksson & Reitman, 1977). However, such improvement does reduce fluctuations in the level of ADP during exercise, thereby attenuating activation of other metabolic pathways (e.g., glycolysis, glycogenolysis, and AMP deamination). This may enable greater utilization of lipids as an energy source, conserving carbohydrates (Boushel et al., 2014). By increasing the fraction of VO\(_{2}\)\(\text{max}\) that can be sustained during prolonged exercise, enhanced mitochondrial respiration will improve performance. The high content of mitochondria may explain why skiers are able to utilize fatty acids to a great extent, even at quite high work intensities, as demonstrated by relatively low respiratory exchange ratios (Mygind et al., 1994; Saltin, 1997).

The mitochondrial volume density of different types of muscle fibers is generally considered to differ markedly. In untrained humans, mitochondrial volume density is 6% in type I, 4.5% in type 2a, and 2.3% in type 2x fibers (Essén-Gustavsson & Henriksson, 1984; Howald et al., 1985), but there is pronounced variability in this respect between fibers of the same type (Hoppeler, 1986). The conventional view is that type I muscle fibers exhibit a much higher mitochondrial capacity than type 2.

Although this is the case for classical type 1 and type 2b fibers, our own recent, as yet unpublished findings indicate that the mitochondrial capacity of type 2a fibers of trained skiers is as great or even greater than that of type 1 fibers. Furthermore, the mitochondrial volume density in the type 2 fibers of trained individuals is equal to (Howald et al., 1985) or greater than (Nielsen et al., 2010) in type 1 fibers of those who are untrained. Thus, the mitochondrial content of the different types of fibers can be influenced markedly by exercise (Hoppeler, 1986; Nielsen et al., 2011), as can the total level of mitochondrial enzymes (Holloszy, 1967; Saltin & Gollnick, 1983).

**Metabolism**

The main fuels for exercise are carbohydrates and fatty acids. Carbohydrate is provided by uptake of glucose from the blood and/or breakdown of muscular depots of glycogen. The latter represent the primary source of energy during exercise and the relationship between the level of glycogen and endurance capacity of skeletal muscle is fundamental (Hultman, 1967; Hargreaves, 2000; Ørtenblad et al., 2013). For instance, the muscles of well-trained individuals (including cross-country skiers) contain up to twice as much glycogen as those of untrained individuals (Ørtenblad et al., 2011; Gejl et al., 2014). There are strong indications that depletion of glycogen during prolonged, exhausting exercise contributes to muscle fatigue by impairing Ca\(^{2+}\) regulation inside the muscle (Ørtenblad et al., 2013). Interestingly, a specific pool of glycogen, located within the myofibrils and more abundant in elite skiers, is used preferentially during skiing and is closely correlated with Ca\(^{2+}\) regulation (Ørtenblad et al., 2011).

The equally well-trained leg and arm muscles of elite cross-country skiers allow comparison of their metabolic properties without the complication of a difference in this respect. It is notable that during cross-country skiing, net lactate uptake is higher and lactate release lower in the legs than the arms, despite similar amounts of work and net glucose uptake (Van Hall et al., 2003). Furthermore, lactate should be considered as an important secondary source of carbohydrate in the blood, as it accounted for 20–30% of total carbohydrate oxidation both at rest and during exercise (Van Hall et al., 2003).

Fatty acids are obtained both from the bloodstream and intramyocellular lipids (IMCL). The muscles of well-trained athletes clearly contain higher levels of IMCL. In cross-country skiers, with highly trained leg and arm muscles, this content is fourfold greater and the ability to oxidize fat is higher in the muscles of the legs (unpublished data), a difference that cannot be explained by the distribu-
Energy production

The ability to produce metabolic energy to generate force and perform external work is a major determinant of endurance sport performance. Until recently, the focus has been primarily on aerobic energy production in mitochondria, but the significance of anaerobic energy derived from glycolysis, along with reutilization of the lactate thus produced, has become increasingly clear. Based on biomechanical calculations, Norman et al. (1989) estimated that metabolic energy turnover on a short (~20 s), steep uphill section during a classical cross-country ski race was equivalent to 100–120 mL O2/kg/min, which is far in excess of the VO2max of the best skiers. McGawley and Holmberg (2014) estimated the anaerobic energy contribution during uphill diagonal skiing (600 m, 187 ± 23 s) by the MAOD (Maximal Accumulated Oxygen Deficit) approach and found an O2 deficit of 44 ± 9 mL/kg. Losnegard et al. (2012) have reported an MAOD of 60 mL/kg for uphill ski skating. Others have tried to quantify anaerobic contributions using peak blood concentrations of lactate (Stöggel et al., 2007; Vesterinen et al., 2009) or increases in lactate concentration (Sandbakk et al., 2011) as rough estimates, but, as will become clear below, such indicators must be used with caution.

