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REVIEW

SPECIAL ISSUE

INTEGRATING BIOMECHANICS, ENERGETICS AND ECOLOGY IN LOCOMOTION

Tools and strategies to improve human locomotion performance and safety throughout history: on ice skates, skis, mountains and the battlefield

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ABSTRACT

Humans have developed tools and strategies to improve locomotion performance and safety throughout history. In particular, unusual environmental conditions and danger have pushed the limits of imagination and initiative, laying the foundations for the development of several tools to enhance locomotion. This Review summarises studies on the biomechanics and energetics of human locomotion on ice and snow, from a historical perspective and in load-carrying conditions. Environmental conditions challenge our locomotor performance: steep mountain paths and snow on the ground increase the metabolic cost of walking, ice increases the risk of falls, and fighting on the medieval battlefield required protection. In these conditions, humans evolved and developed tools and strategies to improve their locomotor performance and safety, typically with a trade-off between increasing the weight carried and reducing the metabolic cost of locomotion and/or increasing safety. Materials engineering and empirical understanding of muscle and locomotion biomechanics have aided performance improvement. In addition, environmental and even genetic changes have contributed to a superior physiological performance at high altitude. This Review presents and discusses findings integrating the biomechanics and energetics of locomotion. Overall, the thought-provoking historical perspective of this work helps to hypothesise some of the current technological and technical limitations to human physiological performance and highlights how improving the latter may well require a wide multidisciplinary approach.

KEY WORDS: Bioenergetics, Biomechanics, History, Human, Ice skating, Locomotion, Medieval armour, Mountaineering, Physiology, Skiing

Introduction

Humans have ingeniously crafted tools and devised strategies to enhance both the efficiency and safety of locomotion throughout history. This ingenuity was often spurred on by challenging environmental conditions and hazards that demanded innovative solutions. These challenges – for example, traversing ice or snow-covered terrain – not only increased the metabolic demands of human locomotion compared with walking on a treadmill (Pandolf et al., 1976) but also increased the risk of falls and injuries. For a given terrain and gradient, the metabolic cost of locomotion (the energy spent for various forms of locomotion, e.g. walking) is also increased by load carrying – for example, in the daily job of Nepalese porters navigating steep mountain paths at high altitude, or on the medieval battlefield, where protective gear was necessary to increase safety. In response to these demands, humans have developed a variety of tools and techniques aimed at enhancing locomotion (Minetti, 2004). These advancements probably evolved by trial and error, often involving a balance between increasing the load carried and reducing the metabolic cost of movement or enhancing safety. Materials engineering played a crucial role in tool development, while empirical insights into muscle function and biomechanics further contributed to their effectiveness.

Furthermore, environmental adaptations and genetic changes contributed to the evolution of superior physiological capabilities, particularly in high-altitude natives (e.g. Horscroft et al., 2017). Here, Nepalese porters have demonstrated remarkable resilience and efficiency of walking while carrying loads at high altitude, and also on frozen ground and snow, providing evidence for the interplay between genetic adaptation and movement strategies (Minetti et al., 2006) to optimise locomotor performance.

This Review summarises research on the biomechanics and energetics of human locomotion, focusing on environments such as ice and snow, and while carrying loads on high-altitude mountains and in body armour. By studying human locomotion in this variety of conditions through a historical lens, we gain insights into the enduring quest of humanity to overcome environmental obstacles and enhance locomotor capabilities.

Human locomotion on ice

Ice has been a surface humans have sought to circumvent for millennia: because of its slipperiness, it increases the risk of falls and injuries, reduces walking speed and elevates the metabolic energy expenditure during walking (Formenti and Minetti, 2008). Nevertheless, dating back as far as 4000 years ago, our ancestors recognised that this slipperiness could be leveraged to their benefit, leading to the beginning of an entirely novel mode of human locomotion: bone skating (Jacobi, 1976; Munro, 1893; Roes, 1963).

Now primarily a tool for sports, ice skates were probably borne out of a necessity to afford faster travel and to reduce the cost of transport in the long winters in Scandinavia (Formenti and Minetti, 2008). This section summarises the physics of friction on ice, and the origins and development of ice skating through the centuries.

Friction on ice

The dynamic coefficient of friction on ice is very limited over a reasonably large temperature range between 0 and −20°C

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(Rosenberg, 2005), thereby reducing the possibility of exerting the horizontal forces on the ground typically required for human locomotion such as walking and running (Alexander, 1992; Roberts et al., 1998).

An early experiment demonstrated that two ice blocks would stick when put together, as if there were a layer of water that froze upon contact between the two ice blocks (Faraday, 1859). A key feature that makes ice slippery, and which still puzzles physicists (Niven, 1959), is this presence of a thin layer of water on its surface (Seife, 1996), even at temperatures below freezing (Kietzig et al., 2010; Watkins et al., 2011). This feature is what makes ice slippery, even when we simply stand on it, as very small perturbations can be sufficient to destabilise our balance (Formenti, 2014). In addition, the pressure under a skate's millimetre-thin blade (Colbeck, 1995; Colbeck et al., 1997) and the friction between blade and ice (Bowden, 1955; Bowden and Hughes, 1939) were proposed as mechanisms that may respectively lead to pressure melting and frictional heating of the superficial layer of ice, contributing to ice skates' limited coefficient of friction. The coefficient of friction on ice typically attains a minimum at −5°C (Albracht et al., 2004; Calabrese et al., 1980; de Koning et al., 1992; Slotfeldt-Ellingsen and Torgensen, 1983), and increases at lower and at higher temperatures as a result of boundary and hydrodynamic friction, respectively (Colbeck et al., 1997; Kietzig et al., 2010).

The origins and evolution of ice skating

Archaeologists agree that the oldest specimens of ice skates were made of animal bones (Heathcote et al., 1892; Muhonen, 2005; Munro, 1893), primarily from horse and cattle, and that they matched the user's foot size. Bone skates were used for millennia, and until as recently as the 18th century in Iceland, Gotland, Hungary and Germany (Roes, 1963), despite manoeuvring difficulties caused by the lack of an edge under the bone. It is possible that the two key features that led to the widespread use of animal bones for manufacturing skates are their low dynamic coefficient of friction (∼0.010) – lower than the coefficient of friction of iron blades (∼0.015; Formenti and Minetti, 2008) – and the widespread availability of animal bones and/or the lack of a better alternative. These features partly compensate for the fact that propulsion was generated from the relatively less powerful upper limbs, which were used to push a pointed stick backwards on the ice, while the lower limbs provided support and balance (Olaus, 1555).

