

Jan-Michael Johansen

Effects of training, age, gender and selected genes on aerobic endurance performance in cross-country skiing





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**Effects of training, age, gender and
selected genes on aerobic endurance
performance in cross-country skiing**

A PhD dissertation in
Ecology

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Abstract

The main objective of this thesis was to investigate the effects of training, age, gender and selected genetic variants on aerobic endurance performance and training adaptations in well-trained cross-country skiers. The skiers recruited for the different studies were either exclusively characterized as national-level cross-country skiers (Study I and III) or recreational- to national-level cross-country skiers (Study II). In all studies, both male and female, young and adult skiers were recruited.

The relationships between performance results from a roller-skiing double poling time trial (TT_{DP}) and a large set of aerobic endurance variables, muscular strength variables and technique-specific characteristics in double poling (DP) were studied in study I. These associations were investigated in young male and female cross-country skiers ($n = 28$). Both dependent and independent of gender, strong correlations were observed between maximal strength in pull-down and TT_{DP} ($r = -0.83, p < 0.01$ and $r = -0.50, p < 0.02$, respectively). Among the aerobic variables, the same were observed for maximal aerobic speed (MAS, $r = -0.80, p < 0.01$) and peak oxygen uptake in DP ($DP-VO_{2peak}$, $r = -0.80, p < 0.01$). Stronger skiers were also associated with higher peak forces ($r = 0.78, p < 0.01$), lower cycle rate ($r = -0.71, p < 0.01$) and shorter contact time ($r = -0.48, p < 0.02$) during double poling.

In study II, effects of a 6 weeks DP-specific high-intensity aerobic training (HIT) intervention was investigated. This intervention was performed without increasing total training volume or HIT volume. Seven recreational-level skiers were recruited for the intervention group, while seven national-level skiers served as controls. All skiers were tested in a 3-km TT_{DP} on a treadmill, maximal oxygen uptake in running ($RUN-VO_{2max}$), $DP-VO_{2peak}$ and oxygen cost of DP (C_{DP}). The intervention group trained DP-specific HIT 3 times per week during the intervention. Significant improvements were observed in MAS (+16.5%, $p < 0.01$), $DP-VO_{2peak}$ (+7.1%, $p < 0.05$), C_{DP} (-9.2%, $p < 0.05$), fractional utilization of $RUN-VO_{2max}$ while DP (+7.3%, $p < 0.05$) and TT_{DP} (+19.5%, $p < 0.01$). The control group did not display any improvements during the intervention.

In study III, the physiological adaptations to six months traditional cross-country ski training were examined. In addition, effects of age, gender and selected genetic variants at baseline and on training adaptations were investigated. All included skiers ($n = 29$) were tested in a large set of physiological and performance variables, and all training performed was registered based on heart rate measures. Even though there were some variations in training characteristics, only minor changes were performed in training by the participants. Thus, no significant training adaptations were displayed over 6 months, with no differences across gender and age. At baseline, gender and age did reveal significant effects on TT_{DP} ($p < 0.01$), MAS, ($p < 0.01$), $DP-VO_{2peak}$ ($p < 0.01$) and maximal strength variables ($p < 0.01$). For the genetic variants, only minor associations were observed at baseline.

Taken together, pooled analyses from study I and III points to the major importance of MAS and maximal strength in upper-body muscles for cross-country skiing performance. In addition, these two variables seemed as important underlying physiological factors for several other performance-related variables.

No physiological adaptations were observed in skiers that did not to minor changes in training characteristics over shorter (6 weeks in study II) or longer (6 months in study III) training periods. However, large improvements were observed in skiers specifically altering their HIT training over short training periods (study II). Gender and age was found to have large effect on initial performance- and physiological capacity, while no effects were evident on training adaptations. For selected genetic variants, minor effects were observed in baseline values.

List of articles

This dissertation is based on the following articles, and will be referred to in the text by roman numbers (Study I, II and III).

Article 1

Sunde, A., Johansen, J-M., Gjøra, M., Paulsen, G., Bråten, M., Helgerud, J. and Støren, Ø. (2019). **Stronger is Better: The Impact of Upper Body Strength in Double Poling Performance.** *Front. Physiol.* 10:1091. doi: 10.3389/fphys.2019.01091.

Article 2

Johansen, J-M., Eriksen, S., Sunde, A., Slette-meås, Ø.B., Helgerud, J. and Støren Ø. (2020). **Improving Utilization of Maximal Oxygen Uptake and Work Economy in Recreational Cross-Country Skiers with High-Intensity Double-Poling Intervals.** *Int. J. Sports Physiol. Perform.* [Ahead of print]. doi: 10.1123/ijsp.2019-0689.

Article 3

Johansen, J-M., Goleva-Fjellet, S., Sunde, A., Gjerløw, L.E., Skeimo, L.A., Freberg, B.I., Sæbø, M., Helgerud, J. and Støren, Ø. (2020). **No Change – No Gain; the Effect of Age, Sex, Selected Genes and Training on Physiological and Performance Adaptations in Cross-Country skiing.** *Front. Physiol.* 11: 581339.

Abbreviations

1RM – One repetition maximum

C – oxygen cost of movement

C_{DP} – oxygen cost of double poling

CR – sub-maximal cycle rate

CT – contact time

DP – double poling

DP-VO_{2peak} – peak oxygen uptake in double poling

HIT – high-intensity aerobic endurance training

HR – heart rate

LIT – low-intensity aerobic endurance training

LT – lactate threshold

LT_% - lactate threshold in percentage of maximal or peak oxygen uptake

LT_v – velocity at lactate threshold

MAS – maximal aerobic speed

MIT – moderate-intensity aerobic endurance training

PF – peak force

RUN-VO_{2max} – maximal oxygen uptake in running

SNP – single nucleotide polymorphism

TT – time trial

VO_{2max} – maximal oxygen uptake

VO_{2peak} – peak oxygen uptake

$\%RUN-VO_{2max}$ – fractional utilization of maximal oxygen uptake in running at peak oxygen uptake in double poling.

$\%VO_{2max}$ – ratio between maximal and peak oxygen uptake

Definitions

Allele	One of at least two versions of a specific gene.
Cardiac output	The product of heart rate and stroke volume, and defines the maximum blood volume pumped by the heart per minute.
Genotype	The pair of alleles for a specific gene located at the two chromosomes within an individual.
Hereditary	An estimate of the genetic contribution in a specific trait that may vary within a population.
Lactate threshold	The point/intensity where blood lactate starts to accumulate exponentially.
Maximal aerobic speed	The product of maximal/peak oxygen uptake and oxygen cost per meter.
Maximal power output	The highest force attained with maximum effort in one muscle contraction divided by time.
Maximal strength	The highest force attained in one muscle contraction.
Maximal oxygen uptake	The rate of oxygen uptake and utilization for aerobic energy turnover by the muscle cells.
One-repetition maximum	The highest weight load a person is capable of lifting one time with maximal effort.
Single-nucleotide polymorphism	Differences in one nucleotide at a specific site in a specific gene inherited in at least 1% of a population.
Work economy	The amount of work/oxygen spent over a given distance at a given velocity.

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1 Introduction

1.1 Cross-country skiing – a demanding aerobic endurance sport

Cross-country skiing is regarded as one of the most demanding aerobic endurance sports (Sandbakk & Holmberg, 2017). Pate and Kriska (1984) and di Prampero (2003) have previously suggested three main determining factors for aerobic endurance performance; maximal oxygen uptake (VO_{2max}), work economy (C) and lactate threshold (LT). The importance of these factors has been extensively confirmed in studies of cross-country skiing (Ingjer, 1991; Sandbakk et al., 2011; Losnegard et al., 2013; Andersson et al., 2017; Sandbakk and Holmberg, 2017), distance running (Conley and Krahenbuhl, 1980; Støa et al., 2010; Støren et al., 2011; Støa et al., 2020), cycling (Lucia et al., 2001; Bentley et al., 2001; Støren et al., 2013) and biathlon (Rundell and Bacharach, 1995; Tønnessen et al., 2015; Laaksonen et al., 2020).

Competitions in cross-country skiing generally range from 2 minutes (sprint) to several hours (e.g. 30/50 km or 90 km Vasaloppet). There have been observed a near 50/50% contribution from aerobic and anaerobic energy supply already at 1 minute of maximal work (Medbø & Tabata, 1989; Gatin, 2001), thus making cross-country skiers highly dependent upon their aerobic metabolism. Accordingly, estimates of 70 – 95% dependency of aerobic energy supply have been reported for various cross-country skiing events (Losnegard et al., 2012a; Andersson et al., 2017; Sandbakk and Holmberg, 2017). However, the variation in terrain typical for cross-country skiing allow skiers to work at intensities above 100% of maximal aerobic energy turnover repeatedly in short uphill sections (Karlsson et al., 2018; Gløersen et al., 2020). The variation in terrain and thus work intensities makes cross-country skiing unlike most of the other endurance sports, which maintain a steadier pace throughout competitions.

In the last 20 years, cross-country skiing competitions have changed rapidly. The inclusion of mass starts and sprint events, better track preparation, better equipment

and waxing, have all contributed to a ~10% increase in average skiing speed since early 1990s (Sandbakk and Holmberg, 2017; Losnegard, 2019). Thus, enhanced demands of maximal strength, force- and power generation, acceleration and maximal speed in modern competitive skiers is evident (Sandbakk and Holmberg, 2014; 2017).

International cross-country skiing is utilizing two separate techniques, classic and freestyle technique, with several sub-techniques in both of them. In response to speed and terrain, cross-country skiers have to alternate between the different sub-techniques (Andersson et al., 2010; 2017). In recent years, the classic technique has been revolutionized by the increased use of the double poling (DP) technique in all sections of the track. Today, in some of the long-distance events (e.g. Vasaloppet) both elite and recreational skiers are solely using the DP technique (Stöggl et al., 2020), while 100% DP is banned for World-Cup races. DP puts more stress on the upper-body and trunk muscles (Hegge et al., 2016), and thus elevating the demands of general and maximal strength even further.

1.2 Physiological determinants of cross-country skiing performance

1.2.1 Maximal and peak oxygen uptake

Bassett and Howley (2000) define VO_{2max} as the highest rate of uptake and utilization of oxygen (O_2) by the muscles for aerobic energy production during strenuous work. VO_{2max} is determined by supply of O_2 to the skeletal muscle, and demand for O_2 in the skeletal muscle (Wagner 1996). The O_2 -supplying variables are the pulmonary system, cardiac output (stroke volume · heart rate) and the O_2 -carrying capacity by the blood (Bassett and Howley, 2000; di Prampero, 2003; Levine, 2008). The demand factors are related to the local skeletal muscle components important in aerobic metabolism, like mitochondrial density and volume and aerobic enzyme activity (Evertsen et al., 1999; Bassett and Howley, 2000; di Prampero, 2003; Levine, 2008). For intensive, whole body

exercise (e.g. cross-country skiing and running), the O_2 -supply is suggested as the bottleneck of VO_{2max} in healthy subjects (Bassett and Howley, 2000; Helgerud et al., 2007). Furthermore, human skeletal muscles have shown an ability to consume more O_2 than supplied by the circulatory system during whole body exercises (Andersen and Saltin, 1985).

VO_{2max} is widely accepted as the most differentiating physiological variable in whole-body aerobic endurance performances (Pate and Kriska, 1984; di Prampero, 2003; Støren et al., 2011; 2013). It has previously been reported that 73% of 3 000 m running performance can be determined solely by VO_{2max} in well-trained endurance athletes (Støren et al., 2011), and 66% of a 23 km laboratory time-trial in elite cyclists (Støren et al., 2013). Accordingly, strong relationships has been observed between VO_{2max} in running (RUN- VO_{2max}) and/or peak oxygen uptake (VO_{2peak}) in any cross-country skiing sub-technique and performance level in both sprint and distance cross-country skiing (Ingjer, 1991; Mahood et al., 2001; Vesterinen et al., 2009; Sandbakk et al., 2011; 2016). Since cross-country skiers utilize the whole-body to create propulsion in all techniques, the demands for O_2 is extremely high in all parts of the body. This puts an enormous stress on the skier's ability to supply the muscle cells with sufficient O_2 (Sandbakk and Holmberg, 2017). Cardiac output of $>40 \text{ L} \cdot \text{min}^{-1}$, stroke volumes $>200 \text{ mL}$ and ventilation of $250 \text{ L} \cdot \text{min}^{-1}$ have been reported in elite male skiers (Ekblom and Hermansen, 1968; Holmberg, 2015). Consequently, both male and female elite cross-country skiers have displayed VO_{2max} values of $>80 \text{ mL} \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$ and $>70 \text{ mL} \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$ respectively, correspondent to some of the highest values ever recorded (Saltin and Åstrand, 1967; Ingjer, 1991; Tønnessen et al., 2015).

Although VO_{2max} is an important factor for cross-country skiing performance, the skier's ability to utilize a high percentage of VO_{2max} ($\%VO_{2max}$) in every sub-technique and overall during a race is proposed as a crucial component in cross-country skiing (Joyner and Coyle, 2008; Sandbakk and Holmberg, 2017). Elite cross-country skiers have displayed high $\%VO_{2max}$ in all sub-techniques, even in the DP technique with relatively less muscle mass involved than in diagonal stride or freestyle sub-techniques (Losnegard

and Hallén, 2014; Sandbakk and Holmberg, 2017; Undebakke et al., 2019). In previous studies, a VO_{2peak} in DP ($DP-VO_{2peak}$) of 80 – 90% of VO_{2max} has been reported (Nilsson et al., 2004; Holmberg et al., 2007; Hegge et al., 2016; Sagelv et al., 2018). Sandbakk and Holmberg (2017) propose that narrowing the gap between VO_{2max} and $DP-VO_{2peak}$ and other sub-techniques, might elevate the overall cross-country skiing performance.

1.2.2 Oxygen cost of skiing and work economy

The ability to consume less energy at a given workload over a given distance, called work economy or oxygen cost of movement (C), is proposed to have major impact on aerobic endurance performance (Pate and Kriska, 1984; di Prampero, 2003; Støren et al., 2013; Støa et al., 2020). In relatively homogenous cohorts of endurance athletes in terms of VO_{2max} , strong correlations between aerobic endurance performance and C are found (Conley and Krahenbuhl, 1980; Luchsinger et al., 2019; Laaksonen et al., 2020). In cross-country skiers, work economy has been reported to determine more than 50% of sprint skiing performance (Andersson et al., 2017). Improvements in aerobic endurance performance after training interventions improving C, without any increase in VO_{2max} , have been reported in cross-country skiers (Hoff et al., 2002; Østerås et al., 2002; Mikkola et al., 2007), cyclists (Sunde et al., 2010) and runners (Paavolainen et al., 1999; Støren et al., 2008).

Work economy seems to be a multi-factorial trait, and high inter-individual variability has been reported both in running and cross-country skiing (Coyle et al., 1992; Losnegard et al., 2012b). Factors like neuromuscular efficiency, amount of movement-specific training and technical abilities have been suggested to influence C in endurance athletes (Scrimgeour et al., 1986; Paavolainen et al., 1999; Hoff et al., 2002; Østerås et al., 2002; Nilsson et al., 2004; Støren et al., 2011). However, Losnegard et al. (2014) also points to additional intrinsic factors not influenced by training history or technical skills. Anthropometrical factors (e.g. calf circumference and leg length) have been suggested to have major impact on running economy (Anderson, 1996; Lucia et al., 2006), females tends to have a better running economy than males (Helgerud et al., 1994; 2010; Støa

et al., 2020), and a higher amount of type I muscle fibers has been suggested to be beneficial for better C (Coyle et al., 1992; Mogensen et al., 2006). Interestingly, Losnegard et al. (2014) reported that the most economical skiers in DP (C_{DP}) were also the most economical skiers in freestyle techniques.

Maximal aerobic speed (MAS) is the product of VO_{2max} divided by C, and have shown to be a better predictor of aerobic endurance performance compared to VO_{2max} or C alone (McLaughlin et al., 2010; Støren et al., 2011; 2013; Støa et al., 2020). In addition, improvements of both or one of these variables, thus an increase in MAS, has corresponded to aerobic endurance enhancement in several studies (Nilsson et al., 2004; Støren et al., 2008; 2012; Sunde et al., 2010; Losnegard et al., 2013; Sandbakk et al., 2013a). Consequently, MAS proves as a useful tool to predict aerobic endurance performance.

1.2.3 Lactate threshold

LT has been defined as the intensity where blood lactate concentration ($[La^-]_b$) starts to accumulate exponentially during prolonged exercise, and is often expressed as a percentage of VO_{2max} (LT%) (Davis et al., 1985). Earlier studies have revealed that LT% appears generally at 75 – 90% of VO_{2max} in endurance athletes (Joyner and Coyle, 2008; Støren et al., 2008; 2012; 2014; Støa et al., 2020). However, even if LT is suggested to be an important contributor to aerobic endurance performance (Pate and Kriska, 1984; Bassett and Howley, 2000), numerous studies have reported that LT% has little to no effect on performance in running and cycling (Helgerud et al., 1994; Støren et al., 2008; 2011; 2012; McLaughlin et al., 2010; Sunde et al., 2010; Støa et al., 2020). The workload or velocity at LT (LT_v) is a more practical way to express LT, both for training purposes and as a predictor of performance. LT_v has been shown to highly predict performance in running and cycling (McLaughlin et al., 2010; Støren et al., 2013; 2014; Støa et al., 2020). In addition, Helgerud et al. (2001) found that the improvements in LT_v after 8 weeks of aerobic training were almost identical to improvements in VO_{2max} and C in soccer players. Later studies have confirmed that LT_v seems to be largely influenced by MAS in

running and cycling, with less impact of $LT_{\%}$ (McLaughlin et al., 2010; Støren et al., 2014; Støa et al., 2020). Additionally, when multiplying $LT_{\%}$ and MAS, Støa et al. (2020) reported that LT_v could be calculated precisely within a range of $0.27 \text{ km} \cdot \text{h}^{-1}$ in 75 well-trained to elite runners. However, little has been reported about the impact of LT_v in cross-country skiers and how this variable may predict cross-country skiing performance.

1.2.4 Maximal strength and force variables

In endurance sports where leg muscles are the predominant force contributors (e.g. running and cycling), significant correlations between maximal strength (1RM) *per se* and performance have been absent in several studies (e.g. Bishop et al., 1999; Støren et al., 2008; 2013; Sunde et al., 2010). However, this does not exclude maximal strength as an important performance contributor (Joyner and Coyle, 2008). In contrast, numerous studies of cross-country skiing, which is dependent of both leg and upper-body muscles, have shown significant correlations between aerobic performance and power output (Rundell and Bacharach, 1995; Gaskill et al., 1998; Nesser et al., 2004; Alsobrook and Heil, 2009; Carlsson et al., 2013) or 1RM in upper-body muscles (Losnegard et al., 2013). This corresponds to results from swimming performance (Keiner et al., 2015), and may indicate that maximal strength *per se* is a stronger performance determinant when upper-body muscles are involved.

One of the high-speed techniques in classical cross-country skiing is the DP technique, where the overall propulsion is generated through the poles (Holmberg et al., 2005). This technique has also been found to generate higher peak forces (PF) through the poles compared to other skiing techniques (Millet et al., 1998). Consequently, numerous studies have identified several DP characteristics that can be related to maximal muscular strength. Stöggl et al. (2011) found that the fastest skiers in DP displayed the highest power outputs in upper-body exercises (bench press and bench pull). Several studies have reported higher PF and a shorter time to PF in faster skiers in DP (Bilodeau, et al., 1995; Holmberg et al., 2005; Stöggl and Holmberg, 2011; 2016). Considering the

short amount of time (~ 0.2 s) to develop maximal forces in DP at high speeds (Stöggl and Müller, 2009), the ability to generate high forces explosively may be crucial for cross-country skiers. In addition, faster skiers have also displayed lower DP cycle frequencies at equal sub-maximal workloads (CR, Zoppirolli et al., 2015) and shorter propulsion phase and longer recovery phases in DP (Holmberg et al., 2005) compared to slower skiers. Thus, these biomechanical and technical differences should be linked to differences in muscular power output and strength as well. In addition, an eventual effect of better DP characteristics on C_{DP} have been suggested (Talsnes et al., 2020a). However, Stöggl et al. (2011) points out that the coordination of both arms and legs during the complex skiing movement and timing of force application may be equally important to utilize the overall strength capacity for cross-country skiers.

The force contribution from leg muscles for propulsion is obvious in most cross-country skiing techniques, since most classical and freestyle techniques includes explosive push-offs by the legs (Stöggl et al., 2011). In DP, Holmberg et al. (2005) showed that a considerable contribution from the legs increased pole forces by $\sim 9\%$ (Holmberg et al., 2006). The contribution of the leg muscles have also been reported to increase progressively with higher DP velocity (Zoppirolli et al., 2017). However, the importance of general maximal strength *per se* and power output in lower limb muscles to cross-country skiing performance over longer distances is still unclear.

1.2.5 Other determining factors of cross-country skiing performance

Anaerobic capacity

The aerobic energy supply in various cross-country skiing events have been estimated to differ from 70 – 95% (Sandbakk and Holmberg, 2017), leaving 5 – 30% of the energy supply provided from anaerobic processes. In longer distances (>5 -km), the anaerobic component is small (5 – 15%) and may therefore be of less importance (Åstrand et al., 2003). However, anaerobic capacity may serve as an important discriminating factor in a homogenous group of cross-country skiers in terms of aerobic capacity (Losnegard et al., 2012a). Losnegard et al. (2013) linked improvements in a 1000-m TT in elite cross-

country skiers to improved anaerobic capacity. The high anaerobic contribution (110 – 160% of VO_{2max}) in short steep uphill sections of a 13.5-km TT in elite cross-country skiers (Karlsson et al., 2018), suggests that the ability to repeatedly utilize and recover anaerobic energy stores rapidly during uphill and downhill sections respectively, may be an important performance-determining factor. However, since anaerobic recovery has to be performed aerobically, this process is thus highly dependent on the overall aerobic capacity, i.e. VO_{2max} , as well as the buffering capacity of H^+ (Stallknecht et al., 1998; Böning et al., 2007). A combined aerobic and anaerobic model have been shown to explain over 80% of the variance in short cross-country skiing races (Losnegard et al., 2013), and long-distance cycling TT (Støren et al., 2013). However, when eliminating the anaerobic component from the model, almost identical results were revealed in Støren et al. (2013). This shows the low impact of anaerobic capacity for longer endurance events.

Anthropometrics

Back in 1992, Bergh and Forsberg concluded that heavier cross-country skiers were favored in most types of terrain, except steep inclines. However, the same study reported high variability in body weight among top-level skiers. Contradictory results have been reported in terms of the importance of factors like body fat, body height, body mass index and body dimensions for cross-country skiing performance in already well-trained or elite adult cross-country skiers (Stöggl et al., 2010; Sandbakk et al., 2011; 2016). One anthropometric variable that seems to be important in adult cross-country skiers is lean mass (Stöggl et al., 2010; Carlsson et al., 2014; 2016). However, lean mass is a good indicator for total muscle mass, and therefore this is related to the overall potential for strength and power output in cross-country skiing (Carlsson et al., 2014).

Gender

In various aerobic endurance sports, overall performance has been reported to be 10 – 15% higher for males compared to females (Pate and Kriska, 1984; Billat et al., 2001;

Etter et al., 2013; Lamberts, 2014). The higher VO_{2max} , due to higher cardiac output, higher blood volumes and hemoglobin levels, higher aerobic and anaerobic enzyme activity, and more muscle mass observed in males, have to a large extent explained these differences (Pate and Kriska, 1984; Evertsen et al., 1999; Sandbakk et al., 2018). Observed gender differences in VO_{2max} in elite endurance athletes have been reported to be ~10 – 20% expressed relative to body mass (Sandbakk et al., 2014; Tønnesen et al., 2015; Støa et al., 2020). However, for cross-country skiing performance, slightly higher gender differences have been observed (~15–20%), due to the higher contribution of poling and upper-body muscles (Sandbakk et al., 2014; Hegge et al., 2016). Thus, more efficient and powerful poling actions in males are suggested to contribute to these differences (Sandbakk et al., 2014). In addition to more muscle mass, relatively more of this muscle mass is located in the upper-body in males compared to females (Janssen et al., 2000; Hegge et al., 2016). Thus a higher potential for power output and maximal strength in upper-body muscles is likely for males.

Studies investigating the impact of gender on skiing economy have revealed no significant gender differences in different sub-techniques (Ainegren et al., 2013; Sandbakk et al., 2013b; Hegge et al., 2016). The results observed in cross-country skiing are to some extent correspondent to several studies investigating running economy, where males have displayed superior economy (Bransford and Howley, 1977; Daniels and Daniels, 1992), or no significant differences have been observed (Billat et al., 2003). The studies investigating skiing or running economy, have expressed C as VO_2 in terms relative to full body weight ($mL \cdot kg^{-1} \cdot min^{-1}$). However, since males and females differ in total body mass, lean mass and fat mass (Sandbakk et al., 2018), this expression may not be appropriate when comparing the two genders. Helgerud et al. (1994; 2010) and Støa et al. (2020) expressed C values where body mass was raised to the power of 0.75 and meters ($mL \cdot kg^{-0.75} \cdot m^{-1}$), to accommodate gender differences in body composition. These studies have observed better running economy in females. Bergh and Forsberg (1992) recommended scaling VO_2 -values to the power of 0.67 for cross-country skiers.

However, few studies have expressed values of skiing economy by use of this scaling method.

In general, studies have mainly examined male cross-country skiers, while female skiers have received less attention (Sandbakk and Holmberg, 2017). Therefore, more studies investigating physiological determinants and the relative importance of these variables on cross-country skiing performance, both dependent and independent of gender, are preferable.

Age

To the best of this author's knowledge, no previous studies have directly compared age-related differences in cross-country skiing performance. However, Ainegren et al. (2013) reported 3-6% difference in relative VO_{2peak} ($\text{mL} \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$) and 8-10% difference in absolute VO_{2peak} ($\text{L} \cdot \text{min}^{-1}$) in various cross-country skiing techniques between junior- and senior male cross-country skiers. The corresponding values for females were 8-11% in both relative and absolute VO_{2peak} . This is somewhat higher values, at least for relative VO_{2max} , compared to age differences observed in VO_{2max} of elite triathletes in cycling (Millet and Bentley, 2004) and elite runners (Saltin et al., 1995). Differences in absolute VO_{2max} -values are mainly influenced by the lower body mass of junior athletes (Saltin et al., 1995; Millet and Bentley, 2004; Ainegren et al., 2013). Millet and Bentley (2004) also reported similar relative body fat values among male and female junior- and senior athletes, and thus differences in VO_{2max} may be a result of differences in muscle mass. Accordingly, significant relationships between muscle mass and VO_{2max} have been observed previously (Kim et al., 2016). In addition, younger skiers still in puberty may still have an in-complete development of the cardiac system (Bjerring et al., 2019; 2020), thus influencing the differences in aerobic capacity between junior- and senior athletes. Furthermore, strong correlations have been observed between VO_{2max} and endurance performance in both junior and senior athletes (Pettersen et al., 2001; Støren et al., 2011; 2013).

Regarding other performance determining factors, Ainegren et al. (2013) found generally no significant differences in skiing economy and LT%, measured as onset of blood lactate accumulation, between male and female junior- and senior cross-country skiers. In terms of strength variables, no studies have directly investigated age-related differences in cross-country skiers.

1.3 Training characteristics and physiological adaptations in cross-country skiers.

Elite male and female cross-country skiers often perform approximately 700 – 950 h of annual training, i.e. 15 – 20 h · week⁻¹ on average, with ~60% of annual training performed from May to October i.e. pre-season (Ingjer, 1992; Losnegard et al., 2013; Tønnessen et al., 2014; Sandbakk et al., 2016; Solli et al., 2017). In addition, both male and female world-class skiers report higher training volumes compared to national-class skiers (Sandbakk et al., 2011; 2016).

1.3.1 Endurance training

Training characteristics

In general, ~90% of the total training volume of cross-country skiers is categorized as endurance training, and remain relatively stable throughout the whole year (Seiler and Kjerland, 2006; Losnegard et al., 2013; Tønnessen et al., 2014; Sandbakk et al., 2016; Solli et al., 2017; 2018). Approximately 80 – 90% of all endurance training is performed as low-intensity training (LIT), i.e. <82% of maximal heart rate (HR_{max}). The remaining proportions of total endurance training is distributed as 2 – 5% at moderate intensities (MIT, 82 – 87% of HR_{max}) and 5 – 10% at high intensities (HIT, >87% of HR_{max}) (Losnegard et al., 2013; Sandbakk et al., 2016; Solli et al., 2017; 2018). This training intensity distribution is comparable to studies of training characteristics of other elite endurance athletes (Lucia et al., 2000; Billat et al., 2001; Esteve-Lanao et al., 2005; Tjelta and Enoksen, 2010; Rasdal et al., 2018)

The training modes of cross-country skiers are mainly divided into ski-specific exercise (on-snow skiing or roller skiing) and un-specific exercise (e.g. running and cycling). Ski-specific training, including both classic and freestyle skiing, progressively is increasing throughout the training year, making up 50% in May to August and 80 – 90% of all endurance training in the competitive season (Losnegard et al., 2013; Solli et al., 2018).