Skeletal muscle continuously produces lactate due to rapid glycolysis, sometimes even when the oxygen supply is adequate. During exercise, the concentration of lactate in the bloodstream depends on the balance between lactate production/release and uptake/utilization by the active muscles. Mygind et al. (1994) reported that elite skiers exhibit substantial blood levels of lactate (10 mmol) after only 5–10 min of a 40-min simulated race and these levels rise only slightly more during the remainder of the race.

Interestingly, we found that regardless of the technique or duration of submaximal classical roller skiing, the arms of elite skiers release more lactate than they take up, while the situation is the opposite for the legs (Van Hall et al., 2003). Because of their large muscle mass and energy requirement, the legs oxidize most of the lactate produced by the whole body (~14.1 mmol/min) and keep the arterial concentration relatively low (~2.5 mmol/L). Clearly, the systemic blood concentration of lactate is not a valid measure of aerobic/anaerobic capacity during exercise or of training status or technique, as it depends heavily on the relative involvement of the arms and legs. Examination of inter-limb differences in lactate production/utilization in greater detail (also during skating) may provide novel insights into metabolic regulation in human muscles and help to improve the training and technical strategies of cross-country skiers (e.g., by intermittently unloading the arms and/or legs).

Training in a physiological context

Table 1 summarizes the training routines of elite male and female cross-country skiers from Norway and Sweden. Endurance training has always been the major component of the overall training routines of cross-country skiers, with extensive low-intensity training and low-to-moderate amounts of medium- and high-intensity training, involving predominantly skiing, roller skiing, and running. These elite skiers train (or compete) 1–4 times per week at medium-to-high intensity. This distribution of endurance training at different intensities has not changed to any great extent during the past three decades.

However, during the past 20 years, much greater emphasis has been placed on specific endurance training of the upper body on roller skis and strength training (both in the gym and more ski-specific), as well as on training ski-specific power and speed. As a consequence of the faster overall speeds in cross-country skiing competitions, the ability to rapidly generate force and power has become more important. In contrast to individual races, sprint and mass-start events place a premium on peak speed during the start, during tactical accelerations and during the final spurt.

Altogether, an appropriate, well-balanced training program should improve maximal aerobic power, the metabolic potential of the muscles and skiing efficiency. High-intensity exercise is essential in this context, while low- and moderate-intensity exercise appear to be necessary for achieving adequate muscle adaptation, as well as a sufficient amount of training.

Table 1. Training routines of Norwegian and Swedish cross-country skiers who won gold medals at the Olympic Games in Sochi 2014 and/or World Championship in Falun 2015 (unpublished data, Sandbakk and Holmberg).

<table>
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<tr>
<th>Training Routine</th>
<th>Total Training Volume per Year (60% May-Oct, 40% Nov-April)</th>
<th>Endurance training (65–75% ski-specific, i.e., roller skiing and skating)</th>
<th>High-intensity (~87% HRmax)</th>
<th>Medium Intensity (80–87% HRmax)</th>
<th>Low-intensity (60–80% HRmax)</th>
<th>Strength and power training</th>
<th>Ski-specific speed training</th>
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<tr>
<td>Total training volume per year</td>
<td>750–950 h</td>
<td>670–830 h</td>
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<td>4–6%</td>
<td>86–89%</td>
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<td>Low-intensity (60–80% HRmax)</td>
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<td>Strength and power training</td>
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<td>Ski-specific speed training</td>
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HR = heart rate.
Conclusions and future perspectives

Research on elite endurance athletes and, in particular, cross-country skiers has provided and continues to provide valuable new insights into the physiology of human exercise, including regulation of energy production and the major factors that determine performance. In particular, the fundamental significance of aerobic capacity with different techniques and anaerobic energy production, as well as oxidation of the lactate thus produced, has become much clearer. Several of these advancements were made possible by Prof. Saltin’s extraordinary creativity and innovative mind, which have inspired several generations of scientists. Like August Krogh, he had a keen intuition for asking the most important questions and designing the appropriate experimental approach, which has yielded important insights into exercise physiology.

At the same time, this new information has made it clear that the optimal training routine for an elite cross-country skier should improve both maximal aerobic power and the metabolic potential of the muscles. High-intensity exercise is essential in this context, while low- and moderate-intensity exercise allow appropriate muscle adaptation and a sufficient amount of training. The optimal mixture and timing of these different types of exercise is presently being unraveled.

Much remains to be done in this exciting field. For instance, differences between men and women in these various respects have not yet been adequately elucidated. Clearly, novel available and developing technologies, including portable monitors, sensors that allow monitoring of movement and technique during both actual training and competitions, and specially designed laboratory environments (treadmill/ergometer, hypoxia, different temperatures) will further broaden our horizons in these contexts. A review similar to the present one written 10 years from now should be exceptionally informative.

Key words: physiology, lung, cardiac output, oxygen uptake, muscle, metabolism, energy, training.

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