By the 13th century, the advent of iron blades facilitated improved manoeuvrability of ice skates, allowing the development of a new skating technique, and consequently exploiting the lower limbs for more powerful propulsive strides. The ice skater maintained an upright posture while moving slowly, bending over at higher speeds to reduce air friction. Without the requirement for the pointed stick for propulsion, the hands and upper limbs were free to support balance and/or carry items. Skaters push off outward and backward against the ice with one foot, while gliding on the other foot. Despite the higher dynamic coefficient of friction of iron on ice compared with bone, the new technology and technique reduced the cost of transport by almost 50% (Table 1) with a proportional increase in the skating speed for a given metabolic power output (the rate of energy expenditure during physical activity).

While the ice-skating technique has not changed dramatically since the introduction of iron blades, new materials (e.g. steel, fibreglass and carbon fibre), design and technology, and technical innovations (e.g. thinner and longer blades, hinges that allow the foot plantar-flexion movement and boots that are part of the ice skate itself) allowed further performance improvements (Houdijk et al., 2000; van Ingen Schenau and Bakker, 1980; van Ingen Schenau et al., 1996) and the widespread use of ice skates for leisure well beyond the geographical area where they originated (Armitage, 1902). Overall, compared with bone skating, these changes led to a reduction in the cost of ice skating to a quarter, and enabled skating on ice to be about four times faster, with a speed of ∼40 km h^{-1} being sustainable for ∼4 h.

Uncoupling between speed of locomotion and velocity of muscle contraction

Centuries before bicycles with gears were invented in the late 19th century (Larkin, 1903), ice skates were the first passive tools to enhance human locomotion by reducing muscle shortening velocity (required to sustain a given speed). Table 2 shows that, for a given metabolic power output (e.g. 'high speed'), the stride frequency associated with more recent ice skate models decreased (e.g. halved), while stride length increased ∼5-fold, with a ∼240% increase in ice-skating velocity (Formenti and Minetti, 2007). This stride length difference is even more striking if we consider a comparison between running and ice skating, where one stride on ice skates could cover ∼6 running strides (1 versus 6 muscular contractions). Taking an experimental approach, our ancestors made the most of some of the biomechanical properties of muscle contraction (Dick et al., 2017), limiting muscle shortening velocity to the range within which muscle can generate its greatest mechanical power (Fenn and Marsh, 1935; Hill, 1922), as suggested by a greater metabolic efficiency, with peak power and efficiency occurring at similar strain rates (Barclay et al., 1993).

Applying bioenergetics data to estimate ice-skating performance through history

Knowing the value for the cost of transport on historical ice skates allows modelling to estimate the maximum sustainable speed and distance that could be covered throughout history. Briefly, this model is based on the assumptions that the cost of transport is speed independent, as for running (Margaria et al., 1963; McMiken and

Table 1. Characteristics of five pairs of skates that represent milestones in the evolution of ice skating as a means of transport

Date	Material	Blade length (mm)	Blade width (mm)	Foot height (mm)	Mass (pair) (g)	Dynamic μ	Metabolic cost (J kg^{-1} m^{-1})
1800 BC	Animal bone	210	14	36	1450*	0.0103±0.0022	4.62±0.91
1200 AD	Ash and iron	230	6	59	1300	0.0147±0.0011	2.46±0.75
1400 AD	Ash and iron	250	6	45	900	0.0112±0.0007	2.01±0.35
1700 AD	Birch and steel	410	1.3	50	950	0.0084±0.0010	1.78±0.28
2004 AD	Fibreglass, carbon fibre, Kevlar, steel	460	1	62	930	0.0058±0.0004	1.32±0.27

The table lists the representative year of the ice skate models that are considered milestones in the development and evolution of ice skating as a means of transport, together with the manufacturing material, blade length and width, foot height from the ice surface and mass. The mean±s.d. of the dynamic coefficient of friction (μ) and the metabolic cost associated with each ice skate model are also presented. As the bone skates did not have a blade, measurements reported here show the dimensions of the underside of the bone, the part that was in contact with the ice while skating. *Mass includes the pole (Formenti and Minetti, 2007).

Table 2. Speed, stride frequency and stride length associated with the use of different historical skates at low and high speeds

	Low speed			High speed		
Date	Speed (m s^{-1})	Stride frequency (strides s^{-1})	Stride length (m)	Speed (m s^{-1})	Stride frequency (strides s^{-1})	Stride length (m)
1800 BC	1.13±0.40	0.50±0.01	2.68±0.52	–	–	–
1200 AD	1.80±0.12	0.63±0.09	2.94±0.44	2.75±0.73	0.90±0.19	3.16±1.01
1400 AD	2.55±0.16	0.54±0.12	4.87±0.92	4.06±0.59	0.65±0.20	6.44±0.93
1700 AD	2.87±0.51	0.57±0.15	5.17±0.53	3.96±0.32	0.68±0.12	5.97±1.71
2004 AD	5.09±1.85	0.40±0.05	13.31±6.09	6.70±2.39	0.45±0.09	15.24±5.55
F (3,8)	6.43	2.39	6.61	4.95	4.25	9.21
P	0.02	0.14	0.01	0.03	0.05	<0.01

Mean±s.d. speed, stride frequency and stride length are presented for the five ice skates considered milestones in the evolution of ice skating, averaged for three participants who were equipped with inertial sensors. Low and high speeds were defined as sustainable for, respectively, 8 and 4 h. A higher speed on the 1800 BC ice skate model was not attainable because of the relatively frequent turns imposed by the geometry of the ice rink. An analysis of variance (ANOVA) was used to determine differences between subsequent skates' models; *F*-values and levels of significance (*P*-values) are reported (Formenti and Minetti, 2007).

Daniels, 1976), and that the fraction of metabolic power available to exercise is inversely proportional to the time of exhaustion (Formenti et al., 2005; Minetti, 2004). Further details of the mathematical analysis and modelling applied here are presented in Minetti (2004).

Fig. 1 shows the estimated maximum sustainable speed over distances associated with historical ice skate models, given a maximum metabolic power of ∼20 W kg^{-1} (Formenti and Minetti, 2007). Data from recent competitions are also presented in Fig. 1 to support the validity of the modelling approach. By the 15th century, for a given metabolic power and time, humans could cover more than twice the distance on ice skates that they could cover when running (Alexander, 2005). This conclusion is based on experiments performed in standardised environmental conditions, such as ice, temperature and (absence of) wind. While this approach was necessary to determine the biomechanical and metabolic differences associated with the use of different ice skates, the results need to be interpreted considering the variety of the actual environmental conditions. For example, the metabolic cost of ice skating could be affected by temperatures altering the ice dynamic coefficient of friction (Rosenberg, 2005), and wind speed and direction altering air friction (van Ingen Schenau, 1982).