Physiological adaptations

The physiological adaptations to aerobic endurance training is frequently reported, especially after HIT interventions. Several interventional studies have reported improved VO_{2max} after HIT in healthy subjects (Helgerud et al., 2007; Tjønnå et al., 2013; Støren et al., 2017) and well-trained to elite endurance athletes (Nilsson et al., 2004; Sandbakk et al., 2013a; Seiler et al., 2013; Rønnestad et al., 2014; 2016; Sylta et al., 2016). The main physiological adaptations contributing to higher aerobic capacity is suggested to be a higher stroke volume (Bassett and Howley, 2000; Helgerud et al., 2007), thus an improved ability for O_2 -supply (Wagner, 1996). In studies of endurance athletes, the same HIT interventions have also induced performance enhancements (Støren et al., 2012; Sandbakk et al., 2013a; Rønnestad et al., 2014; 2016). Although this training method has proved effective, a recent study reported huge inter-individual differences in the response to a demanding HIT protocol in cyclists (Bratland-Sanda et al., 2020).

Few studies have investigated specific training models for improving the $\%VO_{2max}$ and VO_{2peak} in sub-techniques in cross-country skiers. Nilsson et al. (2004) did report an increase in DP- VO_{2peak} with no improvement in VO_{2max} in running (RUN- VO_{2max}), thus showing an improvement of the utilization of RUN- VO_{2max} while DP ($\%RUN-VO_{2max}$). This pointed at a potential for improvements of the $\%RUN-VO_{2max}$ after specific HIT. Enhancement of both VO_{2peak} in cycling and RUN- VO_{2max} have also been observed after HIT performed as running (Støren et al., 2012).

In contrast to HIT, the direct physiological adaptations accompanied by LIT is less documented in well-trained endurance athletes. Several studies have reported that endurance athletes that train more LIT often perform at a higher level (Esteve Lanao et al., 2005; Sandbakk et al., 2011; 2016; Tønnessen et al., 2015). In addition, the observed amount of LIT performed by world-class endurance athletes, including cross-country skiers, thus have been indicative for a high importance of this kind of training (Seiler and Kjerland 2006; Esteve-Lanao et al., 2007; Seiler, 2010; Tønnessen et al., 2014; Sandbakk et al., 2016). However, the physiological components affected by high amounts of LIT, both short- and long-term, and why this type of training is so important is unclear in already well-trained subjects. Adding twice as much LIT, Costill et al. (1991) did not observe any additional effects on physiological variables or performance in swimmers. Evertsen et al. (1999) did not observe superior endurance and enzyme activity adaptations to a training program dominated by LIT (87% LIT) in junior cross-country skiers. This is also correspondent to later findings on added LIT in moderately trained healthy subjects (Helgerud et al., 2007) and well-trained endurance athletes (Enoksen et al., 2011; Stöggl and Sperlich, 2014).

Equivocal results have been reported in adaptations following HIT interventions on C. In studies of less trained individuals (Helgerud et al., 2007; Tjønnå et al., 2013) and in studies of athletes in movements patterns which they are not previously specialized in (Helgerud et al., 2001; McMillan et al., 2005), reveals great improvements in C after HIT interventions. However, studies of already movement-specialized endurance athletes reveal minor effects in C after such interventions (Støren et al., 2012; Rønnestad et al., 2014; 2016; Vandbakk et al., 2017). Actually, Skovereng et al. (2018) showed deteriorations in efficiency after a 12 weeks HIT intervention. In contrast, Nilsson et al. (2004) observed an improved C_{DP} in well-trained cross-country skiers following a 6 weeks HIT intervention performed in DP. Accordingly, Enoksen et al. (2011) did observe significant improvements in running economy among well-trained runners after HIT, although this adaptation did not differ from high-volume LIT training. Scrimgeour et al. (1986) showed that runners with most kilometers during a week also had better running

economy. A relationship between amount of movement-specific training at low- or higher intensities, and better C was thus suggested. Haugnes et al. (2019) have suggested that LIT or MIT can serve as beneficial training methods for C in elite cross-country skiers. Comparable velocities to race speed were observed in flat terrain, thus high amounts of movement-specific training may be possible with such training.

Training interventions have mainly observed minor to no significant changes in $LT_{\%}$ in already healthy or well-trained subjects (Helgerud et al., 2001; 2007; Støren et al., 2012; Enoksen et al., 2011; Rønnestad et al., 2016; Sylta et al., 2016). However, several studies have observed improved LT_v (Helgerud et al., 2001; 2007; Enoksen et al., 2011; Stöggl and Sperlich, 2014; Rønnestad et al., 2014; 2016; Sylta et al., 2016). Interestingly, none of these studies has observed improvements in LT_v without concomitant improvements in VO_{2max} , VO_{2peak} and/or C, thus indicating a close relationship between MAS and LT_v (Støren et al., 2014; Støa et al., 2020).

The optimal distribution of endurance training intensity, in order to improve aerobic endurance variables, is still debated. Seiler and Kjerland (2006) suggests that a polarized training model, including most training in LIT (~80%) and HIT (~20%), may be termed as an “optimal” intensity distribution in most endurance athletes. This is supported by findings of better physiological endurance adaptations after short periods (<3 months) of polarized intensity distribution compared to other training models in well-trained endurance athletes (Neal et al., 2013; Stöggl and Sperlich, 2014). The 9 weeks intervention in Stöggl and Sperlich (2014) displayed a 12% improvement in VO_{2max} after a polarized training distribution, compared to a 2.6% improvement after a pyramidal intensity distribution (LIT > MIT > HIT). However, most long-term studies (>3 months) on training in elite endurance athletes are retrospective or descriptive, and were thus not able to measure the direct physiological effects on performance or physiological variables. Only a couple of studies have been able to investigate the correspondent effects in a large set of endurance variables and performance of cross-country skiers over longer periods (Losnegard et al., 2013; Talsnes et al., 2020a; 2020b).

Losnegard et al. (2013) observed that elite male cross-country skiers improved their 1000-m time after increments in anaerobic capacity and C, while no significant improvements were detected in VO_{2peak} (+1.2%), after nine months of training. Similar findings were reported in Talsnes et al. (2020a) in a group of Chinese endurance athletes (runners and kayakers), transferred to cross-country skiing, after a 6-months ski-specific training program. The athletes in both Losnegard et al. (2013) and Talsnes et al. (2020a) were following a similar training model suggested for optimal adaptations in cross-country skiing, including high proportions of LIT and lower amounts of MIT and HIT. However, studies have revealed that there are large inter-individual differences in the response to such training models (Gaskill et al., 1999; Talsnes et al., 2020b). Although this might be indicative for individual potential for performance development, few studies have investigated concurrent adaptations to a different intensity distribution programs longitudinally in cross-country skiers. Gaskill et al. (1999) and Støren et al. (2012) displayed significant improvements of VO_{2max} and endurance performance after reduced training volumes and increased volumes of HIT. Two successful seasons, differing in total training volume and relative amounts of HIT, were also observed in a highly successful female cross-country skier (Solli et al., 2019). However, higher amount of HIT over longer periods in elite endurance athletes has been criticized for being too demanding and vulnerable to over-training symptoms (Esteve-Lanao et al., 2007; Seiler, 2010).

1.3.2 Strength and speed training

Training characteristics

Cross-country skiers generally dedicate ~10% and 1 – 2% to strength and speed training, respectively (Losnegard et al., 2013; Tønnessen et al., 2015; Solli et al., 2017; 2018). In addition, both male and female world-class skiers report higher volumes of speed and strength training compared to national-class skiers (Sandbakk et al., 2011; 2016).

Solli et al (2017) reported a ~50/50% distribution of maximal strength training and general core stabilization training in the most successful female cross-country skier of

all time. Generally, cross-country skiers perform most strength training from May to October, and reduce the total strength training volume through the competitive season (Losnegard et al., 2013; Tønnessen et al., 2014; Solli et al., 2017; 2018). Speed training is generally reported to be performed in ski-specific sessions, either included in LIT or as independent sessions (Sandbakk et al., 2016).

Physiological adaptations

Improvements of 10 – 30% in 1RM of upper- or lower-body muscles have been observed in shorter strength training interventions (<3 months), in cross-country skiers (Hoff et al., 2002; Østerås et al., 2002; Losnegard et al., 2011; Skattebo et al., 2016) and other aerobic endurance athletes (Støren et al., 2008; Sunde et al., 2010; Aagaard et al., 2011; Rønnestad et al., 2015). These studies mainly used heavy or maximal strength training interventions, with maximal effort in the concentric phase. The interventions were added to the normal endurance training. The physiological adaptations following maximal strength training (1 – 5 repetitions) are mainly suggested to be neural adaptations (Aagaard et al., 2011), such as improved firing frequency and activation of more motor units (Aagaard et al., 2003). The effect on muscle volume has shown to be minor by this type of strength training (Aagaard et al. 2011) combined with the high amounts of endurance training.

The improvements in maximal strength observed in experimental studies have often been accompanied by a significant improvement of endurance performance, without changes in VO_{2max} (Hoff et al., 2002; Østerås et al., 2002; Støren et al., 2008; Aspenes et al., 2009; Sunde et al., 2010; Losnegard et al., 2011; Aagaard et al., 2011). Concurrent improvements of 1RM and C have been observed in several studies of cross-country skiers (Hoff et al., 2002; Østerås et al., 2002), cyclists (Sunde et al., 2010), runners (Paavolainen et al., 1999; Støren et al., 2008) and swimmers (Aspenes et al., 2009). Thus, improved MAS may explain the observed effect on aerobic endurance performance (Støren et al., 2008; Sunde et al., 2010). Contrastingly, later studies have not been able to reveal the same effect on C after heavy strength training (Aagaard et al., 2011;

Losnegard et al., 2011; Rønnestad et al., 2015; Skattebo et al., 2016). However, this may be explained by methodological and interventional differences among the studies, and pointing at the importance of maximal mobilization.

Few studies have investigated the adaptations to the amount of strength training performed in cross-country skiers over longer periods (>3 months). However, a recent study observed ~11% improvements in 1RM in upper-body muscles after a six months training program, including 10% strength training in endurance athletes transferred to cross-country skiing (Talsnes et al., 2020a). Strength improvements were followed by longer cycle lengths and reduced CR in the freestyle technique, and an improved C (Talsnes et al., 2020a).

1.3.3 Gender and age-related differences in training characteristics and adaptations

Gender

Generally, studies reveal no or minor differences in training characteristics between male and female cross-country skiers, both in endurance-, strength- and speed training (Sandbakk et al., 2011; 2016; Losnegard et al., 2013; Solli et al., 2017; 2018). Although differing in several physiological variables at baseline, studies investigating training adaptations in both adult males and females have generally revealed no differences among genders to similar aerobic endurance training programs (Evertsen et al., 1999; 2001; Astorino et al., 2011; Seiler et al., 2013; Støren et al., 2017; Varley-Campbell et al., 2018). Similar findings have also been reported after strength training (Lemmer et al., 2000). In contrast, there have been observed gender differences in training adaptations of younger skiers (Matos and Winsley, 2007). However, studies of training effects have mainly been executed in male cross-country skiers. Hormonal changes and menstrual cycles in females may influence both endurance performance and training adaptations (Bruinvels et al., 2017). Thus, a need for direct comparisons of males and females in training adaptations is warranted in such cohorts (Sandbakk and Holmberg, 2017).

Age

Generally, adult elite cross-country skiers train higher total training volumes compared to younger and junior cross-country skiers. However, the training mode and intensity distribution seems to be similar (Ingjer, 1992; Seiler and Kjerland, 2006; Sandbakk et al., 2011; Losnegard et al., 2013; Skattebo et al., 2016; Solli et al., 2018). The difference in total training volume is most evident between world-class skiers and junior skiers, while the differences in total training volume between national-class and junior skiers are smaller (Sandbakk et al., 2011; 2013a; 2016; Skattebo et al., 2016; Solli et al., 2018). This may be due to the amount of time available for training.

Similar training responses are reported in subjects between 20 – 70 yrs after similar training protocols (Støren et al., 2017). Training adaptations of aerobic endurance (Nilsson et al., 2004; Seiler et al., 2013; Rønnestad et al., 2014; 2016) and strength variables (Østerås et al., 2002; Støren et al., 2008; Sunde et al., 2010; Losnegard et al., 2011) after comparable training protocols, in different age cohorts of well-trained senior endurance athletes, have shown to be similar. This may indicate that the training response within active senior endurance athletes (20 – 40 yrs) do not differ substantially. Comparable improvements in both aerobic capacity and strength variables have been reported in both young cross-country skiers and non-skiers (14 – 18 yrs) after different training interventions (Helgerud et al., 2001; Aspenes et al., 2009; Sperlich et al., 2011; Sandbakk et al., 2013a; Skattebo et al., 2016). However, direct comparisons of training adaptations in junior- and senior endurance athletes has not been performed. In addition to responses related to training *per se*, training adaptations in junior skiers might be affected by maturation and growth (Steiner et al., 2019; Bjerring et al., 2019; 2020). Thus, a potential difference in training response in such skiers seems important to compare.

Previous studies have reported that both younger pubertal endurance athletes and healthy subjects starts to level-off in relative VO_{2max} during puberty, while absolute VO_{2max} continue to increase through adolescence (Ingjer, 1992; Pettersen et al., 2001).

Interestingly, Steiner et al. (2019) did not report superior improvements in VO_{2max} (+20%) in young male endurance athletes and age-matched healthy non-athletes, although endurance athletes had higher initial aerobic capacity. Therefore, an additional effect on aerobic capacity due to maturation in cardiac morphology, hemoglobin mass and muscle mass should be generated in younger skiers (Steiner et al., 2019; Bjerring et al., 2019; 2020). In strength training interventions, improvements in 1RM in control groups consisting of both young males and females (Aspenes et al., 2009; Cunha et al., 2015; Skattebo et al., 2016), also suggesting a potential maturation effect beside training adaptations in strength variables.

1.4 Genetic influence on physiological variables and trainability

Genetic variations have been recognized as an important factor influencing both athletic performance and trainability in humans (Jacques et al., 2019). Earlier studies have revealed that the genetic component and heritability in physical capacity and athletic performance may be as high as 70 – 95% in humans (Klissouras, 1971; De Moor et al., 2007; Jacques et al., 2019). For overall aerobic capacity and adaptations in maximal strength, genetic components have been estimated to account for 50 – 80% of the observed variance (Zhai et al., 2005; Silventoinen et al., 2008; Costa et al., 2012). The pioneering HERITAGE-study by Bouchard et al. (1998) concluded that baseline VO_{2max} was at least 50% inherited. Furthermore, Bouchard et al. (1999) demonstrated that VO_{2max} responses to training were likely to have a 47% genetic component. Taken together, these studies points to a strong genetic contribution in aerobic endurance- or strength capacity, and the trainability of these traits in humans.

Due to technological development, and thus more research, the interest of exercise genomics has grown large over the last decades. To date, over 150 single genetic variants have been associated with athletic performance through either single gene analysis or genome-wide association studies (Ahmetov et al., 2016; Jacques et al., 2019). Thus, it is speculated that genetic screening could be used in elite sports for talent identification (Pickering et al., 2019) and optimization of training programs (Vlahovich

et al., 2017) in near future. Actually, Chinese ministries have announced that genetic screening will be used in identification of genetically favored athletes to represent China under the Winter Olympics in Beijing 2022 using next generation sequencing that will screen the total genome (Lemon, 2018). However, the use of such genetic screening for e.g. talent identification raises serious ethical questions and is not supported by the international scientific community (Camporesi and McNamee, 2016).

Two of the most studied and replicated genes associated with athletic performance are the *ACTN3* and *ACE* genes (Eynon et al., 2011; Guth and Roth, 2013; Jacques et al., 2019). The *ACTN3* gene codes for the α -actinin-3 protein, which plays an important structural role in the sarcomeres in skeletal muscles (Seto et al., 2019). The protein is most abundant in type II muscle fibers, and is suggested to be of crucial importance for explosive and forceful muscle contractions (Del Coso et al., 2019). The R577X polymorphism located at that gene, leads to a protein deficiency in subjects homozygote for the X-allele (XX genotype, North et al., 1999). In Europeans, this is the case for ~19% of the population (Roth et al., 2008; Goleva-Fjellet et al., 2020). Despite this deficiency, X-allele carriers and XX individuals have demonstrated more efficient muscle metabolism and improved fatigue resistance (Head et al., 2015), a tendency of lower percentage of type II muscle fibers (Vincent et al., 2007; Seto et al., 2019) and higher oxidative enzyme activity in type II muscle fibers (MacArthur et al., 2008). Thus, such individuals have been associated with higher aerobic endurance capacity (Yang et al., 2003; Eynon et al., 2012; Seto et al., 2019). On the contrary, subjects with the R-allele or RR genotype have demonstrated higher maximal strength (Erskine et al., 2014) and better strength adaptations after maximal strength training (Pereira et al., 2013; Pickering and Kiely, 2017) compared to XX individuals. Thus, the RR genotype has been observed more frequently in sprint/power athletes compared to the general population and endurance athletes (Yang et al., 2003; Roth et al., 2008; Ahmetov et al., 2016).

The angiotensin I-converting enzyme gene (*ACE*) was the first studied genetic variant that were related to physical performance (Pescatello et al., 2019). The protein encoded

by *ACE* contribute to regulate blood pressure and fluid-electrolyte balance, and may affect the muscle function and metabolism (Puthuchearry et al., 2011; Pescatello et al., 2019). The studied I/D polymorphism of this gene, either insert a 287-bp long nucleotide-strand (I, insertion) or not (D, deletion), and the inherited allele may affect physiological variables differently (Rigat et al., 1990). Traditionally, the I allele have been regarded as beneficial for endurance performance, while the D allele have been regarded as beneficial for strength and power capabilities (Nazarov et al., 2001; Ma et al., 2013; Ahmetov et al., 2016). However, the reported results are contradictory, and do vary among different studies (Tobina et al., 2010; Pescatello et al., 2019). No conclusive associations between VO_{2max} , work economy or cardiac function have been reported for either II, ID or DD genotypes (Pescatello et al., 2019). However, I-allele carriers have been reported to possess a higher percentage of type I muscle fibers (Zhang et al., 2003), and improved capillary density and mitochondrial density following aerobic exercise (Vaughan et al., 2013; 2016; Valdivieso et al., 2017). This should, in turn, elevate the aerobic endurance capacity of I-allele carriers. Although, due to the conflicting evidence of the role of *ACE* polymorphisms in relation to endurance performance, the impact of this gene might be minor (Pescatello et al., 2019).

Genes within the peroxisome proliferator-activated receptor (PPAR) pathways are some of the most studied genetic variants, beside *ACE* and *ACTN3* (Correia et al., 2015; Phua et al., 2018). This group of genes has been suggested to play a central role in energy metabolism, and has thus been studied in relation to VO_{2max} and muscle characteristics (Alvarez-Romero et al., 2020). One of the most studied, the *PPARGC1A* gene, codes for the protein PGC1 α (Petr et al., 2019). This protein plays a crucial role in mitochondrial biogenesis (Correia et al., 2015) and angiogenesis (Ahmetov and Fedotovskaya, 2015). The rs8192678 polymorphism within this gene has recently been associated with sports performance and trainability of aerobic endurance components (Petr et al., 2018; Tharabenjasin et al., 2019). Furthermore, these benefits are mostly seen in carriers of the common Gly-allele (Ahmetov and Fedotovskaya, 2015; Petr et al., 2019), while the minor Ser-allele might be beneficial for power-athletes (Gineviciene et al., 2016). In

addition, *PPARA* and *PPARG* have been studied in relation to athletic performance since these genes codes for proteins related to lipid and glucose metabolism (Phua et al., 2018). Furthermore, two promising genetic variants, the acyl-CoA synthase long-chain member 1 (*ACSL1*) and interleukin-6 (*IL6*) genes, have previously been studied. Bouchard et al. (2011) demonstrated allele differences in the rs6552828 SNP of the *ACSL1*-gene to explain ~6% of VO_{2max} improvements after exercise training, favoring the common G allele. Recently, Harvey et al. (2020) demonstrated a significant association between the rs1474347 SNP in the *IL6* gene and adaptations in VO_{2max} in trained individuals. The protein encoded by this gene has been suggested to contribute in muscle growth (Serrano et al., 2008), myogenesis (Muñoz-Cánoves et al., 2013) and glucose metabolism (Serrano et al., 2008).

Few studies have investigated these polymorphisms in cross-country skiers. Mägi et al. (2016) reported that male skiers exhibited a higher frequency of RR and ID genotype in the *ACTN3* and *ACE* polymorphisms, respectively, compared to sedentary controls. The same study also revealed considerably higher improvements of VO_{2peak} over a 5-year period in the *ACE* ID genotype for females and the *ACTN3* XX genotype for males, although not significant differences in improvements were observed (Mägi et al., 2016). Additionally, genetic comparisons of well-trained cross-country skiers and controls from the exact same geographical area have not been performed. In the region of Southeastern Norway, Goleva-Fjellet et al. (2020), genotyped 831 untrained to moderately trained subjects for *ACE* and *ACTN3* polymorphisms. Thus, making it possible for a comparison of a cohort of cross-country skiers from the same area. Allele frequencies may vary considerably between populations (Marchini et al., 2004; Jacques et al., 2019), thus comparisons of homogenous cohorts are necessary for valid results.

2 Rationale and aims of the studies

Based on the scientific literature presented above, several facets of cross-country skiing performance and training are well described. However, there are still several unanswered questions:

1. How do cross-country skiers respond to a longitudinal training program consisting of the traditionally suggested training characteristics?
2. How do cross-country skiers respond to a short-term specialized HIT training program, targeting DP-specific aerobic capacities?
3. Are there differences in training characteristics, and subsequent adaptations, in well-trained male and female, and young and adult cross-country skiers?
4. Are there differences in the relative importance of physiological variables to cross-country skiing performance in males and females, and in young and adult skiers?
5. Do genetic variants affect physiological factors in a small group of cross-country skiers, and will a cohort differ from a general population in known performance-associated genes?

To address these questions, the main aim of this thesis is to gain further knowledge about cross-country skiing performance, short- and long-term training adaptations in cross-country skiers, and the effect of age, gender and genetic variants by investigating:

- Training adaptations to a long-term training model traditionally used by cross-country skiers in a large set of endurance- and strength variables (Study III).
- Training adaptations to a short-term training model of specific high-intensity aerobic training (Study

- A large set of determinant factors of cross-country skiing performance both dependent and independent of gender and age (Study I and III).
- Age- and gender related differences in training adaptations (Study III).
- Possible influence from selected single genes on determinants of cross-country skiing performance (Study III).

2.1 Study I

Since most studies have been performed on male skiers, evaluations of the relative importance of aerobic endurance variables, strength variables and DP characteristics on DP performance in both males and females is warranted. Cross-country skiers with relatively similar training background, yet heterogeneous in performance level is preferable. Therefore, the aim of this study was to compare different endurance- and strength variables, and DP characteristics with a DP roller-skiing time-trial (TT) in both male and female young competitive skiers. The hypothesis was that maximal upper-body strength would significantly affect DP characteristics and thus performance.

2.2 Study II

Few studies have investigated the effects of specific HIT interventions in sub-technical movement patterns in cross-country skiing, and the subsequent effect on %VO_{2max} and performance. Therefore, the primary aim of this study was to explore the training adaptations on DP-VO_{2peak} and %RUN-VO_{2max} following a 6 weeks HIT intervention in DP among non-specific DP trained, but competitive skiers. Secondary, we wanted to investigate possible effects on C_{DP}, MAS and cross-country skiing performance. The intervention was performed without increasing total HIT volume or total training volume.

2.3 Study III

Few studies have been able to investigate the concurrent training adaptations to training programs designed by the athletes themselves or their coaches. In addition, the subsequent effect of gender, age and genetic variants in physiological variables and adaptations in such skiers have been scarcely documented. Thus, the aim of this study was to 1) investigate the subsequent training adaptations in physiological and performance variables in national-level to elite cross-country skiers following a 6-months training program during the season preparation, 2) explore possible differences between genders and young and adult skiers in both baseline values and training adaptations, and 3) investigate the potential effect of known genetic variants on physiological variables at baseline.

3 Methods and materials

3.1 Subjects

A total of one-hundred and thirteen cross-country skiers were recruited, while seventy-one (45 males and 26 females) were included for statistical analysis in all three studies together. The exclusion of participants were mainly due to insufficient training registration (study III), unable to perform sufficient testing (all studies), and sickness or injuries (all studies). All participants were recruited from Southeastern and Eastern Norway, primarily from skiing high schools or regional cross-country skiing teams. Subject characteristics of participants included in the published articles are presented in Table 1. The studies were either ethically approved by the regional ethics committee of Southeast Norway (Study II), by the institutional research board at the University of Southeastern Norway (Study I) or by both (Study III). All participants gave their written informed consent to participate in the studies, and additional written consents were provided from parents and coaches for subjects under 18 years. The age groups referred to in this thesis were defined as still in or above puberty, and in or above high-school age. This corresponded to 16-18 years old young skiers and ≥ 19 year old adult skiers.

Table 1: Subject characteristics (N = 71)

	Study I	Study II	Study III
N (Int. + Con.)	28 (28 + 0)	14 (7 + 7)	29 (29 + 0)
Level	National	Recreational to national	National to Elite
Age	18.5 \pm 1.3	25.7 \pm 9.5	22.1 \pm 8.4
Gender (Males + Females)	16 + 12	12 + 2	17 + 12
RUN-VO_{2max}			
mL · kg ⁻¹ · min ⁻¹	64.0 \pm 10.4	68.7 \pm 8.4	62.9 \pm 8.0
L · min ⁻¹	4.48 \pm 1.00	5.19 \pm 0.85	4.38 \pm 0.88

Data are mean \pm standard deviation if not otherwise explained for included participants in study I, II and III. N, number of subjects. Int., intervention group. Con., control group. SD, standard deviation. RUN-VO_{2max}, maximal oxygen uptake in running. mL · kg⁻¹ · min⁻¹, milliliter per kilogram per minute. L · min⁻¹, liters per minute.

3.2 Testing procedures

For all three studies, all testing procedures were conducted at the exercise physiology lab at the University of Southeastern Norway, and carried out over two consecutive days. The identical tests for studies I, II and III were measurements of RUN-VO_{2max}, DP-VO_{2peak}, C_{DP} and DP time-trial performance (TT_{DP}). However, TT_{DP} in study II was performed on a treadmill, while performed on an outdoor track in studies I and III. Additionally, LT in DP, maximal strength (1RM) and maximal power were measured in studies I and III. Measurements of DP characteristics (Study I) and jumping variables (Study III) were also performed. In study II and III, subsequent testing sessions (Post-tests) used the same test protocols that were used for baseline testing.

3.2.1 Testing materials

For all studies, a Woodway PPS55 sport treadmill (Woodway, Waukesha, WI, USA), calibrated for speed and inclination, was used for the RUN-VO_{2max} measurements. Heart rate was monitored by Polar s610 monitors (Kempele, Finland) or the participants own heart rate monitors.

In studies I and III, all VO₂-measurements were performed by the metabolic test system Cortex MetaLyzer II (Biophysic GmbH, Leipzig, Germany) with VO₂-measurements every 10 s. Calibration of flow and gas analyzers were performed in accordance to the manufacturer's instructions. [La⁻]_b were collected by a Lactate Scout+ (SensLab GmbH, Leipzig, ray Inc., Kyoto, Japan), which analyzed whole blood lactate concentration. The treadmill used for all DP-tests was a Rodby RL2700E (Rodby Innovation, Vänge, Sweden), modified with rubber belts for use of regular pole tips. For the DP treadmill tests, all participants used the same pair of Swenor roller-skis (Swenor Fibreglass, Sarpsborg, Norway) with the NNN Rottefella binding system (New Nordic Norm; Rottefella, Klokkestua, Norway). For measurements of 1RM, maximal power, jumping variables and force and technique-specific variables in DP, the MuscleLab-system was used (Ergotest Innovation, Porsgrunn, Norway).

In Study II, all VO_2 -measurements were collected by the metabolic test system, Sensor Medics V_{max} Spectra (Sensor Medics, Yourba Linda, CA, USA) with a mixing chamber and VO_2 measurements every 20 s. Calibration of flow and gas analyzers were performed in accordance to the manufacturer's instructions. For the DP tests, a Rodby RL2500E treadmill (Rodby Innovation, Vänge, Sweden) was used, with the same pair of roller skis (Swenor Fibreglass, Sarpsborg, Norway) with either SNS (Salomon Nordic System; Salomon, Annecy, France) or NNN binding system.