Human locomotion on snow

Similar to the case for ice-skates, cross-country skis were first developed to facilitate human transport during the winter season (Formenti et al., 2005). In fact, the energy cost of walking on snow increases linearly with increasing depth of footprint depression (Richmond et al., 2019); compared with no depression, a 45 cm footprint depression increases the cost by 5-fold, due to the increased lift work and balancing difficulty (Pandolf et al., 1976).

Skis were manufactured in countries where daylight is limited in winter, reducing the time available for fishing and hunting, and where snow persisted for several months per year (Bo, 1993). These climatic and environmental conditions increased the cost of walking compared with level treadmill walking (Connolly, 2002; Pandolf et al., 1976), making travelling by foot difficult (Knapik et al., 2002), and hence pushing humans to develop tools to reduce travel time and energy cost of locomotion. Skiing technology and techniques have changed dramatically through history; this section will provide an overview of their development.

The origins and evolution of cross-country skiing

The first evidence for skiing is associated with cave engravings from China and Norway, which suggests that it started more than 10,000 years ago (Dresbeck, 1967). Limited evidence pinpoints the location of the first skis to Southern Siberia and Mongolia, while several specimens were found in Northern Scandinavia (Weinstock, 2005). The oldest well-preserved specimen found so far is from Finland: radiocarbon dating indicates it was made and used ∼3200 BC (Vilkuna, 1984).

For millennia, humans skied with one pole for balancing and propulsion from the upper limbs, with the use of two poles becoming more popular only in the 19th century. Skis and poles were made typically with wood, a readily available material, until the 20th century, when materials engineering contributed to lighter skis that were less prone to breaking (e.g. carbon and glass fibre). The underside of skis was at times covered with animal fur, which reduces the chances of skis sliding backwards and is particularly useful when skiing uphill, albeit also increasing the gliding friction. Shoe or boot bindings were made of leather straps for centuries, limiting the control of the skis until metal and plastic bindings became available.

Table 3 summarises the fundamental characteristics of six ski models that represent the milestones in the development of cross-country skis since the 6th century AD (Formenti et al., 2005). Ski length and width varied widely, ranging, respectively, from ∼3.0 to ∼1.7 m and from ∼15 to ∼4 cm. The weight of the materials remained within a ∼20% range until the 19th century. The support surface area, and consequently the pressure exerted by the skier on snow, remained within a ∼10% range until the 1950s, when trail snow grooming (i.e. packing) started. This change is reflected in the ∼60% reduction of the 1970s ski model surface area compared with that of earlier skis (Table 3). Snow grooming is probably the factor that determined the greatest step-reduction in the metabolic cost of cross-country skiing. More packed snow allowed the use of lighter and thinner skis, reducing the external work required to lift the skis (Steudel, 1990; Willems et al., 1995) and the dynamic coefficient of friction (Colbeck, 1994a,b; Outwater, 1970). While studies of ski friction are (reasonably) performed on snow that does not change between experimental conditions (Bowden, 1955; Colbeck, 1988; Kuroiwa, 1977), it is possible that the metabolic cost associated with historical skis on a groomed snow trail (Formenti et al., 2005) is an underestimation of the actual metabolic cost on natural, non-packed snow.

In addition, packed snow, together with modern bindings and materials that enhanced ski control, allowed the introduction of skating techniques (Hoffman and Clifford, 1990; Smith, 1990, 1992), with a reduction in the metabolic cost of transport compared with classic techniques (Welde et al., 2003). This technical change allowed a step-increase in skiing performance associated with the reduction of muscle shortening velocity required to sustain a given speed of locomotion, as suggested by the greater mechanical power

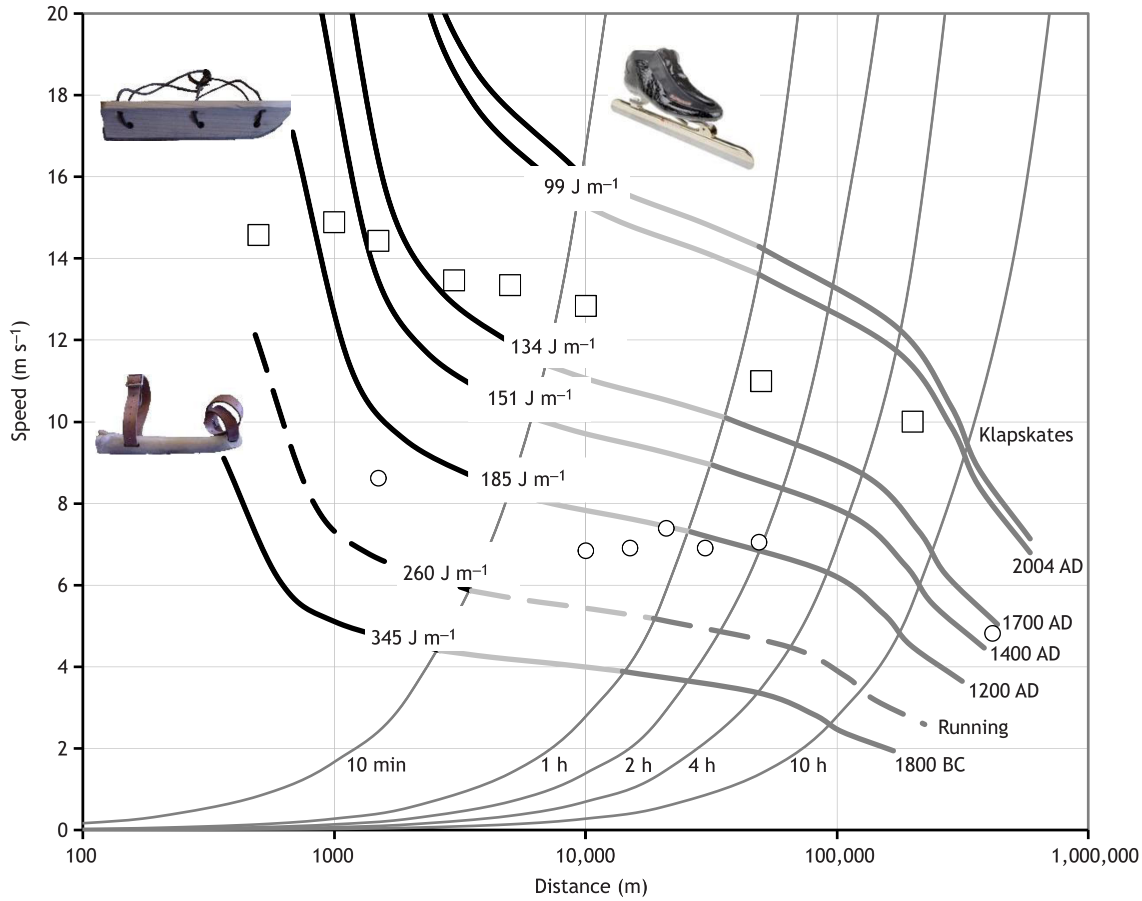

Fig. 1. The maximum sustainable speed on ice skates over distances through history. The greyscale curves represent the maximum speed/distance relationships calculated for a constant metabolic cost for the different skate models. Insets show images of the 1800 BC bone skate, the 1200 AD replica used for the experiments and a klapskate (an ice skate used in speed skating); the skates from 1400 AD and 1700 AD were made of materials similar to the 1200 AD skates, but with longer and thinner blades and tighter straps that improved manoeuvrability. Data for the klapskate were calculated assuming speeds 5% faster than those for the 2004 AD ice skate model. The ice-skating data presented in the curves were calculated from equations provided by Wilkie (1980) (black, 40 s to 10 min), Saltin (1973) (light grey, 10 min to 1 h) and Davies (1981) (dark grey, 1–24 h), assuming a maximum metabolic power available of 21.3 W kg^{-1} (di Prampero, 1986), and that the available fraction of the metabolic power used for a physical activity is inversely related to the time to exhaustion. The grey curves are iso-duration speed/distance pairs; the open squares represent the actual records in ice-skating and the open circles show records for cross-country skiing, reported as a means of comparison. The dashed line represents human running data for world records (from Minetti, 2004), also shown for comparison with the ice-skating data. Example: the energy cost of bone skating (1800 BC) is indicated by the thick 345 J m^{-1} iso-cost line. The intersection between this iso-cost line and the light 10 min iso-time line shows that in 10 min, for an energy cost of 345 J m^{-1}, a skater could cover a distance of 2638 m at an average speed of 4.4 m s^{-1} before exhaustion. Modern ice-skating energy cost is only 99 J m^{-1}, less than one-third of the energy cost associated with skating on bones. Consequently, as indicated by the intersection between the 99 J m^{-1} iso-cost curve and the 10 min iso-time line, a distance of almost 10 km can be travelled in 10 min at an average speed of ∼16 m s^{-1} before exhaustion. Figure modified from Formenti and Minetti (2007).

and reduced metabolic cost (Formenti et al., 2005; Werkhausen et al., 2023).

Applying bioenergetics data to estimate skiing performance through history

Fig. 2 shows the maximum speed/distance relationships for a constant metabolic cost and a maximum metabolic power available of ∼20 W kg^{-1} associated with different historical skis (Formenti et al., 2005). The thick lines from bottom to top illustrate the reduction in the metabolic cost of skiing with more modern ski sets and the associated faster sustainable velocities. For example, the metabolic cost of skiing with the 542 AD skis is indicated by the thick 313 J m^{-1} iso-cost line. The intersection between this iso-cost line and the light '30 min' iso-time line shows that in 30 min, for an energy cost of 313 J m^{-1}, a skier could cover a distance of ∼7 km at an average speed of ∼3.9 m s^{-1} before exhaustion. The metabolic cost of locomotion with the 2004 AD ski set is 154 J m^{-1}. Consequently, in 30 min, a distance of ∼14.4 km can be travelled at an average speed of ∼8 m s^{-1} before exhaustion, as indicated by the intersection between the 154 J m^{-1} iso-cost curve and the 30 min iso-time line. Based on the above-summarised experimental data, it is possible to estimate the likely maximum speed sustainable over a given distance in historical events.

The Vasaloppet in Sweden is a 90 km ski race from Mora to Sälen, established as a race in 1922 and now one of the world's most popular cross-country skiing competitions. The race commemorates Lars and Engelbrekt's 1520 AD pursuit of Gustav Eriksson Vasa, a 24 year old nobleman from Uppsala and the future King of Sweden, sought to lead the fight for independence from the Danes. Between 1922 and 2004, average speed records increased from 3.75 to 6.56 m s^{-1}, as indicated by the arrow connecting the grey squares in Fig. 2. Factors such as improved technology, technique and aerobic training may affect the calculations, yet the vertical range of these speed records from 1890 to 1922 provides support for the correctness

Table 3. Characteristics of six pairs of skis that represent milestones in the evolution of cross-country skiing as a means of transport

Date	Model	Material	Length (mm)	Width (mm)	Underside	Pole(s)	Mass* (kg)	Dynamic μ	Metabolic cost (J kg^{-1} m^{-1})
542 AD	'Mantta'‡	Pine	1680	149	Badger fur	1	5.0	0.151±0.036	4.28±0.64
1300 AD	Asymmetric (long)‡	Birch	3000	97	None	1	5.0	0.085±0.006	3.88±0.55
	Asymmetric (short)‡	Birch	2000	89	Seal skin	–			
1890 AD	End 1800‡	Birch	2870	78	Tar	2	6.7	0.054±0.005	3.17±0.22
1970 AD	Last wood	Hickory	2000	47	Wax	2	2.6	0.020±0.006	2.34±0.19
2004 AD	Modern (DS)	Carbon fibre	2010	46	Wax	2	2.2	0.013±0.004	2.11±0.21
2004 AD	Modern (SK)	Carbon fibre	1840	43	Wax	2	2.0	–	1.92±0.18

The table lists the representative year of the ski models that are considered milestones in the development and evolution of skiing as a means of transport, together with the model, material, length and width, underside coating, number of poles and mass. The mean±s.d. of the dynamic coefficient of friction (μ) and the metabolic cost associated with each ski model are also presented. *Mass includes skis, bindings, boots and pole(s). ‡Replicas of archaeological specimens (the Mantta model refers to a specimen found in Mantta, Finland). DS, diagonal stride; SK, skating (Formenti et al., 2005).

of the metabolic cost measurements and calculations, both in relative and in absolute terms. The current Vasaloppet record is 3 h and 28 min, while a time of 8 h and 10 min is estimated for the 1520 AD feat of Lars and Engelbrekt using the iso-cost curve of the 1300 AD ski (black square in Fig. 2).