3.2.2 Measurement procedures of RUN- $\text{VO}_{2\text{max}}$

RUN- $\text{VO}_{2\text{max}}$ was measured in all studies, by use of an incremental protocol. The initial incline was set to 6% and a starting speed between 8 and 12 $\text{km} \cdot \text{h}^{-1}$ in all studies. The protocols started with increments in incline of 1% every 30 s until 8% was reached (study I and III), or incline increments of 1 – 4% during the first two minutes of the test dependent on the subjects' fitness level (study II). From that point, only speed increased by 0.5 $\text{km} \cdot \text{h}^{-1}$ every 30 s until the end of the test. The test terminated at voluntary exhaustion. A possible flattening of the VO_2 -curve, $\text{HR} \geq 98\%$ of HR_{max} , respiratory exchange ratio (RER) ≥ 1.05 , $[\text{La}^-]_{\text{b}} > 8.0 \text{ mmol} \cdot \text{L}^{-1}$ and Borg scale ≥ 17 were used as criteria to evaluate if a true RUN- $\text{VO}_{2\text{max}}$ was reached. Since the Cortex MetaLyzer measured VO_2 every 10 s, the three highest consecutive measurements were used to determine RUN- $\text{VO}_{2\text{max}}$ (studies I and III). For the Sensor Medics system with measurements every 20 s, the two highest consecutive VO_2 measurements were used (Study II).

3.2.3 Measurement procedures of DP- $\text{VO}_{2\text{peak}}$, C_{DP} , LT and MAS

Three to six submaximal work periods were used to determine C_{DP} (study I, II and III) and LT (studies I and III). In study I and III, the work periods lasted for 4 minutes, while work periods of 5 minutes were used in study II. VO_2 and HR were registered for the last minute of each work period. In studies I and III, each work period was only separated by 1-minute rest for measuring $[\text{La}^-]_{\text{b}}$. The first work period started at an intensity assumed to be approximately 60% of expected DP- $\text{VO}_{2\text{peak}}$, with 4% inclination. For males, this

corresponded to 10 – 11.5 km · h⁻¹, and 6 – 8 km · h⁻¹ for females. For the consecutive work periods the intensity was increased by 1 – 3 km · h⁻¹. In study I and III, the test terminated when lactate values exceeded LT. LT was defined as the lowest measured lactate value + 2.3 mmol · L⁻¹. The VO₂ values from each work period was used to calculate C_{DP} at 70% of DP-VO_{2peak} (study II) or at LT intensity (study I and III).

After five minutes of rest, an all-out test for determination of DP-VO_{2peak} was performed. In study I, a standardized RAMP-protocol was used. The initial speed was set to 6 km · h⁻¹ and 11.5 km · h⁻¹ for females and males, respectively. The inclination of the treadmill was set to 6% throughout the whole test. Increments of 1 km · h⁻¹ every 30 s were made until 10 km · h⁻¹ and 18 km · h⁻¹ was reached for females and males, respectively. From that point, the speed was increased by 0.5 km · h⁻¹ until voluntary exhaustion. In study III, a modified version of the same RAMP-protocol was used. The inclination of 6% was the same, while the initial speed was set to 7 km · h⁻¹ for both genders. The speed was then increased by 1 km · h⁻¹ every 60 s. In both studies, the participants were encouraged to perform their best and received motivational feedback. The test terminated in both studies when the participants were no longer able to maintain their position on the treadmill, and reached a pre-defined mark 1 m behind their original position. Time to exhaustion was registered, and the two highest consecutive VO₂ measurements were used to determine DP-VO_{2peak}. All skiers were connected to a safety harness during testing to avoid accidents.

In study II, an incremental protocol was used to determine DP-VO_{2peak}. The treadmill was set to 4% inclination and 2 to 4 km · h⁻¹ below 80% of expected HR_{max}. The test started with 0.5% increments in inclination every 30 s until approximately 80% of HR_{max} was reached. From that point, only speed was increased by 0.5 km · h⁻¹ every 30 s until voluntary exhaustion. The mean of the two highest consecutive VO₂ measurements was used to determine DP-VO_{2peak}.

In all studies, MAS was defined as the velocity where the horizontal line representing DP-VO_{2peak} meets the extrapolated linear regression representing the sub maximal VO₂

measurements from the C_{DP} and LT test (study I), or calculated by $DP\text{-}VO_{2peak} / C_{DP}$ (study II and III). MAS was expressed as a velocity since the product of the denominations was

$$m \cdot \text{min}^{-1}, \left(\frac{\text{mL} \cdot \text{kg}^{-1} \cdot \text{min}^{-1}}{\text{mL} \cdot \text{kg}^{-1} \cdot \text{m}^{-1}} = \frac{1 \cdot \text{min}^{-1}}{1 \cdot \text{m}^{-1}} = \frac{\text{m}}{\text{min}} \right).$$

3.2.4 Measurement procedures of 1RM, maximal power and jump height

In study I and III, maximal strength and maximal power in leg press (study I) or half-squat (study III) and pull-down were tested. These tests were performed 60 minutes after the $DP\text{-}VO_{2peak}$ protocol. All strength tests used the same incremental protocol; 10 reps at 50% of estimated 1RM, 5 reps at 60%, 3 reps at 70% and 2 reps at 80%. The sub-maximal series were separated by at least 3 min of rest. A slow eccentric movement, followed by a complete stop of movement in the lowest (half-squat and leg press) or highest (pull-down) position for approximately 1 s, proceeded a maximal mobilization in the concentric phase in every repetition. During the sub-maximal series, power output was measured by the MuscleLab system, and the highest power output recorded was used as results for maximal power. Power output results were made possible by measurements of lifting time and distance of work by the MuscleLab-system. One repetition was given at the participants estimated 1RM, after the last sub-maximal series. From that point, the participants performed only 1 repetition per series, and the load increased by 2.5 – 10 kg from subsequent lifts until 1RM was reached. In study III, subsequent tests during the study period used the previously achieved 1RM results to estimate the submaximal %1RM preceding the new 1RM attempts.

In study III, participants performed measurements of jump height 30 min prior to the $RUN\text{-}VO_{2max}$ test. These measurements consisted of three maximal jump series of at least three consecutive attempts in the following order; squat jump (SJ), counter-movement jump (CMJ) and counter-movement jump with armswing (CMJas). The best attempt in every jump series was used as jump height result. A 3 min rest was given between each jump series. The starting position for the SJ test was a 90° angle in the knee-joint, and was controlled by the same test leader in every jump. Specifically for the SJ test, no counter-movements were allowed, while no restrictions were given for the

CMJ and CMJas tests. A force platform (Ergotest Innovation, Porsgrunn, Norway), calibrated in accordance to the manufacturer's instructions, was used for these measurements.

3.2.5 Measurement procedures of force and DP characteristics

In study I, force and DP characteristics were measured simultaneously to the VO_2 and HR measurements in the sub-maximal work periods for determination of C_{DP} and LT. The participants used modified poles with a force transducer integrated in the upper part of the pole. With a sampling rate of 200 Hz and a resolution of 14 bits, an external sender connected to the pole communicated with a 2.4 GHz band and the MuscleLab system. Force through the poles, CR and contact time (CT) were measured by the force transducer. The force measurements were taken from 03:00 to 03:20 minute of every sub-maximal work period, and results were used from the same relative intensity (LT intensity) in all skiers.

3.2.6 Measurement procedures of DP performance

In study I and III, all participants had 1 h rest after termination of the RUN- $\text{VO}_{2\text{max}}$ test before performing a TT_{DP} . TT_{DP} was performed in an outdoor paved roller-skiing course track with a height difference of 11 m. It consisted of six laps of 940 m, thus a total distance of 5.64 km. Only the DP technique was allowed throughout the test. Individual 30 s start intervals, with drafting not legal, and not more than 4 participants on the track at once ensured individual racing. The participants used their own roller skis and additional skiing equipment, and for study III, they used the same equipment for the subsequent tests. Stopwatches registered total time. Different temperature and track-conditions (e.g. wet or dry) can influence the rolling resistance for the roller skis. Therefore, we performed several rolling tests to be able to calculate a correction factor for temperature and humidity. This procedure was used in both studies. After every test day, test personnel performed a rolling test of 50 m in a tucked position. Time was registered by photocells and the MuscleLab-system (Ergotest Innovation, Porsgrunn,

Norway). The wheels were properly warmed-up in 5-10 minutes, and a mean of three 50 m runs were used to calculate the correction factor.

In study II, a 3-km TT_{DP} were performed on the roller skiing treadmill at least 40 min after the RUN-VO_{2max} test. The inclination was set to 4%, and the speed was increased to a level that the participants thought they could sustain for the whole test. Once this speed was reached, the test started. The speed could be increased or decreased by physical signs from the participants at any time. From 2000 m, information of the remaining distance was provided. No participant was given information on time spent at pre- or post-tests. The participants used the same roller-skis (Swenor Fibreglass, Sarpsborg, Norway), and they used the same skis at pre- and post-tests.

3.2.7 Procedures for genotyping of selected polymorphisms (Study III)

In study III, blood samples from the participants were drawn from venous blood at day 1 of baseline testing (April/May). The blood samples were taken when the participants first attended to the laboratory, before any physiological tests were performed. Samples were stored at -20°C in EDTA tubes until DNA extraction. For DNA extraction, we used the DNeasy Blood and Tissue Kit (Qiagen, MD, USA), and for genotyping of all polymorphisms, a Taqman® SNP Genotyping Assay was used. Polymorphisms that were genotyped were *ACTN3* R577X, *ACE* I/D, *PPARGC1A* rs8192678, *PPARG* rs1801282, *PPARA* rs4253778, *ACSL1* rs6552828 and *IL6* rs1474347. For the qPCR, we used the StepOnePlus™ Real-Time PCR System (Applied Biosystems®, CA, USA). The cycling conditions were as follows; 30 s at 60°C and an initial denaturation step for 10 min at 95°C, 40 cycles of 15 s of denaturation at 95°C and annealing for 1 min at 60°C, and termination after 30 s of a final post-read step at 60°C.

3.3 Training intervention and registration

3.3.1 Training registration

In study II and III, the participants reported all endurance training by the exact time in different intensity zones based on heart rate measures. All training was logged in online training diaries (Study III), or in Excel-files handed out to the participants (Study II). In both studies, training intensity was divided into three intensity zones. In study III, LIT was defined and reported as endurance training performed <82% of HR_{max} , MIT as endurance training performed between 82 – 87% of HR_{max} and HIT as endurance training performed >87% of HR_{max} . In study II, the intensity zones were almost identical even though LIT was defined as 60 – 84%, MIT was defined as 85 – 90% and HIT was defined as >90% of HR_{max} as previously used in Støren et al. (2008) and Sunde et al. (2010).

In study II, all training was registered both before and during the 6 weeks intervention period. In study III, the participants in this study were instructed to train according to their own training plans. All training was registered by training intensity, training modality (endurance, strength, speed, jump or other) and training activities (running, roller skiing, cross-country skiing or cycling) 3-months prior to the first testing session (PRE), and during the 6-months study period. The 6-months training period was divided into two separate periods, where the first period spanned from PRE to the follow-up test in July/August (POST1). The second period spanned from POST1 to the last testing session after the 6-months period in October/November (POST2).

In study III, strength training was registered as time from the first set performed in the session to the last set performed. Rest periods between exercises and sets were included. Warm-up and cool-down procedures prior to and post strength exercises were monitored as LIT. Jump training was registered in the same manner as strength training, while speed training was registered as the number of sprints multiplied by 1.5 min.

3.3.2 Training intervention

In study II, the intervention group performed three HIT sessions per week performed only in the DP technique. These sessions were conducted on a roller skiing treadmill (RL2500E, Rodby Innovation, Vänge, Sweden), and supervised by research personnel. The HIT sessions were organized as 4 x 4 min at 90 to 95% of HR_{peak} in DP, separated by 3 min at 70% of HR_{peak} in DP. In addition, each session included a 10 min warm-up and a 3 min cool down. The amount of HIT during the intervention did not differ from the amount of HIT prior to the intervention for this group. The control group was instructed to continue their normal training throughout the intervention period. Training volume and training intensity was controlled by the registration procedures previously described.

3.4 Statistical analyzes

Normality tests and Quantile-Quantile (QQ) plots were used to test for normality in main variables. In all studies, a normal distribution was evident, thus parametric statistics were used. Descriptive analysis were performed to display values as mean and standard deviation (SD), and inter-individual variability as coefficient of variance (CV). In all studies, all correlation analyzes (normal-, partial- and delta correlations) were analyzed by the Pearson correlation test, and displayed as correlation coefficient r . For practical evaluations of correlations, standard error of the estimate (SEE) was obtained from regression analysis (study I and II). To compare means between groups, paired sample T-tests (all studies), independent samples T-tests (all studies) and General Linear Model (GLM) with pairwise comparisons (study III) were used. In study III, a Univariate GLM with Tukey *Post Hoc*-tests was used for evaluation of potential changes in physiological variables for the whole group, within genders and within age groups.

In study III, we used a One-way ANOVA with *Post-Hoc* tests to determine potential associations between genotypes and physiological variables at baseline. Hardy-Weinberg equilibrium (HWE) was tested in all polymorphisms by the Pearson's Chi-square test. Different gender representation in the different genotypes groups, could

affect the observed associations between genotypes and physiological variables. To avoid these bias effects, all female values were multiplied with the average gender difference in the corresponding physiological variable. We were thus able to investigate associations without issues with different gender representation. Multivariate ANOVA analyzes were not performed for the genetic analyzes, due to the low number of participants in this study.

For this thesis, all initially recruited cross-country skiers with valid physiological and performance baseline results were included for descriptive ($n = 109$) and correlation analyzes ($n = 95$). Correlation analyzes across studies were only performed in physiological and performance tests with similar testing protocols (study I + III). All statistical analysis in the published studies and present thesis were performed by using the software program SPSS, version 25.0 (Statistical Package of Social Science, Chicago, USA), and $p < 0.05$ was taken as the level of significance in two-tailed tests.

4 Summary of papers

4.1 Paper I

Stronger is better: The impact of upper body strength in double poling performance.

Paper I investigated the relationships between DP performance and different aerobic endurance- and strength variables, and DP characteristics in young male and female cross-country skiers with similar training background. Twenty-eight (16 males and 12 females) 16-25 year-old competitive cross-country skiers were tested for a large set of physiological variables. The correlations were analyzed both dependent and independent of gender. The study demonstrated strong to moderate correlations between TT_{DP} and maximal upper-body strength, both independent ($r = -0.83, p < 0.01$) and dependent ($r = -0.50, p < 0.02$) of gender. Higher DP PF ($r = 0.78, p < 0.02$), lower CR ($r = -0.71, p < 0.01$) and shorter CT ($r = -0.48, p < 0.02$), were all related to higher maximal strength in upper-body muscles. In addition, MAS was strongly correlated to TT_{DP} , both independent ($r = -0.80, p < 0.01$) and dependent ($r = -0.48, p < 0.01$) of gender. In conclusion, DP performance was largely influenced by maximal upper-body strength and MAS, both in females and males. In addition, DP characteristics were affected by maximal strength in upper-body muscles. Thus, maximal strength training should be highly emphasized by competitive cross-country skiers.

4.2 Paper II

Improving utilization of maximal oxygen uptake and work economy in recreational cross-country skiers with high-intensity double-poling intervals.

Paper II investigated the effect of a specific DP HIT intervention in competitive skiers. The intervention was performed without increased amount of HIT, or total training volume. Seven recreational cross-country skiers (5 males and 2 females) performed a 6 weeks HIT intervention, while seven national-level cross-country skiers (7 males) in the control group trained as normal. In the intervention group, improvements were

observed in DP-VO_{2peak} (7.1%, $p < 0.01$), C_{DP} (9.2%, $p < 0.05$), MAS (16.5%, $p < 0.01$) and 3-km TT_{DP} (19.5%, $p < 0.01$), while RUN-VO_{2max} remained unchanged. Thus, %RUN-VO_{2max} in DP improved by 7.3% ($p < 0.05$). No improvements were demonstrated in the control group. The HIT intervention performed in this study demonstrated effective improvements of DP-specific aerobic variables, and thus DP performance, while overall aerobic capacity was maintained. Although the recreational skiers had a lower overall aerobic capacity than the national-level controls also post-intervention, the improved %RUN VO_{2max} and C_{DP} raised the performance level to the same level as the control group in the treadmill TT. For cross-country skiers aiming for higher DP capacity, or specialization in DP, these results should be of special interest.

4.3 Paper III

No change – no gain; the effect of age, sex, selected genes and training on physiological and performance adaptations in cross-country skiing.

Paper III investigated the training adaptations of well-trained cross-country skiers in numerous physiological- and performance variables both during and after 6 months of training. Potential differences between genders and between young and adult skiers in baseline values and training responses were investigated. In addition, the impact of genetic variants of selected polymorphisms on physiological baseline values was examined. In total, 29 skiers performed all testing (PRE, POST1 and POST2) and reported all training sufficiently.

The results revealed that no physiological or performance variables improved significantly during the 6-months study period. Total training volume and ski-specific training increased significantly ($p < 0.05$), while the training intensity distribution was held constant during the study period (May to October). Baseline differences were demonstrated between genders and between young and adult skiers in TT_{DP} ($p < 0.01$), DP-VO_{2peak} ($p < 0.01$), LT_v ($p < 0.01$) and maximal strength variables ($p < 0.01$). Additionally, RUN-VO_{2max} differed significantly between genders ($p < 0.01$). Although

different at baseline, training adaptations and training progression did not differ either between genders or between young and adult skiers. The selected polymorphisms did show minor effect on physiological baseline values. In conclusion, minor to no effects on training response in the recruited skiers. As the skiers performed very similar relative training programs, with no changes in training intensity distribution, training was shown to have no impact on the physiological adaptations during the six month`s period. At baseline, both gender and age affected physiological variables significantly, while the selected genetic variants did show minor effects.

5 Discussion across studies

5.1 Training characteristics in national-level cross-country skiers

The national-level skiers of study II and all skiers in study III were found to follow general training recommendations for cross-country skiers (Seiler and Kjerland, 2006; Sandbakk and Holmberg, 2017). In study III, mean total training volume was $11.7 \pm 2.8 \text{ h} \cdot \text{week}^{-1}$ from May to July, and $12.6 \pm 2.3 \text{ h} \cdot \text{week}^{-1}$ from August to October in all skiers. This was somewhat higher compared to the comparable national-level skiers (control group) in study II (8.7 ± 4.4 and $8.4 \pm 4.0 \text{ h} \cdot \text{week}^{-1}$ before and during the intervention period, respectively). Accordingly, 13 – 14 $\text{h} \cdot \text{week}^{-1}$ of mean total training volume have previously been reported in national-level skiers (Sandbakk et al., 2011; 2016; Solli et al., 2018). This suggests that the studied cohorts in the present studies were representative for national-level skiers in terms of total training volumes.

In study II and III, most of all endurance training was performed as LIT, i.e. below 82% of HR_{max} , in both recreational- (~75%) and national-level skiers (~83% in study II and ~90% in study III). Competitive cross-country skiers and other aerobic endurance athletes have often been recommended to train relatively high amounts of their endurance training as LIT (Seiler, 2010; Tønnessen et al., 2014; Sandbakk and Holmberg, 2017). Studies have repeatedly demonstrated 80 – 90% of all endurance training to be performed at low intensities, both for world-class and national-class endurance athletes (Billat et al., 2001; Seiler and Kjerland, 2006; Losnegard et al., 2013; Tønnessen et al., 2014; Sandbakk et al., 2016; Rasdal et al., 2018). High amounts of LIT have previously been suggested to play a crucial role in long-term performance development of endurance athletes (Esteve-Lanao et al., 2007; Seiler, 2010; Tønnessen et al., 2014).

In study III, MIT and HIT volumes were observed to be at relatively similar levels throughout the six months study period (5% from May to August, and 5- and 6% from August to October for MIT and HIT, respectively). Thus, neither a clear polarized or pyramidal intensity distribution were evident in these skiers. This is in close agreement

of the pre-season training reported in Losnegard et al. (2013). The national-level skiers in study II demonstrated a more polarized intensity distribution (~83/7/10% LIT, MIT and HIT, respectively). A polarized training intensity distribution (LIT > MIT < HIT) have been suggested to be an “optimal” intensity distribution for endurance athletes (Seiler and Kjerland, 2006; Seiler, 2010). Such training models have also been found to generate more effective physiological- and performance adaptations compared to other training models (Neal et al., 2013; Stöggl and Sperlich, 2014). An obvious explanation for this is not clear, although the characterized “light – hard” distribution of training seems to have a potential for higher amounts and quality of HIT. Comparisons of world-class and national-class cross-country skiers have demonstrated similar amounts of HIT, but more LIT and MIT compared to national-class skiers (Sandbakk et al., 2011; 2016). However, studies have not revealed conclusive results of superior training responses after training interventions increasing either the amount of LIT (Costill et al., 1991; Evertsen et al., 1999; Enoksen et al., 2011; Stöggl and Sperlich, 2014) or MIT (Evertsen et al., 1999; Esteve-Lanao et al., 2007; Stöggl and Sperlich, 2014).

Previous studies have reported ~10% of total training volume devoted to strength training in cross-country skiers (Losnegard et al., 2013; Tønnessen et al., 2014; Solli et al., 2017; 2018). In study II and III, comparable amounts of strength training were observed relative to total training volume and total minutes per week as previous studies. In addition, a 50/50% distribution of heavy strength training and general strength training have been previously reported in female skiers (Sandbakk et al., 2016; Solli et al., 2017). The same pattern was observed in study III, although not presented in the published article.

No major differences in training characteristics were evident between males and females or between young and adult skiers in study III. This confirms previous findings (Sandbakk et al., 2011; 2016; Losnegard et al., 2013; Solli et al., 2018). Young and adult skiers had the same total training volume in study III. In contrast, younger skiers tended

to have lower total training volumes than adult skiers in previous studies (Sandbakk et al., 2013; 2016; Losnegard et al., 2013; Solli et al., 2018).

5.2 Training adaptations to short- and long-term training programs

During six months (May to October) of training, we observed no significant improvements of DP performance, aerobic endurance variables or strength variables in study III. Since only minor changes in training were demonstrated by the included skiers in this study, this was merely as expected. These findings are comparable to the non-improvements demonstrated by the control group in study II. A summary of results in study I, II and III in performance- and physiological variables are presented in Table 2. In contrast, the only skiers that showed significant improvements were the recreational skiers of study II. Even though these skiers did not change total training volume or total HIT volume, they changed the content of HIT-sessions considerably. This may indicate that without considerable changes in training characteristics over shorter or longer training periods, it may be difficult to provoke further improvements of physiological- and performance variables in already well-trained cross-country skiers. No or minor improvements or a leveling-off in performance or physiological variables have been reported earlier over shorter (< 12 weeks, Støren et al., 2008; Sunde et al., 2010; Sandbakk et al., 2013a) or longer periods (> 12 weeks, Ingjer, 1992; Losnegard et al., 2013; Talsnes et al., 2020a), without considerable changes in training in well-trained to elite endurance athletes. However, some of these studies were performed on cross-country skiers on a higher performance level and with superior physiological capacities compared the skiers of the present studies. Thus, the potential for further improvements should be larger in the skiers of study II and III. In addition, it is both interesting and noteworthy that a group of junior skiers in particular does not show improvements in neither the measured physiological variables nor DP performance after ~300 h of training during six months of season preparation.

Table 2. Physiological and performance results in study I, II and III.

Study	I + II + III	II		III	
	Baseline (n=109)	Baseline + delta values Int. group (n=7)		Baseline + delta values (n=29)	
Variables	Mean ± SD	Mean ± SD	Δ (%)	Mean ± SD	Δ (%)
TT_{DP}					
5.64 km (s, n=95)	851.2 ± 116.6	-		875.1 ± 92.8	3.3
3-km (s, n=14)	771.9 ± 153.7	833.6 ± 175.1	19.5 ^{###††}		
Study I+II+III					
RUN-VO_{2max}					
mL · kg ⁻¹ · min ⁻¹	66.2 ± 8.5	65.8 ± 8.8	- 3.8	62.9 ± 8.0	1.9
L · min ⁻¹	4.76 ± 0.93	4.82 ± 0.99	- 3.3	4.38 ± 0.87	2.1
mL · kg ^{-0.67} · min ⁻¹	270.8 ± 39.0	279.8 ± 45.2	- 6.3	254.6 ± 36.1	2.0
DP-VO_{2peak}					
mL · kg ⁻¹ · min ⁻¹	56.5 ± 8.0	51.5 ± 8.1	6.0 ^{#†}	54.3 ± 7.3	2.2
L · min ⁻¹	4.07 ± 0.84	3.80 ± 0.86	7.1 ^{###†}	3.79 ± 0.79	2.6
mL · kg ^{-0.67} · min ⁻¹	231.4 ± 36.4	212.5 ± 36.3	6.4 ^{#†}	220 ± 33.0	2.4
%RUN-VO _{2max}	85.5 ± 7.0	78.7 ± 5.6	7.3 ^{#†}	86.5 ± 7.3	0.4
C_{DP}					
mL · kg ⁻¹ · m ⁻¹	0.187 ± 0.023	0.207 ± 0.016	- 9.2 [#]	0.198 ± 0.021	- 2.5
mL · kg ^{-0.67} · m ⁻¹	0.765 ± 0.096	0.857 ± 0.095	- 9.2 [#]	0.800 ± 0.078	- 2.5
MAS					
km · h ⁻¹	18.5 ± 4.0	15.1 ± 3.2	16.5 ^{###††}	16.7 ± 3.2	4.2
Study I+III					
LT (n=95)					
%DP-VO _{2peak}	81.4 ± 7.5	-	-	82.3 ± 6.5	- 0.7
km · h ⁻¹	15.1 ± 2.7	-	-	13.7 ± 2.5	3.6
1RM strength (kg)					
Leg press (n=44)	282.3 ± 48.0	-	-	-	
Half squat (n=48)	128.0 ± 28.6	-	-	120.8 ± 21.9	8.5
Pull-down (n=95)	90.8 ± 19.0	-	-	87.4 ± 16.5	2.7
Max power (w)					
Leg press (n=44)	607.7 ± 152.2	-	-	-	
Half squat (n=48)	843.4 ± 206.8	-	-	808.6 ± 207.6	2.9
Pull-down (n=95)	481.0 ± 133.3	-	-	473 ± 152.8	3.5

Values are mean ± standard deviation with delta values in percentage. The baseline data for study I+II+III includes all valid data from recruited participants across all studies pooled (n=109) tested by similar protocols in one, two or all studies. Int. group, intervention group. SD, standard deviation. Δ, delta change. TT_{DP}, time-trial in double poling. RUN-VO_{2max}, maximal oxygen uptake in running. DP-VO_{2peak}, peak oxygen uptake in double poling. %RUN-VO_{2max}, fractional utilization of RUN-VO_{2max} at peak double poling. C_{DP}, oxygen cost of double poling. MAS, maximal aerobic speed. LT, lactate threshold. 1RM, one repetition maximum. # *p* < 0.05 significantly different from pre values. ### *p* < 0.01 significantly different from pre values. † *p* < 0.05 significantly different from control group (study II). †† *p* < 0.01 significantly different from control group (study II).

In contrast to the not significantly changed performance capacity of the national-level skiers in study II and III, the recreational skiers (study II) demonstrated a 19.5% improvement in TT_{DP} after a short-term specific HIT-intervention. This improvement is

comparable to the performance enhancements observed in Nilsson et al. (2004) after 6 weeks of specific HIT in DP in a comparable group of skiers, although performed on a DP ergometer. The improvement in TT_{DP} in study II actually raised the performance level up to the national-level control group in that treadmill TT-test. This shows that considerable performance improvements can be made by a short-term training protocol targeting technique-specific capacities in such skiers. However, whether or not the national-level skiers would have demonstrated similar performance enhancements after a similar training protocol is unclear.

5.2.1 Training adaptations in aerobic endurance variables

In study II, the 19.5% TT_{DP} improvement in the recreational skiers was mainly contributed by the 16.5% improvement in MAS. This suggestion is strengthened by the significant correlation between ΔTT_{DP} and ΔMAS ($r = -0.61$, $p < 0.05$) in the same study. This is well in line with previous results where concurrent enhancements of MAS (i.e. concurrent improvements of VO_{2max} and C, or improvements in one variable and maintenance of the other) and endurance performance have been shown (Hoff et al., 2002; Østerås et al., 2002; Nilsson et al., 2004; Støren et al., 2008; Sunde et al., 2010; Losnegard et al., 2013; Sandbakk et al., 2013a). Strong significant relationships were also observed between MAS and TT_{DP} in both study I and III at baseline. Additionally, the present findings supports the suggested determining models of aerobic endurance performance presented in several published works (Pate and Kriska, 1984; Bassett and Howley, 2000; di Prampero, 2003; Joyner and Coyle, 2008). In study III, no significant adaptations were evident in MAS over the six months training period. In line with the results from the control group in study II, we did not observe a significant improvement in TT_{DP} either.

Adaptations in RUN- VO_{2max} and DP- VO_{2peak} .