Similarly, the Birkebeiner (Birchlegs) event in Norway is a 54 km classic technique cross-country skiing race from Lillehammer to Rena, where over 6000 participants ski, loaded with a 3.5 kg mass to simulate the weight of a (very light) 2 year old child to commemorate a heroic act in 1206 AD. Here, two Birkebeiner

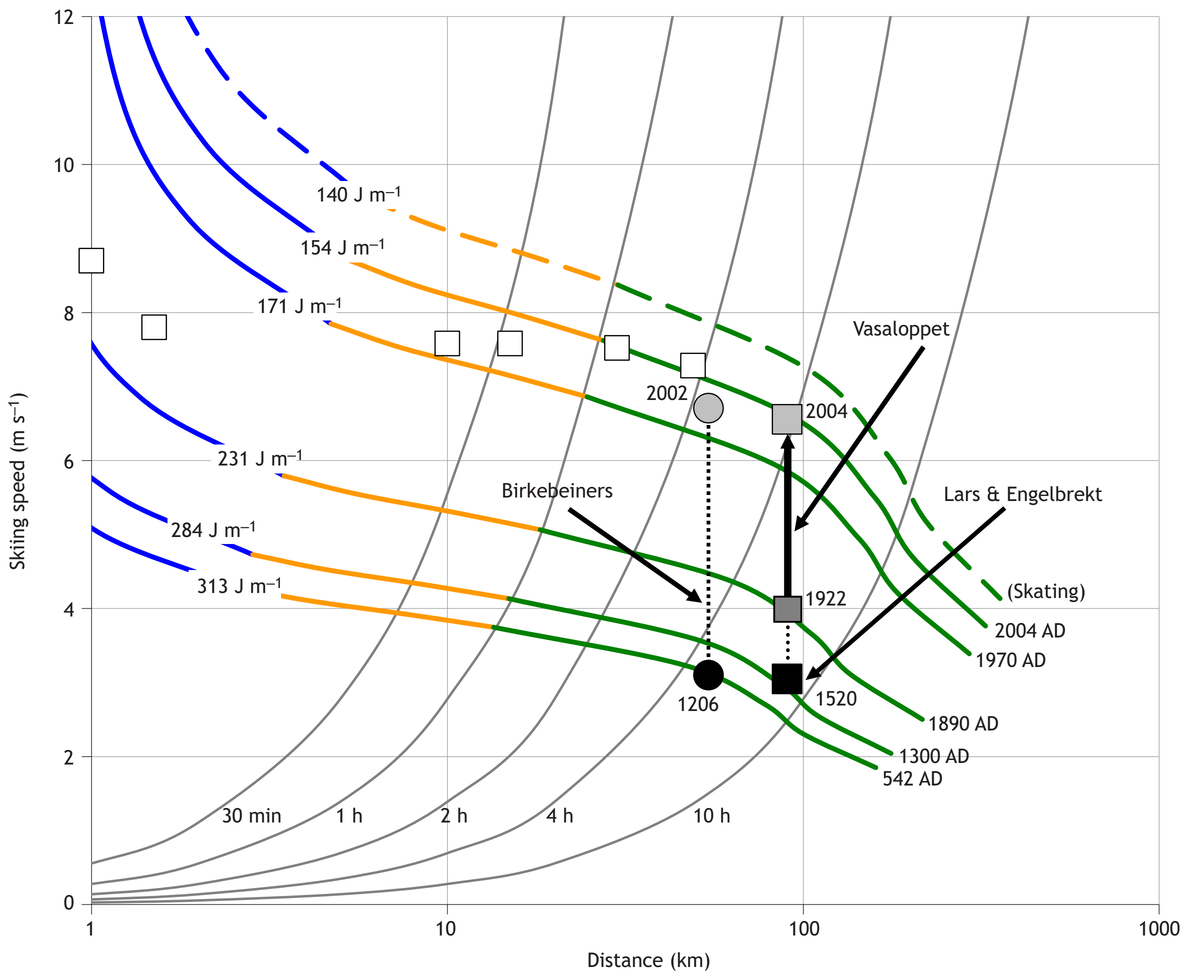

Fig. 2. The maximum sustainable speed on cross-country skis over distances through history. The coloured curves represent the maximum speed/distance relationship for constant metabolic cost; each curve refers to a different ski. Data were obtained by combining the relationship between the time to exhaustion and the available fraction of the metabolic power used, as suggested by Wilkie (1980), Saltin (1973) and Davies (1981) for different exercise periods (blue: 40 s to 10 min; light orange: 10 min to 1 h; green: 1–24 h); see Fig. 1 legend for further details and an example to support the interpretation of the data. In this computational frame, 20.3 W kg^{-1} was assumed as the maximum metabolic power available (di Prampero, 1986). The grey curves show iso-duration speed/distance pairs, and the open squares show records in cross-country skiing (taken from the International Ski and Snowboard Federation website: www.fis-ski.com), from sprint events to endurance races. Grey and black symbols are explained in the main text ('Applying bioenergetics data to estimate skiing performance through history'). Figure modified from Formenti et al. (2005).

warriors rescued the 2 year old prince Hakon Hakonsson from his pursuers by carrying him on a dramatic escape over the snowy mountains. Combining experimental data on the cost of skiing with ancient skis and physiological modelling, the 1206 AD Escape journey would have lasted approximately 5 h (indicated by the black circle in Fig. 2), posing a challenge even for the child.

Biomechanics-based hypotheses for improved ice-skating and cross-country skiing performance

The movement pattern of the lower limbs in ice skating and in the skating technique in cross-country skiing seems to have reached an optimum in terms of muscle shortening velocity (Yu and Herzog, 2023), mechanical power generated and associated metabolic cost (van Ingen Schenau, 1998). The upper limbs are not typically used for propulsion in ice skating, possibly because using the upper limbs (e.g. with poles) could result in a more elevated posture, increasing external resistance at higher speeds ($drag \propto speed^2$), which is the main determinant of total friction (van Ingen Schenau, 1982). In contrast, at relatively slower speeds, the upper limbs contribute significantly to propulsion in cross-country skiing. Here, we hypothesise that the next technical evolutionary step could be to ensure that even the poles maintain continuous movement relative to the ground, for example with miniature, ultralight skis at the distal end of poles that could resemble the skating movement pattern of the skis. The trade-off in this case would result from the potentially increased mechanical power output and increased energetic cost of skiing with the additional, distally loaded mass (Steudel, 1990).

The foot moves as a single anatomical/geometrical element in cross-country skiing and ice skating, avoiding the flexion of the metatarsophalangeal joint (Bobbert and van Ingen Schenau, 1988; van Ingen Schenau and Bakker, 1980). In contrast, the evolution of bipedal locomotion in humans appears to have reduced toe and foot length to decrease the energy cost of locomotion (Webber and Raichlen, 2016), which has also occurred through the mechanical and metabolic advantage associated with the cyclical stretch and recoil of the plantar aponeurosis, plantar-flexor muscles and ligaments of the longitudinal arch observed during stance (Ker et al., 1987), walking (Papachatzis et al., 2023; Smith et al., 2022), jumping (Farris et al., 2015) and running (Holowka et al., 2020). This cyclical stretch and recoil mechanism (illustrated in fig. 1D of Farris et al., 2019), known as the windlass mechanism, is a biomechanical process that is essential for maintaining the structural integrity of the foot's arch, providing support during weight-bearing activities and assisting in the propulsion phase of human locomotion (Huang et al., 2023).

We hypothesise that skates and cross-country skis that allow the movement of the metatarsophalangeal joint could lead to a mechanical power advantage and reduced energy cost of locomotion via the biological springs in the human foot. Stride frequency remaining unchanged, the increase in work per stride allowed by the metatarsophalangeal joint movement would result in an increase in mean power output, leading to a higher ice-skating and cross-country skiing velocity. Changes in stride frequency would be proportional to changes in power output. While the effect size might be limited in the overall locomotor performance, it might be sufficient to improve at least top sports performance (de Koning et al., 2000), as long as the additional degree of movement freedom does not reduce the control of the skate and ski.

Load carrying

Load carrying is a daily job for thousands of people, especially on mountain paths at high altitude, where other forms of transport might be more expensive. Like ice and snow on the ground, steep mountain paths also challenge human locomotion performance, more so when carrying heavy loads at high altitude, where oxygen availability is reduced (i.e. in hypoxic conditions).

Populations have been living at high altitude for several thousand years in East Africa, on the Himalayas and Andes (Aldenderfer, 2003). African women living in Kenya's western flatlands and Nepalese porters and Tibetans living on the Himalayas have developed strategies and adapted in ways that increase their locomotor performance and support life in the hypoxic environment. All these populations carry heavy loads regularly/daily and live at high altitude.

Biomechanics and energetics of load carrying on mountain paths

Human walking is often modelled as an inverted pendulum, as it involves alternate raising and lowering of the body's centre of mass with out-of-phase fluctuations in potential and kinetic energy (Alexander, 1984), like a pendular movement. The exchange of potential and kinetic energy makes walking an economical gait; however, there are energy losses, in particular at the step transitions. The metabolic energy cost of walking increases approximately proportionally with the load carried (Goldman and Iampietro, 1962; Huang and Kuo, 2013; Soule and Goldman, 1969; Soule et al., 1978) and appears to be largely related to the increased mechanical work performed on the body centre of mass at the transition between steps as the direction of the body changes from moving downwards to moving upwards (Huang and Kuo, 2013).

Luo and Kikuyu women in East Africa, surprisingly, can carry loads (on their heads) of up to 20% of body mass on flat ground without a measurable increase in oxygen consumption and energy cost (Maloiy et al., 1986). This more economical walking is probably a result of a greater conservation of mechanical energy caused by a more efficient pendulum-like transfer of energy between gravitational potential energy and kinetic energy of the centre of mass at each step (Heglund et al., 1995). Nepalese porters are even more economical than Luo and Kikuyu women, when carrying ∼60% of their body weight in a basket on their back held via a head strap, on flat ground (Bastien et al., 2005). In contrast with Luo and Kikuyu women, Nepalese porters do not show a greater conservation of mechanical energy compared with Caucasian mountaineers (Bastien et al., 2016). This difference might be expected when considering that Nepalese porters typically carry loads on steep mountain paths, often in the 15% gradient range, where the pendulum-like transfer of energy mechanism cannot be observed (Minetti et al., 1993). The mechanism underlying the Himalayan porters' economy of locomotion must differ from the mechanism observed in Luo and Kikuyu women. For example, the different load-carrying strategies and height of the load might be associated with the different metabolic costs (Dempsey et al., 2023). Overall, these observations suggest that a different locomotor strategy, physiological acclimatisation or biological adaptation underlies the economy of locomotion in Nepalese porters.

Compared with Caucasian mountaineers, Nepalese porters' cost of loaded walking is ∼20% lower, and they can walk ∼60% faster thanks to a ∼40% greater mechanical power (Minetti et al., 2006). Nepalese porters' trunk oscillations have a smaller amplitude, are less variable than in Caucasian mountaineers (Fig. 3), and porters appear to take frequent rests (Chaen and Trapellieni, 2020; Minetti et al., 2006). As the metabolic cost of walking is predominantly attributable to the energy expenditure required for generating muscular force during the stance phase (Griffin et al., 2003), it is also possible that effective load carriage is derived from postures limiting the cost of producing muscle force/moment. Altogether, these data indicate that biomechanical parameters contribute to