For the recreational skiers in study II, the large improvement in MAS was due to a 6% improvement in DP- VO_{2peak} ($mL \cdot kg^{-1} \cdot min^{-1}$) and a 9.2% improvement of C_{DP} . The increase in DP- VO_{2peak} was observed despite no improvements of RUN- VO_{2max} in the

same skiers. Since these skiers did not increase the total training volume or HIT volume, this was as expected. During the intervention period, the recreational skiers substituted all regular HIT with DP-specific HIT. Thus, the specific training load provided during this HIT intervention may have generated DP-specific adaptations. In addition, the DP technique may activate insufficient amounts of muscle mass to tax the overall aerobic system maximally (Holmberg et al., 2007; Undebakke et al., 2019). It is suggested that the primary effect of HIT on improved VO_{2max} in whole-body exercises is an increased stroke volume (Helgerud et al., 2007), thus an improved capacity for O_2 -supply to the working muscles (Wagner, 1996; Bassett and Howley, 2000). The improved DP- VO_{2peak} combined with the maintenance of RUN- VO_{2max} observed in the recreational skiers may reflect a maintenance of stroke volume combined with local adaptations in muscular oxidative capacity or O_2 -demand (e.g. higher oxidative enzyme activity, mitochondrial adaptations) in DP specific muscles.

None of the national-level skiers in studies II and III were able to show significant improvements in RUN- VO_{2max} or DP- VO_{2peak} after their habitual endurance training protocols over shorter (6 weeks) or longer (6 months) training periods. This was merely as expected, since no (study II) or minor (study III) changes in total training volume or total HIT volume were observed. However, the training performed was sufficient to maintain both RUN- VO_{2max} and DP- VO_{2peak} . The already high-level of overall and specific aerobic capacity observed in the national-level skiers, may thus provide limited potential for further improvements in such capacities if considerable changes are not made in training. In contrast, already well-trained endurance athletes have shown positive adaptations in VO_{2max} or technique-specific VO_{2peak} in both short (e.g. Nilsson et al., 2004; Sandbakk et al., 2013a; Rønnestad et al., 2014; 2016; Stöggl and Sperlich, 2014) and long periods (e.g. Gaskill et al., 1999; Støren et al., 2012). However, these previous studies have demonstrated considerable changes in training content, by an increased amount of HIT. An increased focus on HIT volume has been criticized for being vulnerable to over-training symptoms (Seiler, 2010). However, increased HIT volume over one year have revealed large improvements in both performance and VO_{2max} in a

top-level cyclist (Støren et al., 2012) and cross-country skiers (Gaskill et al., 1999), without any overtraining symptoms reported. It is important to point out that the increased HIT volume was combined with decreased total training volume and/or LIT volume in these studies. Thus, it may be suggested that increased amount of HIT and/or reduced total training volume could induce effective adaptations over shorter or longer periods. In contrast, with no change in training, no to minor improvements in VO_{2max} have been observed in such athletes (Losnegard et al., 2013; Sandbakk et al., 2013a; Solli et al., 2017). The latter corresponds to the findings of study III.

The lack of further improvements and stagnation in VO_{2max} or VO_{2peak} in already well-trained athletes have previously been explained by athletes reaching their upper limit for oxidative capacity, often based on genetic potential (Losnegard et al., 2013). Even though this might be true, significant changes in overall training stimuli have demonstrated further enhancements of aerobic capacity in stagnated endurance athletes (Gaskill et al., 1999; Støren et al., 2012). Thus, we might speculate that even though well-trained to elite endurance athletes demonstrate no further improvements in VO_{2max} , this does not necessarily implicate that the upper-limit of aerobic development has been reached.

One novel finding of the present thesis, is the improved ratio between RUN- VO_{2max} and DP- VO_{2peak} observed in the intervention group of study II. To this author's knowledge, this is the first study to demonstrate and present such improvements. Comparing study II with the previous study on cycling by Støren et al (2012) there seems to be at least two possible ways to increase work-specific aerobic capacity. The first method, as demonstrated in study II, is to increase work-specific VO_{2peak} by specific HIT, and leave overall aerobic capacity unchanged. The second method is to increase overall aerobic capacity, by whole-body HIT (e.g. running), and thus leaving the ratio between VO_{2max} and work-specific VO_{2peak} unchanged (Støren et al., 2012).

Adaptations in C_{DP} and LT

The concurrent improvements in $DP\text{-}VO_{2\text{peak}}$ and C_{DP} in study II are in contrast to the results from the skiers in study III, which showed no significant improvements. Additionally, several studies report that athletes may become less energy efficient after training interventions at higher intensities (Vandbakk et al., 2017; Skovereng et al., 2018). However, cross-country skiers (Nilsson et al., 2004) and runners (Enoksen et al., 2011) have shown improved C after HIT, similar to the results observed in study II. Thus, one might speculate that development in C is more or less independent of intensity, since the present studies and previous studies show conflicting results after training at high intensities (>87% of HR_{max}).

The amount of technique-specific training has been suggested to be crucial for further improvement of C in endurance athletes (Scrimgeour et al., 1986). More training may generate several repetitions in race-specific technique (Haugnes et al., 2019). Scrimgeour et al. (1986) showed that the runners performing most kilometers during the week also had better work economy. Losnegard et al. (2013) and Talsnes et al. (2020a) observed improved C in freestyle skiing, which might be explained by increased amount of ski-specific training throughout the study period. Similar patterns of improved C_{DP} and more ski-specific LIT training was indicated in both study II and III. Haugnes et al. (2019) reported that elite junior cross-country skiers actually trained close to race-specific velocities during LIT and MIT at flat and downhill terrain. This suggests that skiers may be able to generate large volumes of training close to race-specific technique, which in turn might improve race-specific work economy. This could be one of the potential benefits of the large volumes of LIT observed in cross-country skiers in the present studies, and frequently reported previously (Seiler and Kjerland, 2006; Losnegard et al., 2013; Tønnessen et al., 2015; Sandbakk et al., 2016; Sandbakk and Holmberg, 2017; Solli et al., 2017; 2018).

The 9.2% improvements in C_{DP} in study II, was in line with previous studies utilizing HIT protocols over shorter periods (Helgerud et al., 2001; 2007; Nilsson et al., 2004;

McMillan et al., 2005). However, the common factor among these studies was that they investigated C in movement patterns not previously specialized by the participants, like e.g. straightforward running in soccer players (McMillan et al., 2005). Increased focus on HIT may not generate improvements in C in technique-experienced endurance athletes (Støren et al., 2012; Rønnestad et al., 2016). Comparatively, the skiers in study III and national-level control group in study II consisted of more experienced skiers, thus improvement potentials may have been less. However, most of them did not put their training focus solely on DP in HIT sessions, and thus a potential for improvements may still be apparent after specific HIT in such skiers.

As previously reported in several studies (Helgerud et al., 2001; 2007; Støren et al., 2008; 2012; Enoksen et al., 2011; Rønnestad et al., 2016; Sylta et al., 2016), $LT_{\%}$ did not change during the six months training period for the well-trained cross-country skiers in study III. In addition, LT_v did not change either. Interestingly, most previous studies (Helgerud et al., 2001; 2007; Enoksen et al., 2011; Stöggl and Sperlich, 2014; Rønnestad et al., 2016) have only demonstrated adaptations in LT_v with concurrent improvements in MAS, which was effectively enhanced by HIT (Helgerud et al., 2001; 2007; Støren et al., 2012; Sandbakk et al., 2013a). Thus, it may be suggested that the recreational skiers of study II also improved their LT_v after the DP-specific HIT intervention.

5.2.2 Training adaptations in strength variables

In study III, no significant muscular strength or power improvements were observed despite a significant increase in the amount of strength training. The strength training (~10% of total training volume) performed by these skiers was thus sufficient to maintain, but not improve the level of maximal strength and power observed in these skiers. These findings are in contrast to Talsnes et al. (2020a), which reported significant improvements in maximal strength in DP-specific muscle groups after six months of training in Chinese cross-country skiers. These results were observed after the same relative amount of strength training as seen in the skiers of study III. One possible explanation to the contradictory results between Talsnes et al. (2020a) and study III,

may be due to the amount of ski-specific strength training performed prior to the studies. While the majority of skiers in study III had performed ski-specific strength training over several years, the Chinese skiers in Talsnes et al. (2020a) were transferred from running, kayaking and rowing. Thus, the potential for strength improvements in ski-specific muscles may have been larger in the Chinese athletes.

In contrast to previous studies (Hoff et al., 2002; Støren et al., 2008; Sunde et al., 2010), no significant relationship between $\Delta 1RM$ and ΔC_{DP} was observed. One obvious explanation for this may be that adaptations in these two factors were lacking and significant correlations may thus be difficult to reveal. However, increased maximal strength may be an important underlying factor for improved technique-specific characteristics like e.g. cycle length and CR (Talsnes et al., 2020a), which in turn may affect skiing economy (Sandbakk et al., 2010; Sandbakk and Holmberg, 2017).

5.2.3 The effect of gender on physiological variables and training adaptations

Gender differences from pooled data from study I and III, including all available baseline data ($n = 95$) is presented in Table 3 and 4. Large gender differences (24.1%) were demonstrated in TT_{DP} . This is somewhat higher than previously reported in well-trained-to elite adult cross-country skiers (Sandbakk et al., 2014; Hegge et al., 2016). However, this was mainly due to the higher gender differences observed in younger skiers (25.9%), since the adult skiers demonstrated performance differences between genders comparable to previous studies investigating adult skiers (16.9%, Sandbakk et al., 2014; Hegge et al., 2016).

As expected, males and females differed significantly in both $RUN-VO_{2max}$ (19.2%) and $DP-VO_{2peak}$ (21.3%), previously explained by a higher cardiac output, higher blood volumes, higher aerobic enzyme activity and more muscle mass in males (Pate and Kriska, 1984; Evertsen et al., 1999; Sandbakk et al., 2018). Thus, combined with an 11.2% better C_{DP} in males, the superior MAS in males (~29%) contributed to the higher

performance level. In addition, the baseline differences between genders in the pooled data material and results from study I, supports the proposition made by Sandbakk et al. (2014) that gender differences increase with higher contribution from upper-body work. The highest gender differences across the present studies were observed in 1RM (30.6%) and maximal power output in pull-down (37.1%). In study I, we observed significant gender differences in DP characteristics (e.g. PF, rate of force development, sub-maximal CR and CT), favoring males.

Table 3. Physiological and performance differences between males and females (Study I and III pooled).

<i>Variables</i>	<i>Males (n = 65)</i>	<i>CV (%)</i>	<i>Females (n = 30)</i>	<i>CV (%)</i>	<i>Gender diff. (%)</i>
TT_{DP} (s)	791.0 ± 57.1	7.2	981.7 ± 105.3	10.7	24.1**
RUN-VO_{2max}					
mL · kg ⁻¹ · min ⁻¹	70.2 ± 5.7	8.1	56.3 ± 4.9	8.7	19.2**
L · min ⁻¹	5.18 ± 0.64	12.4	3.64 ± 0.43	11.8	29.7**
mL · kg ^{-0.67} · min ⁻¹	289.9 ± 24.7	8.5	222.7 ± 19.7	8.8	23.2**
DP-VO_{2peak}					
mL · kg ⁻¹ · min ⁻¹	60.6 ± 5.8	9.6	48.3 ± 4.7	9.7	21.3**
L · min ⁻¹	4.49 ± 0.62	13.8	3.11 ± 0.39	12.5	30.7**
mL · kg ^{-0.67} · min ⁻¹	250.8 ± 25.7	10.2	191.0 ± 18.8	9.8	23.8**
%RUN-VO _{2max}	86.6 ± 7.2	8.3	85.9 ± 5.6	6.5	0.7
C_{DP}					
mL · kg ⁻¹ · m ⁻¹	0.178 ± 0.018	10.1	0.198 ± 0.021	10.6	11.2**
mL · kg ^{-0.67} · m ⁻¹	0.737 ± 0.080	10.9	0.783 ± 0.083	10.6	6.2*
MAS					
km · h ⁻¹	20.6 ± 3.0	14.6	14.7 ± 1.8	12.2	28.6**
LT					
%	80.8 ± 7.9	9.8	82.7 ± 6.7	8.1	1.9
km · h ⁻¹	16.4 ± 1.9	11.6	12.2 ± 1.5	12.3	25.6**
Strength					
1RM pull-down (kg)	100.5 ± 13.4	13.3	69.7 ± 9.9	14.2	30.6**
Power pull-down (w)	544.8 ± 100.0	18.4	342.7 ± 81.4	23.8	37.1**

Values are mean ± standard deviation in physiological- and performance variables tested with similar protocols in study I and III. TT_{DP}, time-trial in double poling. RUN-VO_{2max}, maximal oxygen uptake in running. DP-VO_{2peak}, peak oxygen uptake in double poling. %RUN-VO_{2max}, fractional utilization of RUN-VO_{2max} at peak double poling. C_{DP}, oxygen cost of double poling. MAS, maximal aerobic speed. LT, lactate threshold. 1RM, one repetition maximum. * *p* < 0.05 significantly different from male values. ** *p* < 0.01 significantly different from male values.

This is likely contributed by the higher muscular strength in males, and is well in line with the longer cycle lengths observed by males in Sandbakk et al (2014). Factors like better rate of force development, lower CR and shorter CT has been suggested to positively affect work economy in both cross-country skiers (Hoff et al., 2002; Østerås et al., 2002),

runners (Støren et al., 2008) and cyclists (Sunde et al., 2010). In line with this, we observed that males had significantly better C_{DP} than females. This is in contrast to previous studies in cross-country skiers (Ainegren et al., 2013; Sandbakk et al., 2013b, Hegge et al., 2016). The findings are also in contrast to the findings of better running economy in females compared to males when bodyweight is raised to the power of 0.75 (Helgerud et al., 1994; 2010; Støa et al., 2020). Since propulsion in running is mostly provided by leg muscles, we suggest that the gender differences observed in C_{DP} could be affected by the predominant reliance on upper-body muscles in DP.

In study III, we did not reveal any major effect of gender on training adaptations throughout six months of training. Since both males and females had similar training patterns over the study period, this was as expected. Furthermore, the two females in the intervention group of study II did also show similar training adaptations after DP-specific HIT compared to their male counterparts. We did not measure hormonal differences or register menstrual cycles of the female participants, which probably could influence physical performance and training adaptations (Bruinvels et al., 2017). These findings are in correspondence to previous results of similar training adaptations in males and females after similar training protocols (Evertsen et al., 1999; 2001; Astorino et al., 2011; Seiler et al., 2013; Støren et al., 2017; Varley-Campbell et al., 2018). Thus, our findings suggest that well-trained male and female cross-country skiers do not differ substantially in training adaptations. However, more controlled trials of training adaptations in well trained to elite male and female cross-country skiers are still preferred.

5.2.4 The effect of age on physiological variables and training adaptations

Differences between young and adult skiers in the pooled data from study I and III, including all available baseline data ($n = 95$) are presented in Table 4. A 10% difference in TT_{DP} in favor of the oldest skiers was observed between age groups. However, this age-related difference was less apparent in males (4.2%) compared to females (12.2%).

The age differences in aerobic capacity are in correspondence to the results from Ainegren et al. (2013). This may be due to the differences in body weight between young and adult athletes indicating more muscle mass in older skiers (Saltin et al., 1995; Millet and Bentley, 2004; Ainegren et al., 2013) and the insufficient development of the cardiac system in younger athletes (Bjerring et al., 2019; 2020).

Table 4. Baseline physiological and performance differences between genders and age groups (Study I and III pooled).

Variables	Gender			Age		
	All F vs M (n=30vs65)	Young F vs M (n=21vs35)	Adult F vs M (n=9vs30)	All Y vs A (n=56vs39)	Male Y vs A (n=35vs30)	Females Y vs A (n=21vs9)
TT_{DP}	-24.1**	-25.9**	-16.9**	-10.0##	-4.2#	-12.2##
RUN-VO_{2max}						
mL · kg ⁻¹ · min ⁻¹	-19.2**	-21.2**	-15.1**	-6.7##	-2.3	-9.3##
L · min ⁻¹	-29.7**	-29.7**	-26.4**	-15.0##	-10.4##	-14.4##
mL · kg ^{-0.67} · min ⁻¹	-23.2**	-24.1**	-19.0**	-9.6##	-5.0#	-11.0##
DP-VO_{2peak}						
mL · kg ⁻¹ · min ⁻¹	-21.3**	-19.9**	-18.8**	-8.1##	-5.0#	-6.3
L · min ⁻¹	-30.7**	-28.6**	-29.7**	-16.5##	-12.7##	-11.5##
mL · kg ^{-0.67} · min ⁻¹	-23.8**	-23.0**	-22.5**	-10.9##	-7.8##	-8.1#
%RUN-VO _{2max}	-0.7	+1.3	-4.1	-1.1	-2.6	+2.8
C_{DP}						
mL · kg ⁻¹ · m ⁻¹	+11.2**	+12.4**	+9.4*	+0.5	-1.7	+1.0
mL · kg ^{-0.67} · m ⁻¹	+6.2*	+8.5*	+4.1	-2.5	-4.6	-0.6
MAS						
km · h ⁻¹	-28.6**	-29.3**	-25.3**	-8.0#	-2.8	-7.5
LT						
%	+1.9	+1.6	+4.1	-3.6#	-3.3	-5.8#
km · h ⁻¹	-25.6**	-25.9**	-22.1**	-12.3##	-8.1##	-12.7##
Strength						
1RM pull-down	-30.6**	-27.1**	-32.5**	-17.9##	-15.5##	-9.1
Power pull-down	-37.1**	-34.1**	-37.5**	-19.9##	-16.1##	-11.5

Values are percentage differences in physiological- and performance variables tested with similar protocols in study I and III. F, females. M, males. Y, young. A, adult. TT_{DP}, time-trial in double poling. RUN-VO_{2max}, maximal oxygen uptake in running. DP-VO_{2peak}, peak oxygen uptake in double poling. %RUN-VO_{2max}, fractional utilization of RUN-VO_{2max} at peak double poling. C_{DP}, oxygen cost of double poling. MAS, maximal aerobic speed. LT, lactate threshold. 1RM, one repetition maximum. * $p < 0.05$ female skiers significantly different from male skier values. ** $p < 0.01$ female skiers significantly different from male skier values. # $p < 0.05$ young skiers significantly different from adult skier values. ## $p < 0.01$ young skiers significantly different from adult skier values.

The largest differences among young and adult skiers were seen in maximal strength (17.9%) and power output (19.9%) in pull-down. However, larger age-differences were observed in males compared to females also in strength capacities. Thus, combined with differences in aerobic capacity (Table 4), differences in maximal strength and power

output may be of major importance for the differences observed in performance between young and adult skiers.

The accumulated amount of technique-specific training has previously been proposed to be important for development of superior C (Scrimgeour et al., 1986; Støren et al., 2011; Sandbakk and Holmberg, 2017). However, this is not in line with the present results or with Ainegren et al. (2013), finding similar C among young and adult skiers.

In study III, we did not observe any major differences between young and adult skiers in training adaptations. Since both young and adult skiers had only minor changes to their training during the six months, this was as expected. Interestingly, the younger skiers revealed no improvements in aerobic capacity throughout six months of training. In relative terms, this is in line with previous findings (Ingjer, 1992), although contradictory to intervention studies in pubertal athletes (Helgerud et al., 2001; Sperlich et al., 2011; Sandbakk et al., 2013a). One major difference in these studies is the substantial change in relative training intensity distribution and training content, while skiers in study III more or less maintained the relative intensity distribution. This may have facilitated the contradictory results as previously discussed.

Steiner et al. (2019) has also suggested a significant maturational improvement in aerobic capacity in 16 – 19 year old subjects, independent of endurance training volume. Combined with the observed adaptations to HIT training interventions (Helgerud et al., 2001; Sandbakk et al., 2013a), younger skiers may have a large potential for improvements in overall and specific aerobic capacity through adolescence. According to the results presented in Steiner et al. (2019), the younger skiers of study III should have increased their VO_{2max} by ~3% from maturational factors. However, the six months study period may have been too short to reveal such improvements. Nevertheless, the performed training was not sufficient to develop $RUN-VO_{2max}$ or $DP-VO_{2peak}$ in the present skiers. Thus, coaches of younger skiers should perhaps emphasize development of the aerobic system more systematically from young age, preferably by changing relative intensity distribution or training content over shorter or longer periods.

5.2.5 Summary of findings on long- and short-term training adaptations.

Taken together, no significant improvements in those of the cross-country skiers that were maintaining their training characteristics were observed, especially the relative distribution of intensity and training form (study II and III). The only group of skiers significantly altering their training (recreational skiers in study II) was the only group showing significant improvements. This is pointing at the importance of relative changes in training composition to facilitate further improvements of performance and physiological capacities. It is also pointing at the need for individualized training programs. However, direct comparison of training adaptations between recreational and national- to sub-elite level skiers should be performed with caution. The initial performance- and physiological level may influence the potential for further training adaptations in such cohorts.

Gender and age demonstrated significant effects on physiological- and performance values at baseline. Furthermore, the gender and age differences in performance may be highly contributed by the significant gender and age-differences in aerobic capacity and maximal strength in cross-country skiers. However, the impact of gender and age on training adaptations seemed to be negligible. Previously, most studies have investigated training adaptations in males, thus more direct comparisons between male and female well-trained to elite endurance athletes are still preferable in the future.

5.3 Aerobic endurance determinants of cross-country skiing performance

Baseline correlations between physiological variables, tested with similar protocols in study I and III, and TT_{DP} performance are presented in Table 5. Across all studies, strong correlations were observed between MAS and TT_{DP} performance. These correlations were maintained also when controlling for gender, and within gender (Table 5) and age groups. MAS generally explained 60 – 70% of the variance in TT_{DP} performance across the present studies. Accordingly, MAS has previously been shown to highly predict performance in runners (McLaughlin et al., 2010; Støren et al., 2011; Støa et al., 2020)

and cyclists (Støren et al., 2013). Støren et al. (2011; 2013) showed that MAS determined 86% of the variance in running and cycling performance, thus somewhat higher than observed in the present skiers. This may be explained by the more or less constant speed in those endurance sports. In contrast, cross-country skiing races are characterized by the constantly varying terrain and speed (Sandbakk and Holmberg, 2017; Gløersen et al., 2020). As discussed above, the close relationship between MAS and TT_{DP} was also strengthened by the significant delta correlations between these two factors in study II. This is also in line with previous studies demonstrating concurrent improvements in MAS, and endurance time performance (Nilsson et al., 2004; Støren et al., 2008; 2012; Sunde et al., 2010; Losnegard et al., 2013; Sandbakk et al., 2013a).

Across the present studies, it seemed that $DP-VO_{2peak}$ contributed most in the MAS equation ($MAS = DP-VO_{2peak} / C_{DP}$), and solely explained 66 – 88% of overall performance in the present studies. This is closely in line with the same relative importance of VO_{2max} in both running (Støren et al., 2011) and cycling (Støren et al., 2013). In addition, strong correlations were also observed between $RUN-VO_{2max}$ and DP performance. Thus, both specific and overall aerobic capacity proved to be highly important for performance level in the present skiers. The significant importance of aerobic capacity (i.e. $DP-VO_{2peak}$ or $RUN-VO_{2max}$) was maintained when controlling for gender or within genders (Table 5). However, it seems that males are more dependent on specific aerobic capacity (i.e. $DP-VO_{2peak}$, $r = -0.63$, $p < 0.01$), while females were more dependent on overall aerobic capacity (i.e. $RUN-VO_{2max}$, $r = -0.62$, $p < 0.01$). Since DP puts more stress on the upper-body muscles (Hegge et al., 2016), this might be influenced by the higher age-related differences in upper-body strength observed in males compared to females. Since young and adult females were less different in upper-body strength, overall aerobic capacity consequently may have become more important in female skiers.

The practical significance of MAS for predicting aerobic endurance performance become evident since the skiers with the highest aerobic capacity, not necessarily were the skiers with superior C, as observed in the present studies. Furthermore, in cross-country skiing

events less efficient skiers may compensate with higher aerobic capacity, while skiers with lower VO_{2max} may compensate with superior C (Skattebo et al., 2019). However, MAS balance these eventual differences, and thus generates a better picture of real performance capacity.

Table 5. Baseline correlations between physiological variables and performance (Study I and III pooled, n = 95).

Variables	<i>r</i>	SEE (%)	Within genders	
			Males (n=65)	Females (n=30)
RUN-VO_{2max}				
$mL \cdot kg^{-1} \cdot min^{-1}$	- 0.77** (- 0.44**)	8.8	- 0.36**	- 0.62**
$L \cdot min^{-1}$	- 0.75** (- 0.39**)	9.1	- 0.42**	- 0.47**
$mL \cdot kg^{-0.67} \cdot min^{-1}$	- 0.79** (- 0.47**)	8.4	- 0.44**	- 0.62**
DP-VO_{2peak}				
$mL \cdot kg^{-1} \cdot min^{-1}$	- 0.79** (- 0.53**)	8.4	- 0.60**	- 0.54**
$L \cdot min^{-1}$	- 0.77** (- 0.46**)	8.8	- 0.57**	- 0.43*
$mL \cdot kg^{-0.67} \cdot min^{-1}$	- 0.81** (- 0.54**)	8.1	- 0.63**	- 0.54**
%RUN- VO_{2max}	- 0.15 (- 0.18)	13.6	- 0.33**	0.02
C_{DP}				
$mL \cdot kg^{-1} \cdot m^{-1}$	0.43** (0.16)	12.5	0.33**	- 0.002
$mL \cdot kg^{-0.67} \cdot m^{-1}$	0.27** (0.12)	13.2	0.24	- 0.01
MAS				
$km \cdot h^{-1}$	- 0.76** (- 0.48**)	8.9	- 0.60**	- 0.45*
LT				
%	0.12 (0.05)	13.7	0.26*	- 0.24
$km \cdot h^{-1}$	- 0.80** (- 0.53**)	8.3	- 0.59**	- 0.54**
Strength				
1RM pull-down (kg)	- 0.76** (- 0.42**)	9.0	- 0.48**	- 0.42*
Power pull-down (w)	- 0.68** (- 0.31**)	10.1	- 0.32**	- 0.36

Values are correlation coefficient *r* with partial correlations corrected for gender in parenthesis for physiological- and performance variables tested with similar protocols in study I and III. SEE, standard error of the estimate. RUN- VO_{2max} , maximal oxygen uptake in running. DP- VO_{2peak} , peak oxygen uptake in double poling. %RUN- VO_{2max} , fractional utilization of RUN- VO_{2max} at peak double poling. C_{DP} , oxygen cost of double poling. MAS, maximal aerobic speed. LT, lactate threshold. 1RM, one repetition maximum.

**p* < 0.05 significant correlation.

***p* < 0.01 significant correlation.

LT has been proposed as an important factor determining aerobic endurance performance (Pate and Kriska, 1984; di Prampero, 2003). However, numerous studies report no relationship between LT% and performance in various aerobic endurance sports (Helgerud et al., 1994; Støren et al., 2008; 2011; 2012; McLaughlin et al., 2010; Sunde et al., 2010; Støa et al., 2020). In line with these findings, the pooled correlation analyzes from study I and III did not reveal significant relationships between LT% and cross-country skiing performance (*r* = 0.12). In contrast, LT_v showed strong correlations

to TT_{DP} ($r = 0.80$, $p < 0.01$), thus in line with previous findings (McLaughlin et al., 2010; Støren et al., 2013; 2014; Støa et al., 2020). Furthermore, an equation of MAS multiplied by $LT_{\%}$ precisely calculated LT_v in previous studies on cyclists (Støren et al., 2014) and runners (Støa et al., 2020). By use of the same equation at baseline for the pooled data from study I and III, we found an almost perfect correlation between calculated LT_v and measured LT_v (Figure 1). Consequently, MAS and $LT_{\%}$ could calculate baseline LT_v accurately within a range of $\sim 0.1 \text{ km} \cdot \text{h}^{-1}$.

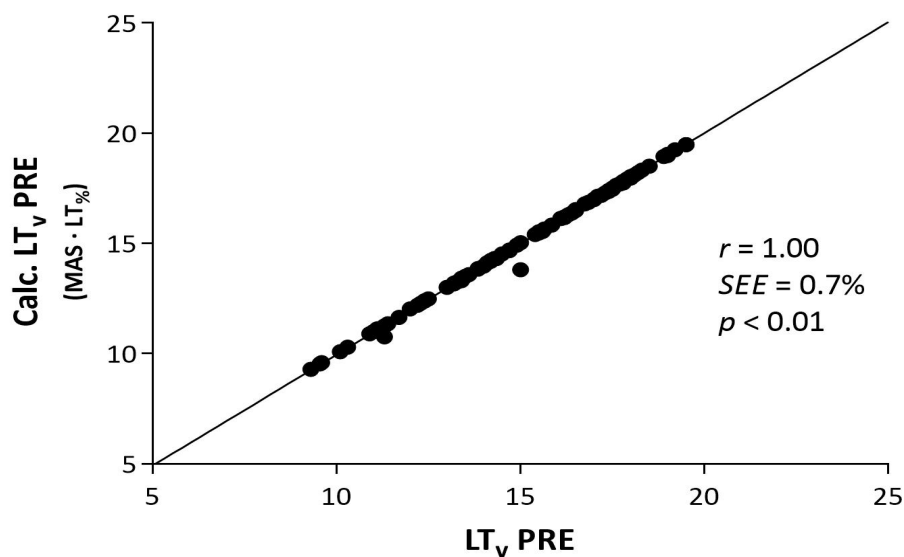


Figure 1. Baseline relationship between lactate measured velocity at lactate threshold (LT_v) and calculated LT_v by the equation: Maximal aerobic speed (MAS) multiplied by $LT_{\%}$ in double poling ($n = 95$). r , correlation coefficient. SEE , standard error of the estimate.