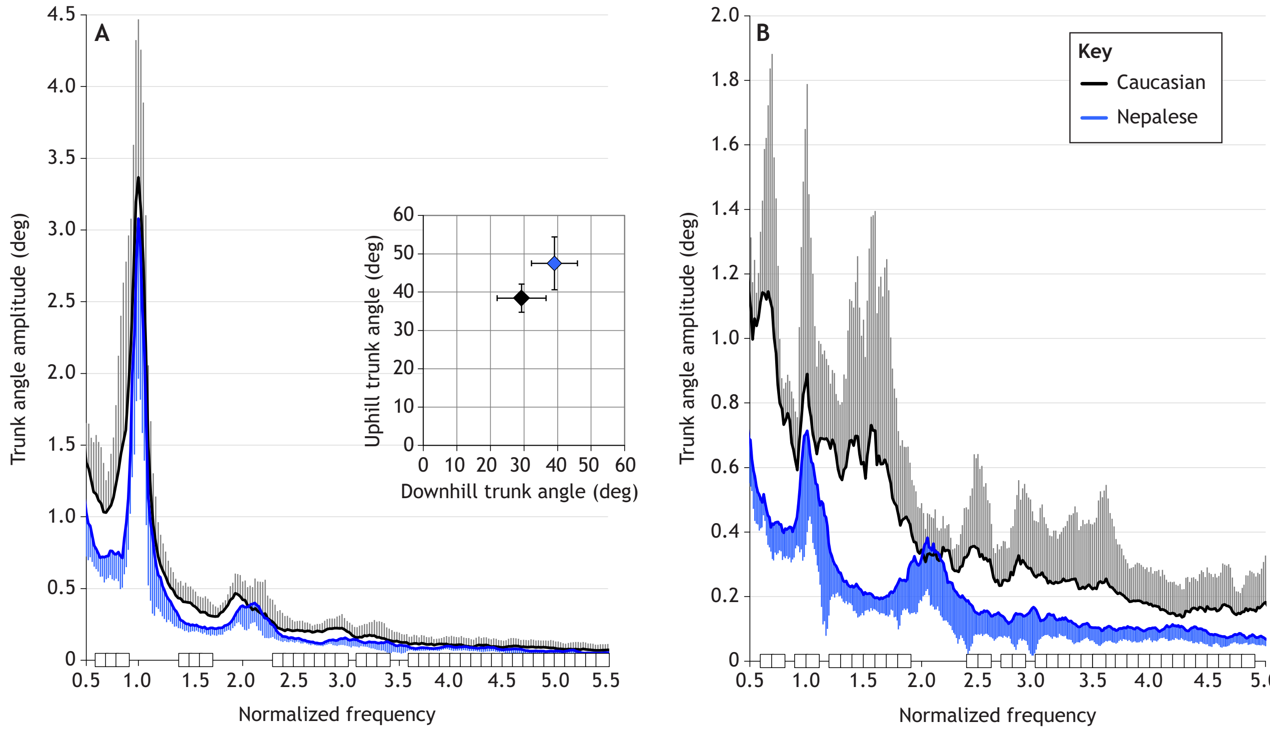

Fig. 3. Trunk angle movement amplitude during walking in Nepalese porters and Caucasian mountaineers. Trunk oscillation frequency spectra for walking (A) uphill and (B) downhill are plotted against normalised frequency (where 1.0 is the prevalent oscillation frequency, corresponding to the step cadence of 0.525 Hz in the mountaineers and 0.650 Hz in the Nepalese porters). Data were collected on 22% gradient mountain paths at 3490 and 5050 m above sea level, where participants carried loads of up to 90% body mass. Vertical error bars represent positive (Caucasian) and negative (Nepalese) amplitude standard deviations. Oscillation variability, compared using Fisher's tests for the same normalized frequency ranges (0.1 intervals), was greater in the Caucasian mountaineers than in the Nepalese porters for most of the investigated range (open squares on the horizontal axes, $P<0.05$). The inset shows the different average trunk angles for the two groups (black diamond, Caucasian; blue diamond, Nepalese) during uphill versus downhill walking (0 deg indicates a vertical trunk). Figure modified from Minetti et al. (2006).

Nepalese porters' superior performance, yet they fall short of explaining the entire performance difference from that of Caucasian mountaineers.

Genetic mutations underpinning adaptation to life and greater exercise capacity at altitude

A large proportion of the difference between the exercise capacity of Nepalese porters, Tibetans and Caucasian mountaineers appears to be explained by alterations in the hypoxia-inducible factor pathway function (Ratcliffe et al., 1998; Wenger, 2000) and their physiological implications at the integrative level (Formenti et al., 2010, 2011; Hoppeler and Vogt, 2001; Perrotta et al., 2020; Petousi et al., 2014). Several mechanisms have been proposed for hypoxia tolerance in humans (Hochachka, 1998), with evidence in Himalayan populations for non-elevated haemoglobin levels (Beall and Reichsman, 1984), probably due to elevated plasma volume (Stembridge et al., 2019), lower pulmonary arterial pressure (Groves et al., 1993), increased levels of exhaled nitric oxide (Beall et al., 2001), higher blood flow and more than 10 times greater circulating concentrations of bioactive nitric oxide products normalising oxygen delivery (Erzurum et al., 2007), increased myoglobin levels and protection from tissue damage caused by reactive oxygen species (Gelfi et al., 2004; Hoppeler et al., 2003). Many of these physiological traits appear to be associated with mutations in *EPAS1* (Beall et al., 2010) and *EGLN1* (Simonson et al., 2010) genes that are involved in the hypoxia-inducible factor pathway (Ratcliffe et al., 1998). More recently, metabolic adaptations were found in Sherpas, allowing a more efficient oxygen utilisation associated with an allele of the *PPARA* gene, leading to better preservation of energy levels in skeletal muscle at high altitudes (Horscroft et al., 2017), which are probably strong determinants of their superior locomotor performance in hypoxia.

Overall, only the combination of knowledge from fields such as biomechanics, energetics, physiology and genetics enabled a finer understanding of the mechanisms underpinning the greater exercise and load-carrying capability in Himalayan populations compared with Caucasian mountaineers.

Load carrying is also required for protection of soldiers' on the battlefield. Humans have manufactured a wide diversity of tools for protection, especially during combat (Knapik et al., 2004). Throughout history, soldiers have carried body armour, protection and weapons totalling between ~15 and ~50 kg during march and combat (Knapik and Reynolds, 2010), with the armour itself reaching its likely heaviest weight of ~44% body weight in medieval times (Askew et al., 2012). At a given walking and running speed, the metabolic cost of locomotion in medieval armour is about twice the cost of unloaded locomotion (Fig. 4). Combining these cost data with maximal physical exercise capacity across lifespan suggests the likely age-related limits that are associated with locomotion in armour on the medieval battlefield. For example, a ~20 year old soldier would be able to walk at a speed of ~1.7 m s^{-1} (~6.1 km h^{-1}). The distribution of the armour load was such that stride kinematics such as swing and stance duration, duty factor and stride frequency were largely unaffected by wearing armour. In contrast, the internal work and mechanical power associated with moving the armoured (i.e. weighted) lower limbs was >60% higher than during unloaded locomotion.

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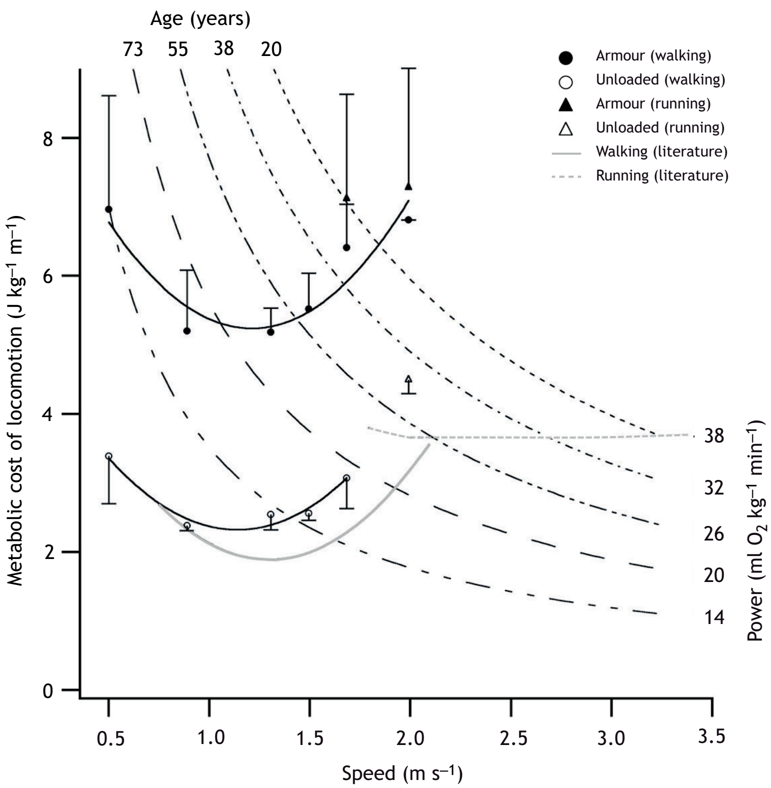

Fig. 4. Metabolic cost of locomotion in medieval armour. Metabolic cost of locomotion is presented across a range of speeds for walking and running in armour (respectively, filled circles and triangles) in comparison with unloaded (open circles and triangles) conditions. Data are means±s.d. The hyperbolae indicate iso-metabolic power (i.e. the product of metabolic cost and speed resulting in the same metabolic power) expressed as ml O_2 kg^{-1} min^{-1}. The age for which the iso-metabolic power is ∼80% of the maximum aerobic metabolic rate is indicated. The intersections between the hyperbolae and the experimental metabolic cost–speed relationship lines indicate the maximum speed that can be sustained for a significant length of time. Published data for the metabolic cost of walking (solid grey line) and running (dashed grey line) on a treadmill are plotted for comparison. Figure modified from Askew et al. (2012).