Due to the frequently reported lack of adaptations in $LT_{\%}$ in well-trained and elite endurance athletes (Helgerud et al., 2001; 2007; Støren et al., 2008; 2012; Enoksen et al., 2011; Rønnestad et al., 2016; Sylta et al., 2016), LT_v was calculated for the subsequent test (POST1) in study III. However, in this calculation the new MAS measured at POST1 was used, while $LT_{\%}$ were taken from PRE-tests. This calculation revealed an almost equally strong correlation between calculated LT_v and lactate measured LT_v (Figure 2), and could predict a new LT_v within a range of $0.7 \text{ km} \cdot \text{h}^{-1}$ ($SEE = 4.8\%$). Thus, the relative importance of LT_v for DP-performance in the present studies, is merely a result of the high correlation between MAS and TT_{DP} .

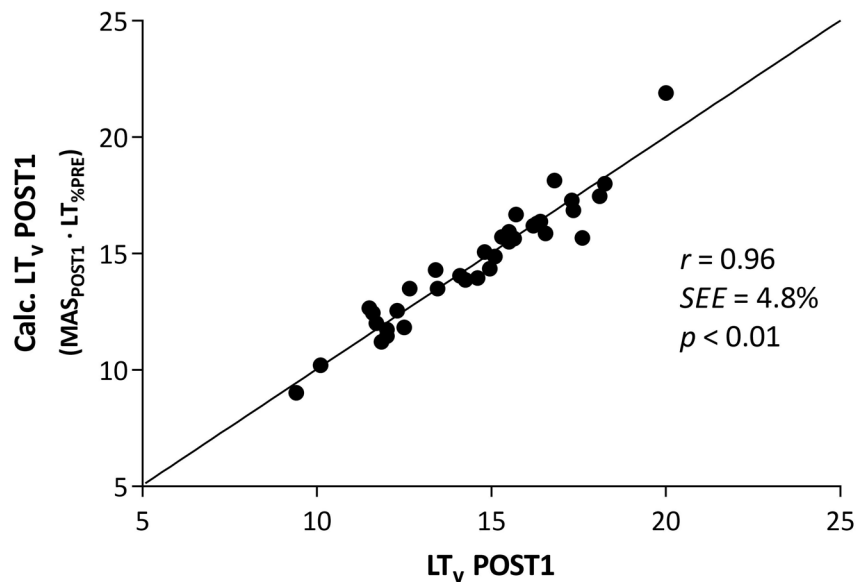


Figure 2. Relationship between lactate measured LT_v at POST1 and calculated LT_v by use of POST1 measurements of MAS multiplied by the PRE $LT\%$. r , correlation coefficient. SEE , standard error of the estimate.

Taken together, cross-country skiing competitions is predominantly determined by MAS, given by the high aerobic energy supply in such competitions (Gastin et al., 2001; Åstrand et al., 2003; Losnegard et al., 2019). The reliance of MAS was strongly evident in all skiers pooled, in males and females, and in young and adult skiers. Thus, a major aim of all cross-country skiers aiming for enhanced performance should be to target MAS (i.e. VO_{2max} and/or C) in their daily training.

5.4 Strength determinants of cross-country skiing performance

Significant correlations between 1RM pull-down and TT_{DP} performance were observed for all skiers in study I and III pooled ($n = 95$), controlled for gender and within genders and age groups. This is in line with a previous investigation of the importance of 1RM strength capacity for cross-country skiing performance (Losnegard et al., 2011). However, the present findings are novel since 1RM in upper-body muscles were related to distance cross-country skiing (~5.5 km). The previous study by Losnegard et al. (2011) found significant relationships between 1RM in upper-body muscles and sprint performance (1.3 km). In addition, the present findings of maximal strength reliance *per*

se in cross-country skiing is contradictory to previous findings in distance running (Støren et al., 2008) and cycling (Bishop et al., 1999; Sunde et al., 2010; Støren et al., 2013). One likely explanation for this is that propulsion is mainly generated through leg muscles in running and cycling, while upper-body muscles is predominant for propulsion in cross-country skiing due to poling actions (Holmberg et al., 2005). To support this, high maximal strength reliance have been observed for swimming performance (Keiner et al., 2015). However, this does not necessarily mean that the stronger skiers perform better in all cases. Stöggl et al. (2011) highlight the timing of force application as important for utilizing the overall strength potential.

In study I, several DP and force characteristics (e.g. PF, CT, CR) were significantly related to TT_{DP} performance. The importance of such factors may also be applicable for the skiers in study II and III, although force and DP characteristics were not measured in these studies. The relationship between technique-specific characteristics and cross-country skiing performance is in correspondence to previous findings in both DP and other skiing techniques (Bilodeau et al., 1995; Holmberg et al., 2005; Stöggl and Holmberg, 2011; 2016; Zoppirolli et al., 2015). The DP and force characteristics were significantly affected by maximal strength in study I. Stronger skiers had higher PF ($r = 0.78$), shorter CT ($r = 0.48$) and lower sub-maximal CR ($r = -0.53$). Thus, maximal strength serve as an important underlying factor for superior technique-specific characteristics and could partly explain the relationship between DP and force characteristics and TT_{DP} performance (Stöggl et al., 2011; Talsnes et al., 2020a). In addition, at a given workload, stronger skiers will generate force at lower percentages of 1RM, and thus probably delay fatigue (Østerås et al., 2002; Støren et al., 2008; Sunde et al., 2010). In other words, stronger skiers can theoretically generate higher propulsion forces at the same relative percentage of 1RM.

Across studies I and III, maximal power output in pull-down significantly affected TT_{DP} performance, and was found to basically follow the impact of 1RM. (Table 5). It was thus no surprise that the stronger skiers also produced the highest power outputs (Østerås

et al., 2002), supported by a high correlation between 1RM and maximal power in pulldown ($r = 0.89, p < 0.01$). Strong relationships between mean power output in upper-body muscles and cross-country skiing performance have previously been demonstrated (Rundell and Bacharach, 1995; Gaskill et al., 1998; Nesser et al., 2004; Alsobrook and Heil, 2009; Carlsson et al., 2013). However, the relationship between maximal power output in one repetition in pull down and DP performance has not been observed before. Since cross-country skiers have very limited time (~ 0.2 s) to generate forces through the poles (Stöggl and Müller, 2009), superior abilities to produce high power outputs over short amounts of time may partly explain this observed relationship. However, as for maximal strength, this is also dependent of the skier's technical abilities to time the force application at exactly the right moment in the technical cycle (Stöggl et al., 2011).

The relationship between 1RM in leg muscles and DP performance has been less investigated. However, force contribution from leg muscles have been documented for the DP technique (Holmberg et al., 2005; 2006; Zoppirolli et al., 2015). In study III, a moderate correlation between half-squat and DP performance ($r = -0.49, p < 0.01$) was demonstrated. However, this correlation disappeared when controlling for gender or doing analyzes within genders. Thus, males being both stronger and faster in the TT_{DP} compared to females may explain the significant correlation between 1RM half-squat and TT_{DP} . This may suggest that 1RM strength in leg muscles is less important for DP performance than upper-body strength. However, it does not exclude an eventual effect of leg strength on performance in cross-country skiing.

5.5 Impact of genetic variants

Study III, investigated associations between seven different SNPs to a large set of physiological variables. The different genetic variants were analyzed for differences in physiological baseline values. Since the skiers in this study did not follow identical training protocols, we were unable to distinguish potential effects of training and/or

single SNPs. Thus, no analyzes of trainability were performed for the present genetic data.

The frequently studied *ACTN3* R577X and *ACE* I/D polymorphisms displayed some associations to physiological variables in this cohort. For the *ACTN3*, a 9.1% higher DP- VO_{2peak} ($p < 0.05$) and a 7.0% higher RUN- VO_{2max} ($p = 0.09$) in X-allele carriers compared to RR-individuals was observed. This was in line with previous findings of XX-individuals displaying superior VO_{2max} values among soccer players (Pimenta et al., 2013). Homozygote cross-country skiers for the X-allele has also shown potential for better longitudinal improvements of VO_{2max} (Mägi et al., 2016). In addition, X-allele carriers and XX individuals have previously been associated with higher aerobic performance capacity (Yang et al., 2003; Eynon et al., 2012; Seto et al., 2019), most likely due to more efficient muscle metabolism associated with this allele (Vincent et al., 2007; MacArthur et al., 2008; Head et al., 2015; Seto et al., 2019). For the *ACE* gene, individuals homozygote for the I-allele (II) displayed ~10% higher relative RUN- VO_{2max} ($p < 0.05$), while DD-individuals had ~14.0% better C_{DP} compared to II-individuals ($p < 0.01$). Although the I-allele have previously been associated with higher aerobic characteristics, e.g. higher capillary and mitochondrial density (Vaughan et al., 2013; 2016; Valdivieso et al., 2017), these differences disappeared when bodyweight were scaled to the power of 0.67. Thus, these differences might be due to differences in bodyweight. Furthermore, DD-individuals did show ~23% higher 1RM in pull-down compared to II-individuals. This is in close agreement with previous investigations (Nazarov et al., 2001; Ma et al., 2013; Ahmetov et al., 2016). Thus, a potential difference in C_{DP} may be explained by the huge differences in upper-body strength across genotypes. Stronger skiers seems to inhibit lower CR and shorter CT (study I), longer cycle lengths (Sandbakk et al., 2014a) and work at a lower relative percentage of 1RM at a given workload (Aagaard et al., 2011; Blagrove et al., 2018). These factors may in turn improve C (Østerås et al., 2002; Støren et al., 2008; Talsnes et al., 2020a).

For the additional SNPs (*PPARGC1A*, *ACSL1*, *IL6*, *PPARA* and *PPARG*) only AA-individuals compared to individuals homozygote for the G-allele in the *ACSL1* polymorphism showed a 10.2% higher RUN-VO_{2max}. The rest showed no associations. However, an interesting case was observed for the *PPARGC1A* polymorphism. Generally, the Ser-allele of this polymorphism has been associated with deteriorated athletic ability and lower endurance status compared to the Gly-allele (Petr et al., 2018; Tharabenjasin et al., 2019). In study III, the skier that displayed the highest RUN-VO_{2max} of all participants, possessed the most unfavorable genotype for this gene, i.e. homozygote for the Ser-allele. Based on single genes, interpretation of physiological capacity should thus be performed with carefulness.

Goleva-Fjellet et al. (2020) genotyped 831 sedentary to moderately trained healthy individuals from Southeastern Norway. Thus, study III provided novel comparisons of competitive national-level cross-country skiers and a general population of the same geographical area in *ACE* I/D and *ACTN3* R577X polymorphisms. No statistically significant differences were detected, but some trends were observed. The skiers displayed slightly higher X-allele and XX-genotype frequencies in the *ACTN3* polymorphism, while they demonstrated slightly lower I-allele and II-genotype frequencies in the *ACE* polymorphism compared to data from Goleva-Fjellet et al. (2020). Both these alleles are previously associated with aerobic endurance capacity (Yang et al., 2003; Eynon et al., 2012; Vaughan et al., 2013; 2016). Taken together, no substantial differences were evident between these two populations. This may implicate that the genetic composition of these two single genes does not determine whether an individual should become a high national-level cross-country skier or not. Consequently, the effect of training and training composition may be of much higher importance for reaching high competitive levels in cross-country skiing than the single genes tested in this study.

Based on the findings of study III and comparisons to a general population, the impact of single genes seems to be minor for physiological capacity and athletic performance level. Findings in previous studies have also reported small effects when investigating

single genes (Jacques et al., 2019). Large sample sizes (e.g. 500 – 1 000 individuals) are often necessary to even demonstrate effects of selected SNPs, thus implicating small effects. Furthermore, when combining several promising performance-related polymorphisms for polygenetic analyzes, it has been shown to be difficult to distinguish elite endurance athletes from general populations (Ruiz et al., 2009). However, this does not mean that the genetic contribution is negligible for athletic performance. Earlier hereditary studies have demonstrated that at least 50% of athletic capacity and trainability is determined by genetic components (Bouchard et al., 1999; Zhai et al., 2005; De Moor et al., 2007; Costa et al., 2012; Schutte et al., 2016). These studies have investigated the result of the complete hereditary impact, where the contribution of every single gene is representing a tiny fraction of that picture.

5.6 Limitations

For associations between single-genes and physiological variables, the sample size of study III is underpowered. Low sample sizes may generate higher possibilities for type I statistical errors, in candidate gene studies like study III (Pitsiladis et al., 2013). Thus, interpreting the genetic results of the present studies have to be performed with caution. On the other hand, one of the main strengths of the genetic analyzes was that the skiers were homogenous in terms of geographical origin (Marchini et al., 2004).

The sample sizes of all studies were however sufficient for a physiological cross-sectional (study I), and for intervention studies (study II and III). For study III, the sample size should be considered large for analyzes of training characteristics and subsequent physiological adaptations in well-trained cross-country skiers over such a long period.

A limitation in study II may be the unequal gender representation. Only two females were initially recruited for the intervention group and control group. Since the two females in the control group were excluded due to sickness or injuries, the two groups were not similar in gender representation. However, studies, including the present thesis, have not been able to demonstrate significant differences in training adaptations

for males and females (Evertsen et al., 1999; 2001; Astorino et al., 2011; Støren et al., 2017). To support this, the statistical results of the main variables in study II were almost unchanged and still significant when analyzing the results with or without the two females.

The impact of learning effects in the performance tests in all three studies cannot be completely ruled out. For the TT_{DP} test used in study I and III, the skiers were not able to perform any familiarization test due to long traveling distances. They were only given the opportunity to inspect the track during warm-up, thus an eventual impact of learning may have influenced the results of subsequent tests (study III). Additionally, although TT_{DP} performance was corrected for weather- and track conditions, it cannot be completely rule out that such conditions not covered by this correction factor could have influenced the results as well. Since most skiers in study II were settled in the same area, they were given more time for familiarization to the roller-skiing treadmill compared to the skiers in study I and III.

5.7 Practical implications

The practical implications based on the findings of this thesis is that MAS and maximal strength in upper-body muscles were the most determining factors for distance cross-country skiing, independent of both age, gender and selected genes. Thus, coaches and cross-country skiers should prioritize the most effective training methods for developing these two factors to reach higher performance levels in their daily training. Increased focus on HIT have shown to be an effective short-term and long-term training method for concurrent improvements in MAS and performance, mainly through development of overall or technique-specific aerobic capacity (Gaskill et al., 1999; Nilsson et al., 2004; Støren et al., 2012; Sandbakk et al., 2013a; Rønnestad et al., 2016). In addition, race technique specific HIT and LIT/MIT (Haugnes et al., 2019) may affect C in specific sub-techniques. Concurrent to the endurance training, maximal strength training with maximal mobilization, high loads with few repetitions (2 – 5), 3 – 4 sets and relatively long pauses between sets (≥ 3 min) have proved most effective for maximal strength

improvements as well as the effects on C. (Østerås et al., 2002; Støren et al., 2008; Sunde et al., 2010; Losnegard et al., 2011)

In addition, increasing the total training volume with most emphasis on low-intensity training, does not necessarily implicate superior adaptations over shorter or longer training periods. Considerable changes in training intensity or modality may be necessary over shorter or longer periods to generate further improvements of performance and physiological variables in already well-trained cross-country skiers. This may be of special interest for skiers experiencing stagnation. Training protocols with specific HIT focus and with maintained total training volume proved as an effective strategy over short periods in the present thesis. In addition, increased HIT focus with decreased LIT and/or total training volume have proved effective over longer periods (Gaskill et al., 1999; Støren et al., 2012). Additionally, this may be applicable for all skiers more or less independent of gender, age or genetic composition in known performance-related genes.

The findings of the present thesis may thus serve as an initial platform for future investigations to elaborate these findings. Thus, future investigations should emphasize experimental studies investigating the effects of considerable changes in training characteristics targeting main determining variables for cross-country skiing performance. This should be executed over shorter periods and over several years on already well-trained male and female, young and adult cross-country skiers. In addition, the impact of genetic variation on athletic performance and trainability needs further elucidation. Thus, studying polygenetic profiles or complete human genomes, including epigenetics and transcriptome may be beneficial scientific approaches. To obtain sufficient levels of statistical power in such investigations, this should probably be organized as multi-center studies.

6 Conclusions

The physiological factors most determining for cross-country skiing performance were MAS and maximal muscular strength in upper-body muscles. This applied independent of both age, gender and selected genes. Gender and age displayed large effects on baseline values for both physiological- and performance variables, although no effect were apparent for training adaptations. In addition, minor effects of known performance-related genes were observed in physiological baseline values. However, national-level cross-country skiers did not differ significantly in frequently studied performance-related genes to a general population of the same geographical area (i.e. Southeastern Norway).

Throughout six months of training with only minor changes in training characteristics, no physiological- and performance adaptations were observed in national-level skiers. Over shorter training periods, considerable and specific changes in HIT content proved effectively to improve DP-specific aerobic capacities.

Taken together, this point to a universal need of significant changes in training characteristics to facilitate further improvements in well-trained cross-country skiers. Training should also mainly prioritize effective training strategies for improving MAS and 1RM in upper-body muscles across all skiers (i.e. males, females, young and adults) to reach higher performance levels.

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Article 1

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Stronger Is Better: The Impact of Upper Body Strength in Double Poling Performance

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The purpose of the present study was to compare time results from a roller-skiing double poling (DP) time trial with different physiological variables, muscular strength variables, and DP characteristics in both male and female young competitive skiers with the same relative training background. In order to do this, 28 (16 women and 12 men) well-trained 16–25-year-old cross-country skiers from three Norwegian high schools for skiers, as well as local high performance competitive skiers from the South-East of Norway were recruited to participate in the study. All participants were tested for; maximal oxygen uptake in running, Peak oxygen uptake in DP, lactate threshold in DP, DP economy, time to voluntary exhaustion in DP, force analyses in DP, one repetition maximum and power output in pulldown, and leg press and a time trial during DP roller skiing. The results expressed strong correlations between roller skiing time trial performance and maximal strength in pull-down, both independent ($r_{xy} = -0.83, p < 0.01$) and dependent ($r_{xy-z} = -0.50, p < 0.02$) of sex. Higher maximal upper body strength was related to higher DP peak forces (PF) ($r_{xy} = 0.78, p < 0.02$), lower DP frequency ($r_{xy} = -0.71, p < 0.01$), and shorter DP contact time (CT) ($r_{xy} = -0.48, p < 0.02$). The practical implications of the present study is to acknowledge maximal upper body strength as a performance determining factor in DP. This point at the importance of including maximal strength training in cross-country skiers training programs.

Keywords: cross-country skiing performance, double poling time trial, upper body strength characteristics, maximal strength, peak force, poling contact time, time performance in cross-country skiing, poling frequency

INTRODUCTION

Cross-country skiing is an aerobic endurance sport, and the contribution from the aerobic system is approximately 70 – 95% (Vesterinen et al., 2009; Støren et al., 2014; Hébert-Losier et al., 2017). Aerobic endurance sports demands a high maximal oxygen consumption (VO_{2max}), and a good work economy, which both contributes to a high velocity at lactate threshold (LT)

Abbreviations: C_{DP} , oxygen cost in double poling; CT, contact time; DP, double poling; HR, heart rate; HR_{max} , maximal heart rate; LT, lactate threshold; MAS, maximal aerobic speed; PF, peak force; RER, respiratory exchange ratio; RER_{peak} , peak respiratory exchange ratio; TT, double poling time trial; VO_2 , oxygen uptake; VO_{2max} , maximal oxygen uptake in running; VO_{2peak} DP, peak oxygen uptake in double poling.

(Costill et al., 1973; Pate and Kriska, 1984; di Prampero, 2003; Sunde et al., 2010; Støren et al., 2014). Cross-country skiing competitions range from intensive sprint with a duration of 2–4 min to distance races of 50 km with a duration of 2–3 h. Five out of six cross-country competitions in the World Cup and the Olympic Games are now mass starts (Skattebo et al., 2016). Mass starts combined with better equipment and track preparation, has led to higher skiing speed in recent years. Higher skiing speed require higher rate of force development and muscular power output (Sandbakk et al., 2014).

Previous studies have focused on determining factors for performance in cross-country skiing and have found strong correlations between $\text{VO}_{2\text{max}}$ and performance (Bergh, 1987; Ingjer, 1991; Mahood et al., 2001; Larsson et al., 2002; Alsobrook and Heil, 2009; Ainegren et al., 2013; Sandbakk and Holmberg, 2014). Pellegrini et al. (2018) have shown that high-level skiers have better work economy than regional level skiers. Even though an important factor for work economy is the skiers technical skills, several studies have found improvements in performance corresponding to a better work economy after maximal strength training (Østerås et al., 2002; Mikkola et al., 2007; Losnegard et al., 2011). This is in accordance with other studies performed in other endurance sports, such as cycling (Sunde et al., 2010), running (Paavolainen et al., 1999; Støren et al., 2008; Balsalobre-Fernández et al., 2016), and swimming (Aspenes et al., 2009).

Some previous studies have shown a relationship between maximal strength *per se* and aerobic endurance performance. In Støren et al. (2013) in cycling, no correlation between maximal strength and performance was found. However, some other studies have found correlation between specifically upper body power output and performance in both long distance and sprint cross-country competitions (Rundell, 1995; Rundell and Bacharach, 1995; Gaskill et al., 1999; Nesser et al., 2004; Alsobrook and Heil, 2009; Stöggl et al., 2011; Carlsson et al., 2016). Also, Stöggl et al. (2010) have found lean trunk mass to correlate to maximal DP speed.

Double poling (DP) is a high-speed cross-country skiing technique. Total racetime now contains a much larger percentage of DP than only a few years ago (Holmberg et al., 2005; Losnegard et al., 2013). DP is also used in more uphill terrain than before. Hoffman and Clifford (1992) found that DP was a more economical technique than kick DP in flat terrain. DP is thus considered a strong performance-determining technique in classic cross-country skiing.

In previous studies on DP in cross-country skiers, some DP characteristics that are linked to maximal muscular strength have been identified (Bilodeau et al., 1995; Holmberg et al., 2005; Stöggl et al., 2007, 2011; Stöggl and Holmberg, 2011, 2016; Danielsen et al., 2015). Although Stöggl et al. (2011) found correlations between power output in bench press and bench pull, and maximal speed in DP, it was first and foremost the timing and instant of force application that accounted for the inter-individual differences. Several studies have found that the fastest skiers produced the highest peak pole forces (Bilodeau et al., 1995; Holmberg et al., 2005; Stöggl and Holmberg, 2011, 2016). Also, Bilodeau et al. (1995) found the fastest skiers to reach their PF in the shortest time, and hypothesized that the

differences in maximal skiing velocity were due to differences in muscular strength. Zoppirolli et al. (2015) found high-level skiers to have a lower DP frequency at the same load as regional-level skiers. Holmberg et al. (2005) found faster skiers to have a shorter propulsion phase and a longer recovery phase when DP at high velocity. Holmberg et al. (2005) also found that the fastest skiers had higher peak pole forces. In contrast to Hoff et al. (1999) and Holmberg et al. (2005) did not find any positive correlation between time to PF and performance in DP. Both Stöggl et al. (2007, 2011), Stöggl and Holmberg (2011), and Jonsson et al. (2019) found that faster skiers produced longer DP cycle lengths (meters) at equal DP frequency, than slower skiers. It may be hypothesized that this was aligned to greater muscular power output.

Male and female athletes at the same relative performance level show sex differences in both $\text{VO}_{2\text{max}}$ (Sandbakk et al., 2014; Stöggl et al., 2019), and maximal muscular strength (Sandbakk et al., 2018). Also greater sex differences have been found in exercises where the upper body is involved (Sandbakk et al., 2014). It is thus crucial to evaluate the relative importance of aerobic endurance variables, muscular strength variables, and DP characteristics on DP performance both independent and dependent of sex. A cohort of competitive cross-country skiers from both sexes with the same relative training background and age, but with heterogeneity in performance level would thus be preferable.

The purpose of the present study was therefore to compare roller-skiing time trial (TT) performance with different physiological variables, muscular strength variables, and DP characteristics in both male and female young competitive skiers with the same relative training background. The hypothesis was that maximal upper body strength would significantly impact DP characteristics and performance.

MATERIALS AND METHODS

Approach to the Problem

The main objective of this cross-sectional study was to evaluate correlations between performance in DP cross-country roller skiing and different physiological variables, muscular strength variables, and DP characteristics in both male and female young competitive skiers with the same training background. Comparisons between male and female skiers as well as correlation analyses both independent of and corrected for sex, were thus performed.

Subjects

A total of 28 (16 women and 12 men) well-trained 16–25-year-old cross-country skiers from three Norwegian high schools for skiers, as well as local high performance competitive skiers from the South-East of Norway participated in this study (Table 1). The study was approved by the institutional research board at the University of South-Eastern Norway (former University College of South-East Norway), and conducted in accordance with the Helsinki declaration. All skiers gave their written consent to participate, after having received information about the study.

TABLE 1 | Characteristics of skiers ($N = 28$).

	All ($N = 28$)		Females ($N = 12$)		Males ($N = 16$)	
	Mean \pm SD	CV (%)	Mean \pm SD	CV (%)	Mean \pm SD	CV (%)
BW (kg)	70.1 \pm 7.5	10.7	65.9 \pm 5.2	7.9	73.2 \pm 7.5**	10.2
Age (years)	18.5 \pm 1.3	7.0	18.3 \pm 1.2	6.6	18.6 \pm 1.4	7.5
VO _{2max} running						
ML·kg ⁻¹ ·min ⁻¹	64.0 \pm 10.4	16.3	53.8 \pm 4.4	8.2	72.2 \pm 5.1**	7.1

Values are mean \pm standard deviation (SD) and coefficient of variance (CV). BW, body weight; Kg, kilograms; VO_{2max}, maximal oxygen uptake; ML·kg⁻¹·min⁻¹, milliliters per kilogram BW per minute. ** $p < 0.01$ different from females.

Parents and coaches to participants under 18 years, also gave their written consent.

Test Procedures

In order to evaluate physiological and technical variables related to performance in DP, the following tests were carried out; VO_{2max} running, VO_{2peak} DP, LT in DP, DP economy (C_{DP}), time to voluntary exhaustion in DP in the ramp VO_{2peak} test, force analyses in DP, one repetition maximum (1RM) and power output in pull-down and leg press, and performance during a DP roller skiing time trial (TT).

The skiers were tested over two consecutive days. Day one consisted of an incremental VO_{2max} test in running and a DPTT test with 1-h rest in between. The subjects started at an intensity of 8–12 km·h⁻¹ and a 6% inclination. Every 30 s the inclination increased by 1% until 8% inclination was reached. Then the speed was increased by 0.5 km·h⁻¹ every 30 s. The test terminated at voluntary fatigue, and additionally heart rate (HR) \geq 98% of HR_{max}, respiratory exchange ratio (RER) \geq 1.05, as well as a plateau of the VO₂ curve was used to evaluate if VO_{2max} was obtained (Åstrand et al., 2003). All VO₂ measurements were made by the metabolic test system, Metalyzer II Cortex (Biophysic GmbH, Leipzig, Germany), with a mixing chamber. The treadmill used for running was a Woodway PPS 55 sport (Waukesha, WI, United States). All HR measurements were made by Polar s610 HR monitors (Kempele, Finland).

The double poling time trial test took place in a paved roller ski course track of 940 m with a height difference of 11 m. The subjects completed six laps, totaling 5640 m. This test was organized as an interval start with 30 s between each subject. The subjects were told to use the DP technique throughout the whole test, and drafting was not allowed (using cycling TT rules). In this test, differences in temperature and humidity in between test days, may lead to differences in rolling resistance. Therefore, we performed a calibration test to calculate a correction factor. One of the test leaders conducted a 50 m roller-timing test with the same roller skis immediately after the time trial test every test day. The test was conducted in a tucked position, with the same test person every day, in a gentle slope, approximately 10%, and with time measured by use of photocell equipment (Musclelab system, Ergotest Innovation, Porsgrunn, Norway). Ten runs were performed for each test, ensuring proper warm up of the wheels, and the average time of the last three runs was used to calculate the correction factor.

The second day of testing consisted of a DP test on a cross-country skiing treadmill, (Rodby RL 2700E, Rodby Innovation, Vänge, Sweden) and two maximal strength tests with 1-h rest in between. The subjects were acquainted to the cross-country skiing treadmill by use of a 30-min workout ahead of the pretest. The first 15–20 min consisted of 3–5 four-minute submaximal work periods. Whole blood lactate concentration was measured with a Lactate Scout+ (SensLab GmbH, Leipzig, ray Inc., Kyoto, Japan). Then C_{DP}, force measurements and DP characteristics were evaluated. By use of a force transducer, measurements of force and DP characteristics, were possible. The force transducers were integrated in the poles and is a part of the Musclelab system (Ergotest Innovation, Porsgrunn, Norway). The dimension of the force transducer was 4 cm of length and 2 cm in diameter, placed 8 cm below the grip bar, as an integrated part of the pole. Outside the force transducer, a sender with the dimension 4 cm \times 4.6 cm \times 1 cm was placed. The total weight of the system added 100 g to the pole. The sender communicated by a Nordic semiconductor Gazell stack with a 2.4 GHz band (Nordic Semiconductor, Norway) with the Musclelab system, with a sampling rate of 200 Hz and a resolution of 14 bits. Over all accuracy was 0.9% of full scale. Test retest reliability was checked at our lab, exhibiting a standard error mean of <1%.

The system was calibrated by use of two different external weight loads on top of the pole placed in a vertical position, while the other end of the pole was placed on the force platform for a secondary control. The reading from the sensor of the pole unloaded was recorded and then the reading from the sensor of the pole with external load was recorded. Force was then computed using the formula $F = (\text{signal} - \text{offset}) \text{ gain}$. The subjects started at a work intensity assumed to represent 50–70% of their VO_{2peak} in DP, corresponding to 4% inclination and 11.5 km·h⁻¹ for men and 6 or 7 km·h⁻¹ for women. Every 4 min after the first step, the speed was increased by 1–3 km·h⁻¹, until the protocol terminated at a lactate level above the subjects' LT. LT was defined as the warm up lactate value (i.e., the lowest measured lactate value) + 2.3 mmol L⁻¹. LT was expressed as the VO₂ in% of VO_{2peak} DP (%VO_{2peak}), whereas the velocity at LT was expressed as km·h⁻¹. This is in accordance with the protocol proposed by Helgerud et al. (1990), using warm up lactate value + 1.5 mmol L⁻¹ with the YSI apparatus. As the constant difference in [La⁻]_b between whole blood and hemolyzed blood is 40%, the 1.5 mmol L⁻¹ measured by YSI equals 2.3 mmol L⁻¹ measured by Lactate Scout+. The

advantage of using individual warm-up values compared with e.g., a fixed 4 mmol L⁻¹, is that this is less vulnerable to day-to-day variations in subjects [La-]_b, as previously discussed in Støren et al. (2014). The force measurements as well as the oxygen consumption measurements for calculating C_{DP}, were made between minute 3:00 and 03:20 in each work period. The force transducer measured force through the poles, DP frequency, and CT. C_{DP} was calculated as oxygen consumption at LT. All DP characteristic measurements were performed at the same relative intensity, i.e., at LT velocity.

Maximal aerobic speed (MAS) was calculated based on the oxygen consumptions measured in the submaximal work periods and the VO_{2peak} in DP, and was defined as the velocity where the horizontal line representing VO_{2peak} meets the extrapolated linear regression representing the sub maximal VO₂ measured in the LT assessment. The same method was used for cycling in Sunde et al. (2010) and in running in Helgerud et al. (2010), with $r > 0.99$ for the regression lines. MAS equals thus VO_{2peak}DP/C_{DP}. Since $\frac{\text{ml}\cdot\text{kg}^{-1}\cdot\text{min}^{-1}}{\text{ml}\cdot\text{kg}^{-1}\cdot\text{m}^{-1}} = \frac{1\cdot\text{min}^{-1}}{1\cdot\text{m}^{-1}} = \frac{\text{m}}{\text{min}}$, VO_{2peak}DP/C_{DP} is expressed as a velocity (m min⁻¹).

One minute after the last submaximal work period, the subjects carried out an all-out test where time to exhaustion and VO_{2peak} in DP were measured. This test was implemented as an incremental ramp protocol. The output speed was set to 11.5 and 6 km·h⁻¹ for men and women, respectively. The inclination was set to 6%, and remained constant through the whole test. The speed was increased by 1 km·h⁻¹ every 30 s until 18 km·h⁻¹ (men) and 10 km·h⁻¹ (women) were reached. The speed was then increased by 0.5 km·h⁻¹ every 30 s until voluntary exhaustion. The subjects were encouraged to perform their best. Voluntary exhaustion was defined as the point where the subjects could no longer manage to keep the position at the treadmill, but slowly moved backward reaching a pre-defined mark 1 m behind their original position on the mill. The time to exhaustion was registered and the mean of the two subsequent highest registered VO₂-values, each representing 10 s intervals by the mixing chamber, was representing VO_{2peak} DP.

After a rest period of minimum 60 min, the subjects were then tested for 1RM and power output in leg press (OPS161 Interchangeable leg press, Vertex, United States), and pulldown (Gym 2000, Vikersund, Norway). From pilot testing in Støren et al. (2008), and later presented in Sunde et al. (2010), no deterioration in 1RM squat was detected 30 min after VO_{2max} and MAS testing in running and cycling, compared to 1RM without these prior tests. Leg press was chosen as a measure of lower body maximal strength for several reasons. More specialized DP related exercises such as hip flexion involves both the lower body, truncus and to some extent the upper body. The more specialized the exercises, the more practice is needed to perform valid and reliable 1RM tests. Only two maximal strength tests, one for the upper body and one for the lower body were chosen, due to the large total number of tests in this study.

Each lift was performed with a controlled slow eccentric phase, a complete stop of movement for approximately 1 s in the lowest position (leg press) or the highest position (pulldown),

followed by a maximal mobilization of force in the concentric phase. The measurements of lifting time, distance of work, and thus power output were performed using the Muscle Lab system (Ergotest Innovation AS, Porsgrunn, Norway). Sensors were placed vertically below the center of the weight loads in both leg press and pulldown, and also at the actual center of the weight loads. Each strength test started using 10 reps at a weight load assumed to be approximately 50% of 1RM. After 3 min of rest: 5 reps at approximately 60% 1RM, then 3 reps at approximately 70% 1RM, 2 reps at approximately 80% and at least 1 rep at estimated 1RM with 3 min rest in between. From there on: 1 rep at a weight load increased by 2.5 – 10 kg from the subsequent lift, followed by 3 min of resting, until reaching 1RM. The time spent in each lift, as well as the work distance was measured. As the external force of each lift is represented by the weight of the lifted bars, the power output can be calculated and expressed as N m s⁻¹ or watt (W).

Statistical Analyses

Normality was tested by use of -plots and found to represent normal distributions for the main variables (TT performance, maximal strength and VO_{2peak} DP). Values were thus expressed descriptively as mean ± SD. Inter-individual variability was expressed as coefficient of variance (CV). Correlations were expressed as the correlation factor r from Pearsons bivariate tests. Based on the correlation coefficient definitions by Hopkins (2000), r values of 0.3–0.5 = moderate, 0.5–0.7 = large, 0.7–0.9 = very large, 0.9 = nearly perfect, and 1.0 = perfect. We have therefor defined strong correlations to be $r > 0.7$ in the present study. However, as the cohort includes both male and female skiers, partial correlation analyses were also performed corrected for sex. The correlation factor in normal correlations independent of- or within sex has thus been denoted r_{xy} , whereas the correlation factor in partial correlations corrected for sex has been denoted r_{xy-z} . The practical (clinical) implication of the relations displayed by the r values, were evaluated by use of standard error of the estimate (SEE). This SEE values were obtained from linear regression analyzes. To investigate differences between males and females, independent sample t-tests were performed. Statistical analyzes were performed using the software program statistical package for social science version 24 (SPSS, IBM, Chicago, IL, United States). A p value <0.05 was accepted as statistically significant in all tests.

RESULTS

Test results in the different variables are presented both as total and per sex in **Table 2**. TT performance was 23% ($p < 0.01$) better in males than in females, and males where 34% ($p < 0.01$) stronger in pulldown than females.

Independent of sex, strong correlations were found between 1RM pulldown and TT performance ($r_{xy} = 0.83$, $p < 0.01$) and maximal power in pulldown and performance ($r_{xy} = 0.81$, $p < 0.01$). The two variables CT ($r_{xy-z} = 0.62$, $p < 0.01$)

TABLE 2 | Test results (N = 28).

	All (N = 28)		Females (N = 12)		Males (N = 16)	
	Mean ± SD	CV (%)	Mean ± SD	CV (%)	Mean ± SD	CV (%)
TT _{DP} (s)	899.4 ± 152.7	17.0	1032.8 ± 134.6	13.0	799.4 ± 61.5**	7.7
VO_{2max} running						
L·min ⁻¹	4.48 ± 1.0	22.3	3.54 ± 0.39	11.0	5.22 ± 0.63**	12.1
ML·kg ⁻¹ ·min ⁻¹	64.0 ± 10.4	16.3	53.8 ± 4.4	8.2	72.2 ± 5.1**	7.1
ML·kg ^{-0.67} ·min ^{-0.67}	259.6 ± 46.4	17.9	213.9 ± 17.9	8.4	296.2 ± 22.8**	7.7
VO_{2peak} DP						
L·min ⁻¹	3.93 ± 0.89	22.6	3.10 ± 0.36	11.6	4.54 ± 0.62**	13.7
ML·kg ⁻¹ ·min ⁻¹	55.7 ± 9.1	16.3	47.3 ± 5.2	11.0	62.0 ± 5.3**	8.5
ML·kg ^{-0.67} ·min ^{-0.67}	226.6 ± 40.5	18.2	188.0 ± 19.8	10.5	255.5 ± 24.1**	9.4
Fract util DP (%VO _{2max})	86.9 ± 7.3	7.9	87.9 ± 5.9	6.7	86.0 ± 8.4	9.8
C_{DP}						
ML·kg ⁻¹ ·meter ⁻¹	0.183 ± 0.023	12.6	0.192 ± 0.020	10.4	0.177 ± 0.023	13.0
ML·kg ^{-0.67} ·meter ⁻¹	0.742 ± 0.087	11.7	0.763 ± 0.084	11.0	0.727 ± 0.089	12.2
MAS (km h ⁻¹)	18.6 ± 4.1	22.0	14.9 ± 1.7	11.4	21.4 ± 3.0**	14.0
LT						
%VO _{2peak}	79.0 ± 9.0	11.3	81.1 ± 4.3	5.3	78.3 ± 11.4	14.6
Km·h ⁻¹	14.6 ± 2.7	18.5	12.1 ± 1.2	9.9	16.5 ± 1.7**	10.3
Km·h ⁻¹ calc. (MAS·%VO _{2peak})	14.6 ± 2.7	18.5	12.1 ± 1.3	10.0	16.5 ± 1.8**	10.4
Force_{DP}						
Peak (N)	381.8 ± 124.0	32.5	277.6 ± 80.7	28.8	459.9 ± 87.7**	19.1
Average during CT (N)	169.3 ± 47.8	28.2	145.6 ± 37.7	25.9	187.1 ± 47.7**	25.5
RFD (N·s ⁻¹)	2620 ± 1233	47.0	2063 ± 1230	59.7	3038 ± 1091*	35.9
DP						
Freq. at LT (St·meter ⁻¹)	0.239 ± 0.055	23.0	0.286 ± 0.047	6.5	0.204 ± 0.027**	13.2
Freq. at LT (St·s ⁻¹)	0.938 ± 0.100	10.7	0.956 ± 0.137	14.3	0.925 ± 0.060	6.5
CT (s)	0.353 ± 0.073	20.7	0.388 ± 0.092	23.7	0.327 ± 0.040*	12.2
Maximal strength						
1RM pull-down (kg)	86.2 ± 19.3	22.4	66.0 ± 8.8	13.2	99.7 ± 10.3**	10.3
1RM leg-press (kg)	278.1 ± 54.9	19.7	235.6 ± 37.5	15.9	303.7 ± 47.8**	17.0
Power pull-down (W)	439.2 ± 122.3	27.8	323.1 ± 54.1	16.7	516.5 ± 87.9**	17.0
Power leg-press (W)	609.7 ± 157.2	25.8	466.6 ± 70.2	15.0	694.0 ± 130.3**	18.7

Values are mean ± standard deviation (SD) and coefficient of variance (CV). TT_{DP}, double poling time trial on roller skis; S, seconds; BW, body weight; Kg, kilograms; VO_{2max}, maximal oxygen uptake; L·min⁻¹, liters per minute; ML·kg⁻¹·min⁻¹, milliliters per kg BW per minute; ML·kg^{-0.67}·min^{-0.67}, milliliters per kg BW raised to the power of 0.67 per minute; DP, double poling; VO_{2peak}, peak oxygen uptake during DP; Fract Util, fractional utilization of VO_{2peak} vs. VO_{2max}; C_{DP}, oxygen cost of DP at LT; ML·kg⁻¹·meter⁻¹, milliliters per kg BW per meter; ML·kg^{-0.67}·meter⁻¹, milliliters per kg BW raised to the power of 0.67 per meter; MAS, maximal aerobic speed calculated as peak oxygen uptake during DP divided on C_{DP}; km·h⁻¹, kilometers per hour; LT, lactate threshold; N, Newton; CT, contact time; RFD, rate of force development; N·s⁻¹, Newton per second; Freq, frequency; St·meter⁻¹, strokes per meter; S, seconds; 1RM, one repetition maximum; W, watt. *p < 0.05 different from females. **p < 0.01 different from females.

and % of 1RM pull down during DP ($r_{xy-z} = -0.56$, $p < 0.01$) expressed the highest correlation with TT performance when corrected for sex. Within each sex, PF in DP ($r_{xy} = -0.65$, $p < 0.05$) among males, and CT ($r_{xy} = 0.85$, $p < 0.01$) among females expressed the highest correlations with TT performance. In Tables 3, 4, the potential relationships between test results and TT performance are presented both dependent and independent of sex, as well as within sexes.

The skiers with the highest 1RM pulldown also had the highest PF ($r_{xy} = 0.78$, $p < 0.01$) during DP. The same skiers also had the shortest CT ($r_{xy} = 0.48$, $p < 0.05$), and the lowest DP frequency measured as strokes per meter ($r_{xy} = -0.71$, $p < 0.01$). Relationships between

maximal strength in pulldown and selected variables possibly related to maximal strength are presented in Table 5.

DISCUSSION

The main findings in the present study are the correlations between roller skiing DPTT performance and maximal strength in pull-down, both independent and dependent of sex. Higher maximal upper body strength was related to higher PF in DP, lower DP frequency, and shorter CT.

The novelty of the present study was the finding of a strong correlation between maximal strength (1RM) in pulldown

TABLE 3 | Correlations with time trial performance ($N = 28$).

	Not corrected for sex			Corrected for sex	
	r_{xy}	SEE (%)	p	r_{xy-z}	p
VO_{2max} running					
L·min ⁻¹	-0.77	10.9	< 0.01	-0.37	0.07
ml·kg ⁻¹ ·min ⁻¹	-0.77	11.0	< 0.01	-0.31	0.12
ml·kg ^{-0.67} ·min ^{-0.67}	-0.79	10.4	< 0.01	-0.38	0.06
VO_{2peak} DP					
L·min ⁻¹	-0.78	10.7	< 0.01	-0.42	0.05
ml·kg ⁻¹ ·min ⁻¹	-0.77	11.0	< 0.01	-0.38	0.03
ml·kg ^{-0.67} ·min ^{-0.67}	-0.80	10.4	< 0.01	-0.44	0.02
C_{DP}					
ml·kg ⁻¹ ·meter ⁻¹	0.40	15.8	0.04	0.24	0.23
ml·kg ^{-0.67} ·meter ⁻¹	0.28	16.5	0.14	0.19	0.34
MAS (km h ⁻¹)	-0.80	10.3	< 0.01	-0.48	0.01
LT					
%VO _{2peak}	0.22	16.8	0.26	0.16	0.44
Km·h ⁻¹	-0.78	10.7	< 0.01	-0.40	0.04
Km·h ⁻¹ calc. (MAS·%VO _{2peak})	-0.77	10.7	< 0.01	-0.39	0.04
Force_{DP}					
Peak (N)	-0.75	11.5	< 0.01	-0.41	0.04
Average during CT (N)	-0.45	15.5	0.02	-0.19	0.33
RFD (N·s ⁻¹)	-0.42	15.4	0.03	-0.19	0.35
%of 1RM pull-down	-0.65	13.4	< 0.01	-0.56	< 0.01
DP					
Freq. at LT (St·meter ⁻¹)	0.55	14.3	0.01	-0.07	0.73
Freq. at LT (St·s ⁻¹)	-0.18	16.9	0.36	-0.48	0.01
CT (s)	0.69	12.5	< 0.01	0.62	< 0.01
Maximal strength					
1RM pull-down (kg)	-0.83	10.5	< 0.01	-0.50	0.02
1RM leg-press (kg)	-0.53	15.3	0.01	-0.09	0.68
Power pull-down (W)	-0.81	10.7	< 0.01	-0.49	0.02
Power leg-press (W)	-0.68	13.2	< 0.01	-0.27	0.21

Values are correlation coefficient (r), significant level (p), and standard error of the estimate (SEE). Kg, kilograms; VO_{2max}, maximal oxygen uptake; L·min⁻¹, liters per minute; ml·kg⁻¹·min⁻¹, milliliters per kg BW per minute; ml·kg^{-0.67}·min^{-0.67}, milliliters per kg BW raised to the power of 0.67 per minute; DP, double poling; VO_{2peak}, peak oxygen uptake during DP; C_{DP}, oxygen cost of DP at LT; ml·kg⁻¹·meter⁻¹, milliliters per kg BW per meter; ml·kg^{-0.67}·meter⁻¹, milliliters per kg BW raised to the power of 0.67 per meter; MAS, maximal aerobic speed calculated as peak oxygen uptake during DP divided on C_{DP}; km·h⁻¹, kilometers per hour; LT, lactate threshold; N, Newton; CT, contact time; RFD, rate of force development; N·s⁻¹, Newton per second; Freq. % of 1RM pull-down, percentage of one repetition maximum in pull-down during one full DP cycle; Frequency. St·meter⁻¹, strokes per meter; 1RM, one repetition maximum; W, watt.

per se and roller skiing time trial performance in a cohort of competitive cross-country skiers from both sexes with the same relative training background and age, but with heterogeneity in performance.

Correlations With TT Performance Independent of Sex

For the strength variables, strong correlations were found between 1RM pulldown and TT performance ($r_{xy} = 0.83$) and maximal power output in pulldown and performance ($r_{xy} = 0.81$). SEE was 10.5 and 10.7, respectively. The r^2 values indicate that both variables predicts TT performance by 69%, and the SEE shows this to be outside a margin of approximately 10.5% of either 1RM or power output results. The 10.5% corresponds to 9 kg in pulldown. This implies that if one skier was at least 9 kg's stronger than

another in pulldown, he or she would perform better in TT. Regarding DP characteristics, PF ($r_{xy} = -0.75$), PF during DP as a percentage of 1RM ($r_{xy} = -0.65$) and CT during DP ($r_{xy} = 0.69$) correlated best with TT performance. The relationship between PF and TT is in accordance with previous studies demonstrating that faster skiers had higher PF, or that higher PF related to peak skiing speeds (Bilodeau et al., 1995; Holmberg et al., 2005; Stöggl and Holmberg, 2011, 2016; Stöggl et al., 2011). The two single physiological variables regarding aerobic endurance that correlated best with TT performance were VO_{2max} in running and VO_{2peak} DP expressed as ml·kg^{-0.67}·min⁻¹ ($r_{xy} = 0.79$ and $r_{xy} = 0.80$, respectively). The SEE value of 10.4%, implies that if one skier had at least 23 ml·kg^{-0.67}·min⁻¹ higher VO_{2peak} DP than another, he or she would perform better in TT. There was also a strong correlation between velocity at LT and performance ($r_{xy} = 0.78$).

TABLE 4 | Within sex correlations with time trial performance.

	Males (N = 16)		Females (N = 12)	
	r_{xy}	<i>p</i>	r_{xy}	<i>p</i>
VO_{2max} running				
L·min ⁻¹	-0.39	0.16	-0.49	0.11
ML·kg ⁻¹ ·min ⁻¹	0.16	0.57	-0.70	0.01
ML·kg ^{-0.67} ·min ^{-0.67}	-0.10	0.71	-0.66	0.02
VO_{2peak} DP				
L·min ⁻¹	-0.57	0.02	-0.46	0.13
ML·kg ⁻¹ ·min ⁻¹	-0.26	0.33	-0.51	0.09
ML·kg ^{-0.67} ·min ^{-0.67}	-0.43	0.09	-0.53	0.08
C_{DP}				
ML·kg ⁻¹ ·meter ⁻¹	0.53	0.03	0.07	0.82
ML·kg ^{-0.67} ·meter ⁻¹	0.40	0.12	0.08	0.81
MAS (km h ⁻¹)	-0.62	0.01	-0.56	0.06
LT				
%VO _{2peak}	0.51	0.04	-0.27	0.40
Km·h ⁻¹	-0.18	0.51	-0.71	0.01
Km·h ⁻¹ calc. (MAS·%VO _{2peak})	-0.23	0.42	-0.74	0.01
Force_{DP}				
Peak (N)	-0.65	0.01	-0.31	0.33
Average during CT (N)	-0.17	0.54	-0.26	0.41
RFD (N·s ⁻¹)	0.13	0.63	-0.38	0.22
% of 1RM pull-down	-0.44	0.10	-0.18	0.62
DP				
Freq. at LT (St·meter ⁻¹)	0.38	0.14	-0.23	0.47
Freq. at LT (St·s ⁻¹)	0.46	0.07	-0.75	0.01
CT (s)	-0.21	0.44	0.85	< 0.01
Maximal strength				
1RM pull-down (kg)	-0.52	0.05	-0.52	0.12
1RM leg-press (kg)	-0.24	0.39	0.02	0.95
Power pull-down (W)	-0.47	0.08	-0.76	0.01
Power leg-press (W)	-0.27	0.34	-0.47	0.21

Values are correlation coefficient (*r*) and significant level (*p*). Kg, kilograms; VO_{2max}, maximal oxygen uptake; L·min⁻¹, liters per minute; ML·kg⁻¹·min⁻¹, milliliters per kg BW per minute; ML·kg^{-0.67}·min^{-0.67}, milliliters per kg BW raised to the power of 0.67 per minute; DP, double poling; VO_{2peak}, peak oxygen uptake during DP; C_{DP}, oxygen cost of DP at LT; ML·kg⁻¹·meter⁻¹, milliliters per kg BW per meter; ML·kg^{-0.67}·meter⁻¹, milliliters per kg BW raised to the power of 0.67 per meter; MAS, maximal aerobic speed calculated as peak oxygen uptake during DP divided on C_{DP}; km·h⁻¹, kilometers per hour; LT, lactate threshold; N, Newton; CT, contact time; RFD, rate of force development; N·s⁻¹, Newton per second; Freq. % of 1RM pull-down, percentage of one repetition maximum in pull-down during one full DP cycle; Frequency. St·meter⁻¹, strokes per meter; 1RM, one repetition maximum; W, watt.

All of these correlations were found in the heterogeneous cohort including both sexes.

Correlations With TT Performance Corrected for Sex

When corrected for sex, the aerobic endurance variables decreased substantially in predicting TT performance. The two variables CT ($r_{xy-z} = 0.62$) and PF as a percentage of 1 RM pull down during DP ($r_{xy-z} = -0.56$) expressed the best correlation with TT performance when corrected for sex. When correcting for sex, the cohorts are more homogeneous since males and females results are clustered in to two groups. This was apparent when comparing coefficient of variance (CV) (Table 2). The CV for VO_{2max} (running) and VO_{2peak} DP when including both sexes, were both 18%. When separated into males and females,

the CV values were cut in half. This phenomenon was not so obvious regarding strength and DP characteristics.

Correlations With TT Performance Within Sexes

Both normal and partial correlations were performed in the present study. When partial correlations were still significant, this would strengthen the normal correlations by showing that it was not confounded by sex. However, the partial correlations only showed to what extent the normal correlations were confounded by sex, and so correlations with TT performance were also analyzed within sexes. These correlations should be handled with caution, due to the low number of skiers within each sex. The division into two separate groups also caused a greater degree of homogeneity in almost all variables. As a result of

TABLE 5 | Correlations with maximal strength in pull-down ($N = 28$).

	Not corrected for sex			Corrected for sex	
	r_{xy}	SEE (%)	p	r_{xy-z}	p
C_{DP}					
MI·kg ⁻¹ ·meter ⁻¹	-0.36	21.5	0.08	-0.18	0.40
MI·kg ^{-0.67} ·meter ⁻¹	-0.20	22.5	0.36	0.02	0.94
MAS (km h ⁻¹)	-0.74	15.2	<0.01	-0.21	0.32
Force_{DP}					
Peak (N)	0.78	14.2	<0.01	0.50	0.01
Average during CT (N)	0.39	21.1	0.05	0.09	0.64
RFD (N·s ⁻¹)	0.31	21.8	0.13	0.02	0.92
% of 1RM pull-down	-0.54	19.3	0.01	-0.40	0.05
DP					
Freq. at LT (St·meter ⁻¹)	-0.71	16.1	<0.01	-0.20	0.35
Freq. at LT (St·s ⁻¹)	-0.09	22.9	0.66	0.08	0.72
CT (s)	-0.48	20.1	0.02	-0.29	0.17
Maximal strength					
Power pull-down (W)	0.92	8.9	<0.01	0.77	0.02

Values are correlation coefficient (r), significant level (p), and standard error of the estimate (SEE). C_{DP}, oxygen cost of DP at LT; MI·kg⁻¹·meter⁻¹, milliliters per kg BW per meter; MI·kg^{-0.67}·meter⁻¹, milliliters per kg BW raised to the power of 0.67 per meter; MAS, maximal aerobic speed calculated as peak oxygen uptake during DP divided on C_{DP}; km·h⁻¹, kilometers per hour; N, Newton; CT, contact time; RFD, rate of force development; N·s⁻¹, Newton per second. % of 1RM pull-down, percentage of one repetition maximum in pull-down during one full DP cycle; Freq, frequency; St·meter⁻¹, strokes per meter; 1RM, one repetition maximum; W, watt.

this and the low number in each group, correlations across sexes were weakened or disappeared. Those analyzes are merely included for informative reasons, but not addressed further in this discussion. Maximal strength in pulldown had approximately the same correlation with TT performance in both males and females. However, the relationships between the utilization of this maximal strength and TT performance seemed to differ, as CT correlated well in females but not males, and PF in DP correlated well in males but not females.

Both males and females had approximately the same correlation between MAS and TT performance. However, TT performance seemed to depend mostly on VO_{2peak} but not C_{DP} in females. In males, TT performance seemed to depend mostly on C_{DP}, but not VO_{2peak}.

VO_{2max}, C_{DP}, and MAS

The importance of a high VO_{2max} in running for TT performance in the present study, is in accordance with several previous studies (Bergh, 1987; Ingjer, 1991; Mahood et al., 2001; Larsson et al., 2002; Alsobrook and Heil, 2009; Ainegren et al., 2013). This is also demonstrated by cross-country skiers' high values of VO_{2max}; 80–90 ml·kg⁻¹·min⁻¹ and 70–80 ml·kg⁻¹·min⁻¹ for men and women world-class cross-country skiers, respectively (Sandbakk et al., 2014). The VO_{2max} values in the present study were 53.8 ± 4.4 ml·kg⁻¹·min⁻¹ and 72.2 ± 5.1 ml·kg⁻¹·min⁻¹ for women and men, respectively. Regarding the skiers cost of skiing, the present study found that C_{DP} did not correlate well with TT performance (Table 2). The low impact of C_{DP} in the present study is further highlighted when including C_{DP} in the MAS equation (VO_{2peak} DP/C_{DP}). MAS did not correlate better with TT performance than VO_{2peak} DP alone ($r_{xy} = -0.80$), independent of sex.

Lactate Threshold

Maximal oxygen consumption at LT in% of VO_{2peak} DP did not correlate with TT performance in the present study. However, velocity at LT correlated strongly ($r_{xy} = -0.78$) with TT performance. This is in accordance with Støren et al. (2014) on cyclists. In Støren et al. (2014) it was shown that velocity at LT, as measured in the present study, also could be calculated by the product of MAS and LT in% of VO_{2peak}, while LT in% of VO_{2peak} alone did not explain LT velocity. The same results were echoed in the present study. When applying the same equation for velocity at LT (MAS LT%), this correlated nearly perfect ($r_{xy} = 0.99$) with the actually measured LT velocity. This implies that it is not LT *per se*, but rather VO_{2peak} that predicts TT performance.