In addition to the locomotor limitations, wearing medieval armour limited locomotion by impairing breathing, restricting the normally associated increase in respiratory tidal volume. As for the metabolic cost of locomotion, ventilation increased ∼2-fold when walking at 1.7 m s^{-1} while wearing medieval armour compared with unloaded locomotion, largely driven by a 2-fold increase in the respiratory rate, as tidal volume was similar between the two conditions (Askew et al., 2012). The highest average ventilation measured during walking in medieval armour was ∼100 l min^{-1}, and was associated with an average tidal volume of ∼2 l, the latter being ∼35% lower than reference values in unloaded exercise (Neder et al., 2001). It is likely that the chest restrictions imposed by medieval armour restricted the natural dorsoventral and mediolateral expansion of the thorax (Callison et al., 2019), limiting the inspiratory capacity (Askew et al., 2012), an impairment still observed when wearing modern body armour (Armstrong and Gay, 2016).

Fast-forward to health and performance of modern soldiers

Body armour remains in use on the battlefield and its weight has decreased substantially (Knapik et al., 2004), but the overall combined load of body armour and other equipment has not changed in recent years (Sessoms et al., 2020), hence remaining a limiting factor for the health and performance of modern soldiers. From a biomechanical perspective, the centre of mass of modern armour is closer to the soldier's centre of mass, unlike medieval armour, which was characterised by heavy metal plates covering the forearms and legs. This added mass distribution difference probably underpins the relatively lower cost of locomotion in modern compared with medieval armour: at 1.34 m s^{-1} on a 0 deg treadmill, these two forms of load carriage were associated with a net cost of, respectively, 16.3 ml O_2 kg^{-1} min^{-1} (Gregorczyk et al., 2010) and 26 ml O_2 kg^{-1} min^{-1} (Askew et al., 2012). Several technological and technical inventions can reduce the cost of carrying loads; for example, exoskeletons (Bryan et al., 2021; Collins et al., 2015; Lee et al., 2018; Mooney et al., 2014), rubber bands to suspend the backpack load (Rome et al., 2006), alterations in the distribution of loads to be carried (Arellano et al., 2020) and different load carriage systems (LaFiandra et al., 2003).

In addition to tools that reduce the energy cost of locomotion, energy can be harvested during locomotion, mostly from movement, and converted to electricity. For example, backpacks where the load is suspended can convert mechanical energy from the vertical movement of carried loads into electricity (7.4 W) during walking (Rome et al., 2005). Whilst not reducing the overall metabolic cost of locomotion, this type of solution is helpful in situations where the battery life of small electronic equipment is critical, as electricity harvested during locomotion can reduce the reliance on batteries for equipment operation.

In this sense, beyond energy harvested from locomotion, chemistry and materials engineering advances are offering unprecedented opportunities. Novel findings in the mechanisms of contact electrification (Baytekin et al., 2011) supported the development of triboelectric nanogenerators (TENG) (Fan et al., 2012; Wang, 2021), which demonstrated instantaneous energy conversion efficiency of ∼70% (Chen and Wang, 2017) and can use biomechanical energy to support the function of mobile and wearable electronics (Niu et al., 2015; Pu et al., 2015). TENG and piezoelectric nanogenerators (PENG) are becoming more widely used in smart textiles for electricity generation (Chen et al., 2020), together with other forms of energy-harvesting technologies (Fig. 5). This novel approach can support the use of small electronics such as GPS and mobile communications in the battlefield, and may also afford the real-time monitoring of vital signs (Ma et al., 2016). Self-powered, wearable sensing technology may be fundamental in preventing soldiers' deaths during missions in the field; for example, from exertional heat stress (Buller et al., 2021; Carter et al., 2005) and exposure to high-altitude hypoxia (Crandall et al., 2019; Purkayastha and Selvamurthy, 2000). While we have come a long way from mail armour, research

Fig. 5. Smart textiles for energy harvesting. Overview of smart textiles for energy harvesting, and variables that can be measured during human locomotion. Different forms of energy including movement, heat, biochemical and radiation can be harvested by fusion of textiles and generators, and converted into electricity for wearable electronics. TENG, triboelectric nanogenerator; PENG, piezoelectric nanogenerator; TEG, thermoelectric generator; BFC, biofuel cells; SC, solar cells; HG, hybrid generators. Figure reprinted with permission from Chen et al. (2020), American Chemical Society.

and development in body armour continue to progress rapidly, with potential implications for various applications in the medical field.

From a broader perspective, recent technology advances provide tools to study the biomechanics and energetics of human locomotion beyond what could have been explored only a few years back. Novel technologies afford the study of human movement and physiology in finer detail, in environments and climatic conditions previously unexplorable, generating knowledge on which new hypotheses can be postulated and new technologies developed. For example, long term (i.e. weeks) measurements of respiratory parameters and body heat via light-weight, portable sensors (Fig. 5) in soldiers during field missions can provide real-time, context-specific insights on breathing, body temperature and their changes. This information could then be used to modify materials, design and load carriage conditions to reduce physiological constraints of locomotion and improve locomotion performance in soldiers.

Conclusions

This review has highlighted some examples of ingenuity and innovations that have supported improvements in human locomotion performance and safety through history. From frozen lakes and rivers to snow-covered lands, steep mountain paths in hypoxia and the medieval battlefield, challenges imposed to human locomotion have been the stimuli for the development of tools, technologies, strategies and techniques to reduce the cost of locomotion and increase safety. In particular, the innovations and step changes presented for the development of ice skating and skiing provide examples for how humans learnt to get the most out of the biomechanical properties of the muscular system, with greater power in the lower limbs, and of skeletal muscle contraction, probably maintaining muscle shortening velocity within the slow range where contraction is more efficient. Based on our biomechanical and energetics measurements, we hypothesise that muscle shortening has played an important role in the improvement of human locomotion performance, yet we acknowledge that many other muscle contractile parameters affect the energetic cost of locomotion. All these innovations occurred well before the biomechanical and physiological properties of muscle contraction were formally described. The improvements in human locomotion that took place over millennia, combined with the understanding of muscle contraction mechanics and physiology gained in the last century, provide the basis for future enhancement to human locomotion on Earth and beyond.

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