Maximal Strength

Although C_{DP} correlated weakly with TT performance in the present study, variables previously shown to affect work economy in other sports (Saunders et al., 2004; Støren et al., 2008; Sunde et al., 2010), such as maximal strength and movement cycle characteristics correlated well with performance in the present study. This indicates that during DP the% of 1RM pulldown, CT, PF, and 1RM pulldown and power output in 1RM pulldown actually affected TT performance *per se* and not merely via C_{DP}. That maximal strength *per se* is related to TT performance, is in contrast to previous studies in running and cycling (Støren et al., 2008, 2013). One possible explanation for this difference is that DP relies much more on upper body work than running and cycling. Blagrove et al. (2018) and Fletcher and MacIntosh (2017), discussed that an improvement in force-generating capacity would theoretically allow athletes to sustain a lower percentage of maximal strength during running. It is likely that this also applies to the cross-country skiers during DP in the present

study. A higher 1RM pulldown would therefore imply a lower percentage of 1RM during DP, at a given work load. Thus the % of 1RM pull down correlated good to TT performance in the present study ($r_{xy} = -0.65$).

Maximal Strength and DP Characteristics

The skiers with the highest 1RM pulldown also had the highest PF ($r_{xy} = 0.78$) during DP (Table 4). The same skiers also had the shortest CT ($r_{xy} = 0.48$), and the lowest DP frequency measured as strokes per meter ($r_{xy} = -0.71$). Also CT correlated with LT velocity ($r_{xy} = -0.53$), indicating that the fastest skiers had the shortest CT, although CT did not correlate with TT directly. Therefore, this shortened CT in faster skiers might be basically explained by the higher skiing speeds. A shorter CT and a lower frequency allows for a shorter contraction time and a longer transit time during each DP cycle. This could theoretically lead to better circulation and thus O_2 and substrate deliverance as well as better clearance of lactic acid (Barrett-O'Keefe et al., 2012). On the other hand, the indication of the fastest skiers having the shortest CT, could partly explain the correlation between CT and 1RM pulldown.

Upper Body vs. Lower Body Maximal Strength and Power Output

Even though DP may be considered a whole body exercise involving muscle mass from feet to neck, the leg press results in the present study seemed to have much less impact on TT performance and MAS than pulldown. This does not necessarily imply that lower body muscles do not have an impact on DP. Based on EMG activity in lower body muscles, Holmberg et al. (2005) showed that DP requires more than upper body work. Also power was measured for the strength variables in the present study. In pulldown, the impact of power more or less followed the impact of 1RM on TT performance and MAS. It is not surprising that the strongest also produced most power output, and this is in accordance with previous studies (Østerås et al., 2002).

Power output was calculated as the product of force and work distance divided by time. The power output results in leg press in the present study may seem low. This is due to the measurements of work distance being performed vertically when the lifting direction is diagonal in the leg press apparatus. In studies where the lifting direction is vertical like squat in e.g., Støren et al. (2008) and Sunde et al. (2010), power output results in runners and cyclist were shown to be approximately 100% higher than in the present study.

Sex Differences

Since the male and female participants in the present study represented a higher and a lower TT performance level, a comparison of the results from the two sexes may be used to discuss the importance of factors predicting DP performance. The male and female skiers were at the same age, and being recruited from the same teams and high schools, their training background was relatively similar. TT performance was 23%

better in males than in females. The sex difference in the present study was therefore in accordance with results from Sandbakk et al. (2014) in DP, finding a 20% sex difference in a ramp DP protocol to exhaustion. The 23% sex difference in the present study corresponded to a 30% higher MAS in males. As VO_{2peak} can be expressed as $ml.kg^{-1}.min^{-1}$, and DP as $ml.kg^{-1}.m^{-1}$, the product of denominations equals $m.min^{-1}$, which may also be expressed as $km.h^{-1}$. The gender difference in MAS, could therefore be explained by 18% difference in VO_{2peak} DP, and a none significant 8% difference in C_{DP} . These differences is somewhat lower than presented in Sandbakk and Holmberg (2017).

Males were 34% stronger in pulldown than females, which is a somewhat lower difference than the 50% reported in Sandbakk et al. (2014). An interesting question is to what extent this influence the sex differences in MAS. Although a strong correlation between MAS and pulldown exist, the correlation weakens when corrected for sex. This could imply that the correlation was merely a product of males both being stronger and having a higher MAS than females. However, we cannot rule out that the higher MAS in males were at least partly due to a higher strength in pull down. On the other hand, the relationship between 1RM pulldown and TT performance corrected for sex is better than the relationship between 1RM pulldown and MAS. This may indicate that maximal strength could be important independent of MAS.

Practical Implications

The practical implications of the present study is to acknowledge maximal upper body strength as a possible performance determining factor in DP. We suggest including maximal strength training in the cross-country skiers training programs, but the effect of this needs further evaluation in future studies. We recommend few repetitions (2–5) in 3–5 series with maximal mobilization in the concentric phase, with relatively long (2–3 min) pauses in between. These principles have in previous studies been shown to improve work economy as well as maximal strength (Østerås et al., 2002; Støren et al., 2008; Sunde et al., 2010).

CONCLUSION

In conclusion maximal upper body strength was shown to have a significant impact on DP roller skiing performance, both dependent and independent of sex, and both dependent and independent of C_{DP} . Higher maximal upper body strength was related to higher DP peak forces, lower DP frequency and shorter CT.

DATA AVAILABILITY

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

This study was carried out in accordance with the recommendations of the Institutional Review Board (IRB) at the University of South-Eastern Norway with written informed consent from all subjects. All subjects gave written informed consent in accordance with the Declaration of Helsinki. The protocol was approved by the Institutional Review Board (IRB) at the University of South-Eastern Norway.

AUTHOR CONTRIBUTIONS

AS, J-MJ, ØS, JH, GP, and MB participated significantly in the planning and designing of the study. AS, J-MJ, ØS, and JH

participated in the data analysis and writing of the manuscript. AS, ØS, J-MJ, and MG participated in the data collection and analysis. All authors read and approved the manuscript.

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Conflict of Interest Statement: JH was employed by the company Myworkout.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Article 2

Johansen, J-M., Eriksen, S., Sunde, A., Slette-meås, Ø.B., Helgerud, J. and Støren Ø. (2020). **Improving Utilization of Maximal Oxygen Uptake and Work Economy in Recreational Cross-Country Skiers with High-Intensity Double-Poling Intervals.** *Int. J. Sports Physiol. Perform.* [Ahead of print]. doi: 10.1123/ijsp.2019-0689.

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Improving Utilization of Maximal Oxygen Uptake and Work Economy in Recreational Cross-Country Skiers With High-Intensity Double-Poling Intervals

Jan-Michael Johansen, Sondre Eriksen, Arnstein Sunde, Øystein B. Slettemeås, Jan Helgerud, and Øyvind Støren

Purpose: To investigate the effect of a double-poling (DP) high-intensity aerobic interval-training (HIT) intervention performed without increasing total HIT volume. This means that regular HIT training (eg, running) was replaced by HIT DP. The aim was to explore whether this intervention could improve peak oxygen uptake in DP, the fractional utilization of maximal oxygen uptake (VO_2max) in DP, oxygen cost of DP, maximal aerobic speed, and a 3-km DP time trial. **Methods:** Nine non-specially-DP-trained cross-country skiers (intervention group) and 9 national-level cross-country skiers (control group) were recruited. All participants were tested for VO_2max in running, peak oxygen uptake in DP, oxygen cost of DP, and time-trial performance before and after a 6-wk, 3-times-per-week HIT DP intervention. The intervention group omitted all regular HIT with HIT in DP, leaving the total weekly amount of HIT unchanged. **Results:** Seven participants in each group completed the study. VO_2max in running remained unchanged in both groups, whereas peak oxygen uptake in DP improved by 7.1% ($P = .005$) in the intervention group. The fractional utilization of VO_2max in DP thus increased by 7.3% ($P = .019$), oxygen cost of DP by 9.2% ($P = .047$), maximal aerobic speed by 16.5% ($P = .009$), and time trial by 19.5% ($P = .004$) in the intervention group but remained unchanged in the control group. **Conclusions:** The results indicate that a 6-wk HIT DP intervention could be an effective model to improve DP-specific capacities, with maintenance of VO_2max in running.

Keywords: cross-country skiing, peak oxygen uptake, oxygen cost of double poling, time-trial performance, maximal aerobic speed

Cross-country skiing is an aerobic endurance sport, with competition durations ranging between 2 and 120 min.¹ In addition, Vasaloppet and other classical-style long-distance races, which nowadays are performed solely by double poling (DP) both by elite and recreational skiers, have an even longer duration from ~240 (winner times) to 360 min (random recreational times). This implies 70% to 99% dependency on aerobic metabolism, in which maximal oxygen uptake (VO_2max), fractional utilization of VO_2max , and work economy are regarded, across all these disciplines.²⁻⁹

Double poling is one of the main classical-style subtechniques being used in 50% to 100% of the distance in classical cross-country skiing events.^{10,11} Although 100% DP is mostly banned from World Cup races, this is allowed in long-distance races such as Vasaloppet. DP puts more stress on the upper body and trunk¹² compared with other skiing techniques,¹³ and a high-fractional utilization of VO_2max ($\%\text{RUN-VO}_2\text{max}$) is needed to perform well in DP.¹ Accordingly, previous studies have found peak oxygen uptake in DP (DP- VO_2peak) to be approximately 80% to 90% of VO_2max in running (RUN- VO_2max).^{12,14-17}

No studies have investigated the effect of training designed specifically to improve $\%\text{RUN-VO}_2\text{max}$ in DP, although Nilsson et al¹⁵ found a 4% increase in DP- VO_2peak without any changes in RUN- VO_2max after 6 wk of aerobic interval training on a DP ergometer. This means that $\%\text{RUN-VO}_2\text{max}$ should have increased as well. Sandbakk and Holmberg¹ have previously proposed that cross-country skiers should attempt to elevate their $\%\text{RUN-VO}_2\text{max}$ in subtechniques, like DP, to enhance their performance. An improvement in $\%\text{RUN-VO}_2\text{max}$ should theoretically improve DP performance, even if RUN- VO_2max and/or oxygen cost of DP (C_{DP}) remain unchanged. It can, therefore, be hypothesized that DP-specific high-intensity aerobic interval training (HIT DP) could improve $\%\text{RUN-VO}_2\text{max}$ in nonspecially DP trained, but competitive, cross-country skiers. HIT DP may also improve C_{DP} , maximal aerobic speed in DP (MAS), and DP time-trial performance (TT) in such a cohort of skiers.

Therefore, the primary aim of this study was to investigate the effects of 6 wk of HIT DP in nonspecially DP trained, but competitive, skiers on DP- VO_2peak and $\%\text{RUN-VO}_2\text{max}$, without increasing total HIT volume or total training volume. A secondary aim was to investigate if this intervention also could improve C_{DP} , MAS, and TT.

Methods

Subjects

Nine recreational-level cross-country skiers (7 males and 2 females) were recruited to the intervention group, and 9 national-level cross-country skiers (7 males and 2 females) were recruited to

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a control group. This study was carried out in accordance with the recommendations of the regional ethics committee of Southeast Norway (REK) with written informed consent from all subjects. All subjects gave written informed consent in accordance with the Declaration of Helsinki. The protocol was approved by the regional ethics committee of Southeast Norway (REK). During the training period and during testing prior to the intervention period, 4 subjects (2 males from the intervention group and 2 females from the control group) were excluded due to illness or injuries not related to the intervention. Thus, in total, 14 subjects were included for the statistical analyses. Subject characteristics of the remaining participants are presented in Table 1.

Design

The present study was a 6-wk, 3 times per week, HIT DP intervention, with a pre–post design and a control group. During the intervention period, both the intervention group and the control group trained as normal, with one exception: the intervention group replaced all HIT training (eg, running) with HIT DP.

Methodology

The 14 regional- to national-level cross-country skiers were assigned into 2 groups based on competition level, 1 intervention group (recreational level) and 1 control group (national level). A pretest preceded the intervention period. The intervention group replaced all other HIT (mostly running and cycling) with DP-specific HIT, exclusively during the intervention period (Table 2). The control group continued their training as normal (Table 2). After the 6 wk, a posttest, including the same tests as in the pretest, was performed. All tests and the training intervention were performed from August to October (ie, preseason).

The subjects were tested on 2 consecutive days both before and after the 6-wk period. A Rodby RL2500E roller skiing treadmill (Rodby Innovation AB, Vänge, Sweden) calibrated for inclination and speed was used in all the DP tests. Only 2 pairs of roller skis

(Swenor wheel type 2 Fiberglass; Swenor, Sarpsborg, Norway) were used by all subjects during the roller skiing tests in this study, with 1 of 2 binding systems: SNS (Salomon Nordic System; Salomon, Annecy, France) or NNN (New Nordic Norm; Rottefella AS, Klokke, Norway). Each subject used the same pair during the pretest and posttest.

All oxygen uptake (VO_2) measurements were performed using a Sensor Medics V_{max} Spectra (Sensor Medics 229; SensorMedics, Yourba Linda, CA) with a mixing chamber and with measurements in every 20 s. Before each test, the metabolic test system was calibrated. Certified calibration gases (26% and 16% $\text{O}_2/4\% \text{CO}_2$) and ambient air were used to calibrate the gas analyzers. The flow sensor was calibrated with a 3-L calibration syringe (Hans Rudolph Inc, Kansas City, MO). According to the manufacturer, the Sensor Medics V_{max} Spectra is accurate within a range of $\pm 3\%$. However, test–retest variations in the present laboratory are shown to be less than $\pm 1\%$, with an SEM of 0.1 to 0.2 in different tests, as reported in Helgerud et al.¹⁸ Heart rate was measured by Polar s610 heart rate monitors (Polar Electro Oy, Kempele, Finland).

All participants performed 2 treadmill familiarization sessions. The first session consisted of 45 min with different speeds, 1 to 2 d prior to pretesting. The second session was performed prior to the first test on the first day of testing. This session consisted of at least 25 min of DP at a low intensity, $<70\%$ of maximal heart rate (HR_{max}). After the second familiarization session, the first day of testing consisted of measurements of heart rate and VO_2 during 5-min DP sessions (4% inclination) at 3 different submaximal speeds for determination of C_{DP} . The subjects started with a speed assumed to be approximately 60% of their DP- VO_2 peak. The speed increased by $1.5 \text{ km}\cdot\text{h}^{-1}$ between each session. C_{DP} at 70% of DP- VO_2 peak was calculated by the VO_2 data from these submaximal 5-min sessions.

After 5 min of rest, a DP- VO_2 peak test was performed using an incremental protocol starting at 4% inclination and 2 to 4 $\text{km}\cdot\text{h}^{-1}$ below 80% of expected HR_{max} . Every 30 s, the inclination increased by 0.5% until reaching approximately 80% of expected HR_{max} . Then, the speed was increased by 0.5 $\text{km}\cdot\text{h}^{-1}$ every 30 s until voluntary exhaustion. DP- VO_2 peak was set as the mean of the highest 2 consecutive 20 s measurements of VO_2 . The following criteria were used to evaluate if VO_2 peak was reached: voluntary exhaustion, flattening of the VO_2 curve, respiratory exchange ratio ≥ 1.0 , and peak heart rate (HR_{peak}) in DP 3 to 5 beats below HR_{max} . HR_{peak} was defined as the highest heart rate obtained during the DP- VO_2 peak test. HR_{max} was defined as the highest HR obtained regardless of movement pattern, and for all participants achieved in running. All participants knew their HR_{max} prior to their participations. Whether or not this was true, HR_{max} was controlled by the RUN- VO_2 max test at day 2, where HR_{max} was defined as the

Table 1 Characteristics of Cross-Country Skiers

Variable	Intervention group (n = 7)		Control group (n = 7)	
	Mean (SD)	CV, %	Mean (SD)	CV, %
Age, y	29.1 (12.5)	43.1	22.3 (3.1)	13.6
Weight, kg	73.5 (10.1)	13.8	77.5 (5.5)	7.1
Height, cm	178.4 (9.5)	5.3	185.4 (4.8)	2.6

Abbreviation: CV, coefficient of variation.

Table 2 Training Data Before and During Intervention ($\text{min}\cdot\text{wk}^{-1}$)

	Intervention group (n = 7)		Control group (n = 7)	
	Before	During	Before	During
Endurance training, min				
60–84% HR_{max}	287.1 (181.4)	222.3 (91.1)	382.1 (209.9)	346.0 (187.7)
85–90% HR_{max}	54.3 (67.0)	55.1 (70.7)	35.6 (38.5)	30.9 (45.8)
$\geq 90\%$ HR_{max}	28.9 (35.5)	32.0 (21.3)	47.3 (33.5)	39.6 (26.2)
Strength training, min	28.0 (26.9)	36.9 (44.6)	58.0 (50.2)	84.3 (70.6)
Total training	398.2 (280.8)	346.8 (213.6)	524.7 (263.1)	502.4 (238.3)

Abbreviation: HR_{max} , maximal heart rate.

highest heart rate obtained during the RUN-VO₂max test + 3 beats. MAS was defined as the product of DP-VO₂peak divided by C_{DP}. As DP-VO₂peak may be expressed as mL·kg⁻¹·min⁻¹, and C_{DP} may be expressed as mL·kg⁻¹·m⁻¹, the product of the denominations was m·min⁻¹.

The second day of testing consisted of a RUN-VO₂max test and a TT performance test in DP. A Woodway PPS55sport (Woodway, Waukesha, WI), calibrated for inclination and speed, was used for the RUN-VO₂max test. An incremental protocol, starting at 6% inclination, was used in this test. The initial speed was set to 8 (females) and 10 km·h⁻¹ (males). During the first 2 min of the test, inclination was increased by 1% to 4%, dependent on the subjects' fitness levels. From that point, only speed was increased every 30 s by 0.5 km·h⁻¹ until voluntary exhaustion. RUN-VO₂max was defined as the mean of the highest 2 consecutive 20 s measurements of VO₂. The following criteria were used to evaluate if RUN-VO₂max was reached: voluntary exhaustion, flattening of the VO₂ curve, respiratory exchange ratio ≥1.05, and HR_{peak} 3 to 5 beats below HR_{max}.

After 40 min of rest, a TT in DP, at 4% inclination, was performed on the same treadmill as the first day. The speed increased to what the subjects thought they could manage to sustain through the whole test, and the test started when this speed was obtained. During the test, the subjects could give physical signs with fingers or head to increase or decrease the speed. All participants were given feedback on the remaining distance from 2000 m, but not on time spent. Heart rate was measured every minute from 3 min and to the end of the test. The time used on this TT was used as the performance result.

Training

To control the weekly training performed by the participants, each subject had to report the exact amount of time in the different training intensity zones 60% to 84%, 85% to 90%, and >90% HR_{max} both before and during the 6-wk period. The 3 zones are representing moderate exercise, exercise at approximate lactate threshold, and HIT, as previously used and described in Støren et al.¹⁹ and Sunde et al.²⁰ All training in the intervention group and in the control group was reported for the last 6 wk prior to the baseline testing. During the intervention period, the control group was instructed to continue their normal training. This training was logged and did not differ from their normal training prior to the intervention (Table 2).

The HIT intervention consisted of 3 DP training sessions per week. Each session contained 4 × 4 min at 90% to 95% of HR_{peak} DP on a treadmill with 4% inclination and was supervised by research personnel. Each session started with a minimum of a 10-min warm-up, and ended with a minimum of a 3-min cooldown, and each 4-min period was separated by 3 min at 70% HR_{peak}. The inclusion criterion for adherence was set to a mean of 2 out of 3 sessions per week (ie, 67%; 12 sessions). The amount of HIT DP during the intervention period equaled the total amount of HIT (running and cycling) performed prior to the intervention.

Statistical Analysis

Normality was tested by Q–Q plots and the Shapiro–Wilk test for %RUN-VO₂max and TT performance and found to be normally distributed. Although a low number of participants, parametric statistics were, therefore, used. Based on previous findings, HIT can be expected to improve VO₂max by approximately 10% in

recreational athletes. With 7 subjects and a SD of the same size as the improvement (10%), the statistical power was calculated to be 84% given an alpha error level of 5%. Statistical analysis was performed using the software program SPSS (version 24; Statistical Package for Social Science, Chicago, IL). Descriptive analysis was performed for display of mean, SD, and 95% confidence intervals. Paired samples *t* tests and independent samples *t* tests were used for comparing means within groups and between groups. Pearson correlation tests were used to identify relationships between variables and displayed by the correlation coefficient *r* and standard error of estimate. In all cases, *P* < .05 was set as the level of significance in 2-tailed tests.

Results

The intervention group completed, on average, 14.4 (2.3) (80%) of the 18 planned HIT DP sessions. The mean weekly effective training volume (pauses and brakes excluded) before the intervention period was 6.6 (4.7) and 8.7 (4.4) h for the intervention and control group, respectively. Neither training volume nor training intensity changed from before to during the 6-wk intervention period in any of the 2 groups (Table 2).

In the intervention group, DP-VO₂peak (L·min⁻¹) increased by 7.1% (*P* = .005) from pretest to posttest, whereas no change was found in the control group (Table 3, Figure 1). The intervention group also improved C_{DP} by -9.2% (*P* = .047), MAS by 16.5% (*P* = .009), and TT performance by -19.5% (*P* = .004). None of these variables changed in the control group. %RUN-VO₂max improved by 7.3% points (*P* = .019) in the intervention group, whereas no increase was found in the control group (Figure 1). No significant difference in either groups was found in RUN-VO₂max, body weight, RER_{peak}, or HR_{peak} in DP after the intervention (Table 3).

A strong correlation was found between TT performance and MAS (*r* = .83, standard error of estimate = 11.6%) at baseline (Figure 2). When performing a partial correlation corrected for group (intervention and control), the correlation was still strong (*r* = .81, *P* < .001). Also ΔMAS and ΔDP-VO₂peak (L·min⁻¹) correlated with the ΔTT performance (*r* = .61, *P* = .021 and *r* = .67, *P* = .009, respectively). Baseline correlations are presented in Table 4.

Discussion

The main novelty of the present study was that a 6-wk HIT DP intervention was an effective model to enhance DP-specific capacities, with maintenance of RUN-VO₂max. Concurrent improvements in DP-VO₂peak, %RUN-VO₂max, and C_{DP} after the work-specific HIT intervention were found, and these improvements proved to be highly performance determining, as shown by large improvements in MAS and TT performance. It is noteworthy that these improvements were achieved without any increase in the total amount of training in general or in the total amount of HIT.

TT Performance and MAS

Although the intervention group improved their TT by -19.5%, the control group was left unchanged. As the control group initially had 15% better TT performance than the intervention group, the improvement of the intervention group resulted in the same TT level as the control group after the intervention, with maintenance of RUN-VO₂max. To our knowledge, this is the first study to

Table 3 Physiological Results in the Intervention and Control Groups

Variable	Intervention group (n = 7)			Control group (n = 7)			Between (P)
	Pre	Post	Within (P)	Pre	Post	Within (P)	
3-km TT							
Time, s	833.6 (175.7)	671.0 (101.1)	.004**	710.1 (106.7)	692.3 (104.8)	.096	.002****
DP-VO ₂ peak							
mL·kg ⁻¹ ·min ⁻¹	51.5 (8.1)	54.6 (8.6)	.030*	58.0 (7.4)	57.7 (7.2)	.830	.047***
mL·kg ^{-0.67} ·min ⁻¹	212.5 (36.3)	226.1 (36.4)	.017*	243.5 (32.1)	242.0 (30.6)	.746	.028***
L·min ⁻¹	3.80 (0.86)	4.07 (0.82)	.005**	4.49 (0.68)	4.44 (0.62)	.615	.014***
HR _{peak}	180 (11)	181 (10)	.647	183 (9)	181 (11)	.386	.322
RER _{peak}	1.08 (0.09)	1.03 (0.02)	.201	1.05 (0.04)	1.07 (0.05)	1.000	.045***
RUN-VO ₂ max							
mL·kg ⁻¹ ·min ⁻¹	65.8 (10.9)	63.3 (8.8)	.085	71.6 (3.9)	71.2 (4.2)	.735	.223
mL·kg ^{-0.67} ·min ⁻¹	279.8 (45.2)	262.1 (36.1)	.129	300.6 (18.0)	298.5 (20.2)	.642	.335
L·min ⁻¹	4.82 (0.99)	4.71 (0.83)	.294	5.54 (0.50)	5.49 (0.53)	.539	.697
HR _{peak}	183 (9)	183 (9)	1.000	190 (6)	189 (7)	.188	.435
RER _{peak}	1.06 (0.03)	1.07 (0.04)	.917	1.05 (0.03)	1.05 (0.04)	.129	.956
%RUN-VO ₂ max							
%	78.7 (5.6)	86.0 (2.4)	.019*	80.9 (7.8)	80.9 (6.4)	.592	.015***
C _{DP}							
mL·kg ⁻¹ ·m ⁻¹	0.207 (0.016)	0.188 (0.015)	.047*	0.204 (0.039)	0.208 (0.019)	.707	.117
mL·kg ^{-0.67} ·m ⁻¹	0.857 (0.095)	0.778 (0.055)	.046*	0.855 (0.163)	0.873 (0.084)	.722	.116
MAS							
m·min ⁻¹	252.1 (52.5)	293.6 (59.8)	.009**	297.5 (85.8)	281.6 (57.5)	.298	.007****

Abbreviations: %RUN-VO₂max, fractional utilization of RUN-VO₂max at DP-VO₂peak; TT, time trial on roller skis; Between (P), P values of between-groups differences; C_{DP}, oxygen cost of DP at 70% of DP-VO₂peak; DP, double poling; DP-VO₂peak, peak oxygen uptake in DP; HR_{peak}, peak heart rate; MAS, maximal aerobic speed; RER_{peak}, peak value of respiratory exchange ratio; RUN-VO₂max, maximal oxygen uptake in running; TT, time trial; Within (P), P values of within-group differences. *Significantly different from pretest value (P < .05). **Significantly different from pretest value (P < .01). ***Significantly different from Δ control value (P < .05). ****Significantly different from Δ control value (P < .01).

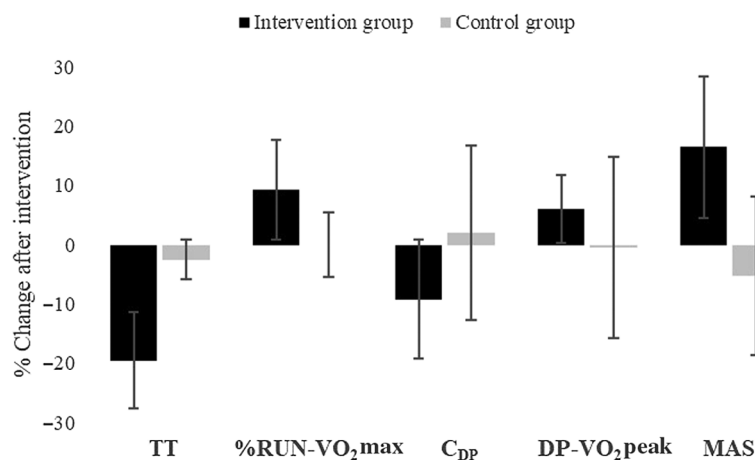


Figure 1 — Percentage change after the intervention period in physiological characteristics and TT performance in the intervention group and the control group. %RUN-VO₂max indicates fractional utilization of maximal oxygen uptake in double poling; C_{DP}, oxygen cost of double poling; DP-VO₂peak, peak oxygen uptake in double poling; MAS, maximal aerobic speed; TT, time trial.

demonstrate recreational-level skiers reaching the level of national-level skiers in TT performance after only 6 wk of specialized training. The improvement in time performance is in line with Nilsson et al,¹⁵ who found a 16% improvement in mean power during a 6-min DP performance test on a DP ergometer after HIT DP 3 times a week for 6 wk. We suggest that the improvement

in TT performance in the present study was due to the improvement in MAS, which was at the approximate same level. This is in accordance with the framework of Joyner and Coyle,⁷ defining performance velocity as the product of performance VO₂ (VO₂max and lactate threshold), performance O₂ deficit, and gross mechanical efficiency.

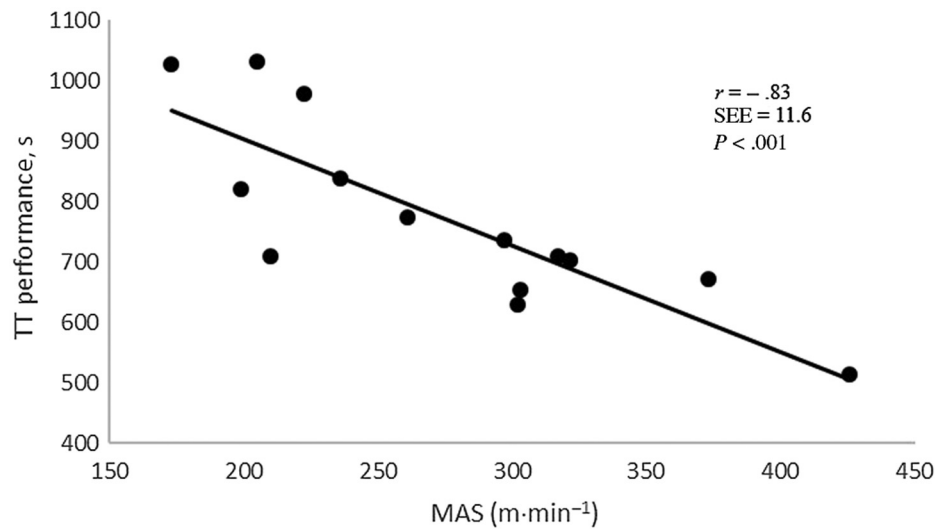


Figure 2 — Relationship between baseline MAS and TT performance. The correlation is statistically significant ($P < .001$). MAS indicates maximal aerobic speed; SEE, standard error of estimate; TT, time trial.

Table 4 Correlations Between Physiological Data and 3-km Time-Trial Performance

	<i>r</i>	SEE, %	<i>P</i>
Age, y	.43	18.8	.130
Height, cm	.01	20.3	.498
Body weight, kg	-.20	20.7	.972
DP-VO ₂ peak			
mL·kg ⁻¹ ·min ⁻¹	-.94	7.2	<.001**
mL·kg ^{-0.67} ·min ⁻¹	-.88	9.9	<.001**
L·min ⁻¹	-.72	14.4	.004**
RUN-VO ₂ max			
mL·kg ⁻¹ ·min ⁻¹	-.84	11.2	<.001**
mL·kg ^{-0.67} ·min ⁻¹	-.81	12.1	<.001**
L·min ⁻¹	-.64	16.0	.014*
%RUN-VO ₂ max	-.37	19.3	.197
C _{DP}			
mL·kg ⁻¹ ·m ⁻¹	.67	17.7	.056
mL·kg ^{-0.67} ·m ⁻¹	.68	17.8	.063
MAS, m·min ⁻¹	-.83**	11.6	<.001**

Abbreviations: %RUN-VO₂max, fractional utilization of VO₂max at VO₂peak in DP; C_{DP}, oxygen cost of DP at 70% of VO₂peak; DP, double poling; DP-VO₂peak, peak oxygen uptake in DP; RUN-VO₂max, maximal oxygen uptake in running; SEE, standard error of estimate.

* $P < .05$. ** $P < .01$.

As MAS is the product of DP-VO₂peak divided by C_{DP}, the improvement in MAS should be due to the improvement in DP-VO₂peak and C_{DP}. Several studies have shown an improved MAS after improvement in either VO₂peak or work economy, leaving the other variable more or less unchanged.^{14,19–24} When improving both variables at the same time, as in the present study, it was natural that the improvement in MAS was large. However, it may also be hypothesized that the improvement in %RUN-VO₂max observed in the intervention group also played a role in the large TT improvement seen in this group.

DP-VO₂peak and %RUN-VO₂max

The improvement in DP-VO₂peak observed in the intervention group seemed to be highly DP specific, as RUN-VO₂max did not change in either groups. This may reflect that the skiers adapted specifically to the load they were provided. Likely, DP did not provide enough muscle mass to tax the aerobic system to the same extent (eg, running).⁷ As discussed in Joyner and Coyle,⁷ performance VO₂ may be a strong performance indicator, and this may be understood as the aerobic capacity in the specific movement patterns being an equally great performance predictor compared with overall aerobic capacity (RUN-VO₂max). This is further supported by the significant correlation between increase in DP-VO₂peak and improvement in TT observed in this study.

The maintenance of RUN-VO₂max was as expected, as the intervention group did not increase total training volume or HIT volume (Table 2). They merely substituted their regular HIT volume (running and cycling) with HIT DP. On the other hand, HIT DP that was performed at 90% to 95% of HR_{peak} in DP, and thus approximately 88% to 93% of HR_{max}, proved to be a sufficient training stimulus to maintain overall aerobic capacity. The improvement in DP-VO₂peak, therefore, lifted the specific aerobic capacity of the nonspecially DP-trained subjects almost to the level of the more skilled subjects in the control group, despite a still much lower overall aerobic capacity. Together with the improvement in time performance in the present study, these results highlight the possibility for enhancing DP performance by improving specific aerobic capacity and maintaining overall aerobic capacity. This is well in line with the discussion of Sandbakk and Holmberg¹ that a better ability to utilize overall aerobic capacity in subtechniques like DP may be a key determinant for performance. The findings in the present study may also have further implications for the last months of preparation for cross-country skiers aiming for peak performance in specific DP events.

It has been previously presented in Støren et al²¹ that VO₂peak in cycling was improved after HIT performed as running. In Støren et al,²¹ VO₂peak in cycling followed an improvement in RUN-VO₂max, without an increase in %RUN-VO₂max. However, the intervention group in the present study increased %RUN-VO₂max by 7.3% points as a result of the improvement in DP-VO₂peak.

To our knowledge, this is a novel finding highlighting the importance of specific HIT training to improve %RUN-VO₂max in any cross-country skiing subtechnique, and thus performance as shown in the present study. This finding also specified that there may be at least 2 ways to improve work-specific VO₂peak. The first way, as demonstrated in Støren et al²¹ in cycling, is by improving overall aerobic capacity and leaving the percentage of work-specific VO₂peak unchanged. The second way, as demonstrated in the present study, is increasing work-specific VO₂peak and leaving the overall aerobic capacity unchanged.

The results from the present study are in contrast to results from previous studies who did not find significant improvements in %RUN-VO₂max in DP after interventions, including increased upper body endurance training.^{15,17,25} However, these interventions were not directly comparable with that of the present study, as they were using either a DP ergometer,¹⁵ additional upper body muscular endurance training,¹⁷ or sprint intervals.²⁵

The results from the present study showed a low %RUN-VO₂max at baseline (79% in the intervention group and 81% in the control group) compared with previous studies,^{14–17,25} ranging from approximately 80% to 90%. However, in the study of Hegge et al,¹² female cross-country skiers showed %RUN-VO₂max values in DP closer to our findings. One possible explanation for the low %RUN-VO₂max at baseline in the present study could be that the nonspecially DP-trained skiers had performed less roller skiing DP training prior to the study compared with previous studies, but this could hardly explain the low %RUN-VO₂max among the national-level skiers. However, as the national-level skiers also had quite low %RUN-VO₂max at baseline, we may speculate that they would benefit from having periods with extra DP focus as well.

Oxygen Cost of Double Poling

One of the main novelties of the present study was the concurrent improvements in DP-VO₂peak and C_{DP}. This combination is in contrast to previous studies showing slightly reduced work economy or gross efficiency when boosting VO₂max over a short period, as in Skovereng et al²⁶ and Vandbakk et al.²⁵ Skovereng et al²⁶ found a moderate correlation between improved VO₂max and deteriorated gross efficiency in cycling, which may indicate a deteriorated work economy, although care should be taken when comparing oxygen cost results with gross efficiency results. One possible explanation of the contrasting results observed in the present study and Vandbakk et al²⁵ was that Vandbakk et al used sprint intervals, that is, a much shorter interval duration and a much higher intensity than in the present study. On the other hand, the mean intensity for 4 × 4-min protocol in Skovereng et al²⁶ was 89% HR_{max}. This is in line with the durations and intensities of the present study, which was 90% to 95% of HR_{peak} in DP, and thus approximately 88% to 93% of HR_{max}. However, the results from the present study are in agreement with the findings in Nilsson et al¹⁵ who found improved work economy after HIT, where the intensity was 85% of maximal power output, which is a slightly higher intensity than reported in Skovereng et al²⁶ and the present study. Thus, when comparing results from the present study with the results from Vandbakk et al,²⁵ Skovereng et al,²⁶ and Nilsson et al,¹⁵ improvement or deterioration of C_{DP} seems to have little to do with the training intensity, bearing in mind that in all these studies, the intensities were above 85% of HR_{max}. It is, however, speculated in Skovereng et al²⁶ that training at moderate intensity (ie, approximately at the lactate threshold) may be more beneficial to

improve work economy or efficiency at these intensities, whereas very high-intensity training aimed to primarily improve VO₂peak with less amount of such moderate training may lead to decreased work economy or efficiency.

The improvement in C_{DP} in the intervention group in the present study is in close agreement with several previous studies, showing improvements of approximately 5% to 10% after 4 to 8 wk of HIT.^{15,22–24,27} Some of these previous results are from interventions in movement patterns the participants have not been previously specialized in, like straightforward running in soccer players.²² HIT interventions performed in athletes in their specific movement patterns may not result in oxygen cost improvements, as shown in Støren et al.²¹ McMillan et al²⁴ have showed a good example of the specificity in oxygen cost improvements, where an HIT intervention performed on a soccer-specific dribble track did not result in improvements in running economy tested on a treadmill. As the skiers in the intervention group in the present study consisted of athletes competing at the regional level, they were familiar with DP movement patterns, but had not previously performed HIT DP regularly. Therefore, more DP in general in the intervention group could be one of the main reasons for the improvement in C_{DP}.

Methodological Concerns

As the intervention group only included 7 subjects, there are possibilities of type II statistical errors. On the other hand, the improvements are large, and the low number of participants thus decreases the possibilities of type I errors. At the beginning of the intervention period, the 2 groups were different in gender representation. When analyzing the intervention group both with and without the 2 women, mean improvement in DP-VO₂peak was the same (0.27 vs 0.27 L·min⁻¹) and with approximately same SD (0.17 vs 0.19 L·min⁻¹). This was echoed in the results regarding %RUN-VO₂max and TT performance. Between-groups differences (intervention vs control) were thus approximately the same and still statistically significant both with and without women in the intervention group. However, as the intervention group without the 2 women only consisted of 5 subjects, the *P* values regarding within-group differences were somewhat worsened, although still significant in the intervention group (*P* = .035, *P* = .016, and *P* < .001 for DP-VO₂peak, %RUN-VO₂peak, and TT performance, respectively).

We cannot completely rule out that some of the improvements seen in the intervention group, compared with the control group, are due to better familiarization with the treadmill from pretest to posttest. However, the improvements in TT were at approximately the same level as the improvement in MAS. This suggests a physiological explanation for the TT improvement rather than a result of treadmill familiarization. In addition, the subjects got 2 familiarization sessions (45 and 25 min) before the first test, which was an incremental submaximal step test for measuring C_{DP}. Thus, the subjects got at least 90 min of familiarization before the DP-VO₂peak test. As the TT was performed on day 2, we considered the skiers well familiarized with the treadmill testing.

Practical Implications

The present study has shown that HIT DP may be an effective way to improve DP-VO₂peak, C_{DP}, and time performance in DP among

recreational cross-country skiers. In addition, the intervention maintained overall aerobic capacity, which was as expected as overall HIT volume did not increase during the HIT intervention. Therefore, the maintenance of RUN-VO₂max suggests that this training regimen may be sufficient to maintain it. We, therefore, suggest a training regimen with HIT DP as a supplement to, and not a substitution for, regular HIT, to improve both specific and overall aerobic capacity. This should be of special interest for skiers aiming for specialization in DP and for those who need to further develop their DP capacity.

The control group differed from the intervention group at baseline in RUN-VO₂max and TT performance, but not in %RUN-VO₂max. This indicates a potential for improvement in %RUN-VO₂max also in skiers at a national level. We, therefore, suggest investigating the effects of the same HIT DP intervention as in the present study on skiers on a national level in future studies.

Conclusion

A 6-wk HIT DP intervention was shown to be an effective training model to improve DP-specific capacities, with maintenance of RUN-VO₂max. Accordingly, HIT DP should be considered an effective training strategy to enhance DP performance in competitive skiers at a recreational level and should be of special interest for skiers aiming to specialize in or develop DP capacity.

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Article 3

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No Change – No Gain; The Effect of Age, Sex, Selected Genes and Training on Physiological and Performance Adaptations in Cross-Country Skiing

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The aim was to investigate the effect of training, sex, age and selected genes on physiological and performance variables and adaptations before, and during 6 months of training in well-trained cross-country skiers. National-level cross-country skiers were recruited for a 6 months observational study (pre – post 1 – post 2 test). All participants were tested in an outside double poling time trial (TT_{DP}), maximal oxygen uptake in running (RUN-VO_{2max}), peak oxygen uptake in double poling (DP-VO_{2peak}), lactate threshold (LT) and oxygen cost of double poling (C_{DP}), jump height and maximal strength (1RM) in half squat and pull-down. Blood samples were drawn to genetically screen the participants for the *ACTN3* R577X, *ACE* I/D, *PPARGC1A* rs8192678, *PPARG* rs1801282, *PPARA* rs4253778, *ACSL1* rs6552828, and *IL6* rs1474347 polymorphisms. The skiers were instructed to train according to their own training programs and report all training in training diaries based on heart rate measures from May to October. 29 skiers completed all testing and registered their training sufficiently throughout the study period. At pre-test, significant sex and age differences were observed in TT_{DP} ($p < 0.01$), DP-VO_{2peak} ($p < 0.01$), C_{DP} ($p < 0.05$), MAS ($p < 0.01$), LT_v ($p < 0.01$), 1RM half squat ($p < 0.01$), and 1RM pull-down ($p < 0.01$). For sex, there was also a significant difference in RUN-VO_{2max} ($p < 0.01$). No major differences were detected in physiological or performance variables based on genotypes. Total training volume ranged from 357.5 to 1056.8 min per week between participants, with a training intensity distribution of 90–5–5% in low-, moderate- and high-intensity training, respectively. Total training volume and ski-specific training increased significantly ($p < 0.05$) throughout the study period for the whole group, while the training intensity distribution was maintained. No physiological or performance variables improved during the 6 months of training for the whole group. No differences were observed in training progression or training adaptation between sexes

or age-groups. In conclusion, sex and age affected physiological and performance variables, with only a minor impact from selected genes, at baseline. However, minor to no effect of sex, age, selected genes or the participants training were shown on training adaptations. Increased total training volume did not affect physiological and performance variables.

Keywords: endurance training, skiing performance, training adaptations, double poling, maximal oxygen uptake, lactate threshold, work economy, genomics

INTRODUCTION

Cross-country skiing is regarded as one of the most demanding aerobic endurance sports, where male and female athletes have displayed some of the highest maximal oxygen uptakes (VO_{2max}) ever recorded (Sandbakk and Holmberg, 2017). VO_{2max} , often measured in running (RUN- VO_{2max}), is suggested as a main predictor for cross-country skiing and overall endurance performance (Pate and Kriska, 1984; Ingjer, 1991; di Prampero, 2003; Støren et al., 2013; Sandbakk and Holmberg, 2017; Sunde et al., 2019; Johansen et al., 2020). However, in cases where RUN- VO_{2max} is relatively homogenous or held constant, differences in work economy (C) (Conley and Krahenbuhl, 1980; di Prampero, 2003) and/or maximal strength (Hoff et al., 2002; Støren et al., 2008; Sunde et al., 2010, 2019) are regarded as major contributors for differentiating performance in endurance athletes.

Although the main determining factors for cross-country skiing performance are relatively clear, the best way to develop these physiological factors over longer periods in every individual skier is still under investigation (Stöggl and Sperlich, 2015). Traditionally, endurance training makes up almost 90% of the total training for competitive cross-country skiers, while the rest is strength training and speed training (Losnegaard et al., 2013; Stöggl and Sperlich, 2015; Sandbakk et al., 2016). The endurance training during season preparation for both junior and senior cross-country skiers is characterized with high volumes of low-intensity training (LIT) and low to moderate volumes of moderate- (MIT) and high-intensity training (HIT). This has been regarded as an “optimal” intensity distribution for developing higher performance capacity in cross-country skiers (Ingjer, 1992; Seiler and Kjerland, 2006; Sandbakk et al., 2016; Solli et al., 2017). Stöggl and Sperlich (2014) suggests that a polarized training intensity distribution, with high LIT volumes (~80%) and relatively high HIT volumes (~20%) with low volumes of MIT, would be more beneficial for further improvements of well-trained endurance athletes, compared to training models with higher volumes of MIT. Additionally, higher volumes of HIT are considered as a more efficient way to elevate VO_{2max} compared to LIT, both in well-trained to elite cross-country skiers and recreational skiers (Nilsson et al., 2004; Helgerud et al., 2007; Støren et al., 2012; Rønnestad et al., 2014, 2016; Stöggl and Sperlich, 2014; Johansen et al., 2020).

Ingjer (1992) observed that young cross-country skiers started to level-off in VO_{2max} at age 19–20 following a training regime similar to that described above, at least in values relative to body mass. Following the same training pattern year after

year has not proven to be an effective strategy to increase VO_{2max} further in well-trained and elite adult cross-country skiers (Gaskill et al., 1999; Solli et al., 2017). In Gaskill et al. (1999) and Støren et al. (2012), major changes in the relative intensity distribution of the endurance training led to significant improvements in VO_{2max} and performance in well-trained endurance athletes. However, a recent study showed substantial differences in training response to the same HIT protocol among well-trained cyclists (Bratland-Sanda et al., 2020). This points to the need for better individualization of training programs.

Earlier studies have mainly explored training characteristics in cross-country skiers retrospectively, with no opportunity to investigate the direct physiological effect of the athlete's training. However, the study of Losnegaard et al. (2013) performed several tests through the preparation phase and the competitive season in elite male cross-country skiers competing at an international and national level. The study revealed improvements in skiing economy (V2 skating), O_2 -deficit and skating performance on a time trial on a roller-skiing treadmill. No improvements were observed in VO_{2max} . These were the results of a traditional high volume LIT and low to moderate volume of MIT and HIT regime. However, mainly retrospective studies have been performed on sub-elite and junior cross-country skiers over longer time periods (>10 weeks). No studies have investigated training characteristics and the subsequent physiological effects in both sub-elite senior and junior cross-country skiers competing at a national and regional level over longer periods.

Sex differences in performance determining factors in cross-country skiing is generally reported to be between 10 and 30%, where greater sex differences are shown when the upper-body is used more extensively (Sandbakk et al., 2014; Hegge et al., 2016; Sunde et al., 2019). Sex differences have been examined in recent years among cross-country skiers, however, sex comparisons in training responses to a similar training regimen is not well examined in well-trained cross-country skiers. Previous investigations have revealed no difference in training responses between males and females following the same training program in both sedentary and well-trained individuals (Astorino et al., 2011; Støren et al., 2017; Varley-Campbell et al., 2018), suggesting that this may also be the case for well-trained cross-country skiers. Although both junior and senior skiers have been investigated separately (Ingjer, 1992; Sandbakk et al., 2010, 2016; Losnegaard et al., 2013), direct comparisons of training responses in these age-groups have not been executed previously in cross-country skiers. Investigations of both sex and age-related

differences in training responses may be crucial to understand differences in training adaptations, and further improve the quality of the individualization of training programs.

The genetic component of sports performance and trainability has received increasing attention the last two decades. Sports performance is considered a complex trait, influenced by many genes. A number of single nucleotide polymorphisms (SNPs) have been associated with various aspects of athletic ability and sports performance. Two polymorphisms that have been intensely investigated are the *ACTN3* R577X and *ACE* I/D (Jacques et al., 2019). The *ACTN3* gene codes for α -actinin-3, a protein expressed in fast-twitch muscle fibers. The common R577X polymorphism leads to the deficiency of the protein in individuals with the XX genotype (North et al., 1999), which is the case for around 19% of Caucasians (Roth et al., 2008; Goleva-Fjellet et al., 2020). Lack of the α -actinin-3 has been associated with increased muscle endurance, and decreased maximal power generation (MacArthur et al., 2008). The *ACE* gene encodes the angiotensin I-converting enzyme, having a role in the regulation of blood pressure, fluid-electrolyte balance and affecting the muscle function (Puthuchearu et al., 2011; Pescatello et al., 2019). *ACE* seems to play a role in exercise induced adaptations and the I allele has been regarded as the endurance allele (Ma et al., 2013; Pescatello et al., 2019). Few studies have investigated these polymorphisms in relation to cross-country skiing performance. Magi et al. (2016) found higher frequencies of the *ACTN3* RR and *ACE* ID genotype in male skiers compared to controls. In addition, male skiers with XX genotype tended to exhibit greater increase in VO_{2peak} over a 5-year period. The same finding applied to female skiers with the ID genotype. Orysiak et al. (2013), on the other hand, did not find any associations between the *ACE* I/D and VO_{2max} in well trained winter sports athletes. No previous studies have compared the genotype distribution for selected genes between regional to national cross-country skiers and the normal population within the same region. Goleva-Fjellet et al. (2020) genotyped *ACE* and *ACTN3* in a cohort representing the region of South East Norway, making it possible to compare this with an athletic cohort.

The *PPARGC1A* rs8192678 SNP has also gained attention in exercise genetics. The protein encoded by the gene, *PGC1 α* (peroxisome proliferator-activated receptor gamma co-activator-1-alpha), induce the mitochondrial biogenesis and modulate the composition and functions of the mitochondria (Austin and St-Pierre, 2012). Recent reviews have concluded that the rs8192678 polymorphism is associated with aerobic trainability and sports performance (Petr et al., 2018, 2020; Tharabenjasin et al., 2019). Peroxisome proliferator-activated receptor genes, e.g., *PPARG* (rs1801282) and *PPARA* (rs4253778), have also been investigated in relation to trainability and athletic ability (Petr et al., 2018, 2020). According to Bouchard et al. (2011) the rs6552828 SNP of the acyl-CoA synthase long-chain member 1 gene (*ACSL1*) could explain around 6% of the training response of VO_{2max} to standardized exercise training programs. A recent study by Harvey et al. (2020) reported that the rs1474347 polymorphisms in the interleukin-6 (*IL6*) gene was associated with training induced improvements in VO_{2max} in both moderately and well trained participants.

To the best of our knowledge, no study have investigated effects of sex, age, training and selected genes on physiological and performance adaptations in the same study. Therefore, the primary aim of this study was to investigate training adaptations in physiological and performance variables in well-trained cross-country skiers after 6 months of training during season preparation (i.e., May to October). Secondly, we wanted to investigate possible differences between gender and age groups in baseline values and training adaptations during the study period. Thirdly, we wanted to investigate the effects of specific candidate genes on physiological and performance variables at baseline. We hypothesized that age and sex would influence on baseline values, but not training adaptations, and that differences in training would impact training adaptations. Further, we hypothesized that the distribution of the selected genetic variants would represent the distribution of the general population for this region and not impact physiological or performance values at baseline.

MATERIALS AND METHODS

Experimental Approach

The main purpose of this study was to evaluate changes in physiological and performance variables after 6 months of training (May to October) in well-trained cross-country skiers. We also wanted to compare baseline values and training induced changes in males and females, and young and older skiers, as well as in skiers with different genotypes. Therefore, the participants were instructed to train according to their own training programs worked out by themselves or their coaches prior to the research project, and report their daily training for the whole 6 months period. They were tested for a number of physiological, strength and performance variables over 2 days at three occasions; before (PRE), mid-way (POST1) and after (POST2) the study period. The test battery consisted of measurements of $RUN-VO_{2max}$, VO_{2peak} in double poling (DP- VO_{2peak}), time to exhaustion (TTE), oxygen cost of double poling (C_{DP}), lactate threshold in double poling (LT), jump height, 1RM and maximal power tests in half squat and pull-down and performance in a 5.64 km double poling time trial (TT_{DP}). At baseline, blood samples were drawn to assess gene status in selected genes.

Subjects

A total of 46 well-trained cross-country skiers (30 males and 16 females), differing in age (16–48 years) and performance-level, were recruited for the whole study. The study's medical doctor approved all participants for participation. However, 17 skiers were excluded because they were not able to fulfill the requirements of three testing sessions during the study period due to sickness or injuries or did not report their training habits sufficiently. Thus, 29 skiers were included in the statistical analyzes. To investigate age-related effects the included skiers were divided in two age groups (16–18 and ≥ 19 years). These groups were defined as either in, or above puberty, and also corresponding to in, or above high-school age. The ≥ 19 group included skiers from 19 to 48 years. All subjects were recruited by invitation to high-schools for skiers in Southeastern Norway

or regional cross country ski teams. The included skiers differed substantially in performance level, from medium-junior level to top national level. The best male and female skiers had finished top 10 in numerous VISMA ski classics races (i.e., Vasaloppet and Marcialonga) and/or top 30 in the Norwegian national championship, and the slowest skiers finished in the lower part of national junior competitions. Subjects' characteristics are summarized in **Table 1**.

The study was conducted in accordance with the Declaration of Helsinki, and evaluated and approved by the regional ethics committee of Southeast Norway (REK 2017/2522) and the institutional research board at the University of South-Eastern Norway (former University College of South-Eastern Norway). After having received information about the study, all participants gave their written informed consent before participation. Parental written consent was collected for skiers below 18 years.

Test Procedures

In order to evaluate changes in physiological and performance variables related to the skiers training, all participants were tested at three separate occasions. PRE were performed in April/May, POST1 were performed in July/August, and POST2 were conducted in October/November. All testing procedures were the same at all testing sessions.

All tests were performed on two consecutive days. The participants were instructed to do only light training the last 24 h before testing, and no food or nutritious drinks were allowed 1 h before the first test. In between tests, the participants were allowed to eat a light meal of energy-rich food and drinks. The last meal before testing and food intake in-between tests were registered, and all participants were asked to consume the same food in the subsequent testing sessions (POST1 and POST2). All preparation procedures were the same at all three testing sessions. The tests were also conducted at approximately the same time of day (± 2 h) at PRE, POST1 and POST2 to avoid circadian differences.

The first day of testing consisted of three maximal jump height tests, an incremental running test for determining RUN-VO_{2max}, and a TT_{DP}. Before the jump tests, the participants performed a self-conducted warm-up procedure of at least 10 min. This

warm-up was registered and repeated at POST1 and POST2. Then they performed three separate jump tests in the following order: squat jump (SJ), counter-movement jump (CMJ) and counter-movement jump with arm swing (CMJas). For the SJ tests, the knee-angle were 90° and this was controlled by the same test leader at all tests. No counter-movements were allowed in this particular test, whereas no counter-movement restrictions were given for the CMJ and CMJas tests. All participants were given at least three consecutive attempts in each jump-test, and the best attempt was registered as the result. At least 3 min of rest were given between the separate jump tests to ensure sufficient restitution. All jump-tests were performed by use of a force platform (Ergotest Innovation, Porsgrunn, Norway) for jump height measurements. The force platform was calibrated in accordance with the manufacturers' manual before each test. Jump height was calculated by the following equation,

$$h = \frac{v_v^2}{2 \times g} \quad (1)$$

where h is jump height, v is the velocity at take-off, which again is based on calculation of force multiplied with time divided by mass, and g is gravitation (Ergotest Innovation, Porsgrunn, Norway).

After at least 20 min of rest, the participants started a 10 min self-conducted warm-up procedure before an incremental VO_{2max} test in running. This warm-up was registered and repeated at POST1 and POST2. The RUN-VO_{2max} test was conducted by the same procedures as presented in Sunde et al. (2019). Briefly, the participants started at an intensity of 6% inclination and 7–8 km · h⁻¹ and 9–10 km · h⁻¹ for female and male, respectively. The test started with 1% increase in inclination every 30 s until 8% was reached, whereas only speed was increased by 0.5 km · h⁻¹ every 30 s after that. All participants were instructed to run to voluntary fatigue, and the three highest subsequent VO₂ measurements were used to calculate VO_{2max}. Heart rate (HR) \geq 98% of HR_{max}, respiratory exchange ratio (RER) \geq 1.05, blood lactate concentration ([La⁻]_b) \geq 8.0 mmol · L⁻¹, rate of perceived exertion (Borg scale 6–20) \geq 17, and flattening of the VO₂ curve was used to evaluate if VO_{2max} was reached. The metabolic test system, MetaLyzer II Cortex

TABLE 1 | Subjects characteristics.

Variable	Total (n = 29)	Males (n = 17)	Females (n = 12)	16–18 years (n = 16)	\geq 19 years (n = 13)
Age (yr)	22.1 \pm 8.4	24.1 \pm 10.2	19.3 \pm 4.1	17.3 \pm 0.8	28.0 \pm 9.8
Weight (kg)	69.4 \pm 9.3	73.2 \pm 8.6	64.0 \pm 7.8**	64.4 \pm 6.7	75.5 \pm 8.5§§
Height (cm)	176.2 \pm 8.9	181.1 \pm 7.1	169.3 \pm 6.3**	173.8 \pm 7.7	179.2 \pm 9.7
RUN-VO_{2max}					
mL · kg ⁻¹ · min ⁻¹	62.9 \pm 8.0	67.4 \pm 6.7	56.5 \pm 4.5**	61.1 \pm 8.0	65.2 \pm 7.7
L · min ⁻¹	4.38 \pm 0.88	4.92 \pm 0.68	3.60 \pm 0.37**	3.94 \pm 0.70	4.92 \pm 0.79§§
Training					
min · week ⁻¹	241.0 \pm 162.6	604.2 \pm 153.1	462.1 \pm 142.9*	529.4 \pm 180.6	557.9 \pm 138.7

Values are mean and SD. Yr, years. Kg, kilograms. Cm, centimeters. RUN-VO_{2max}, maximal oxygen uptake in running. mL · kg⁻¹ · min⁻¹, milliliters per kilogram bodyweight per minute. L · min⁻¹, liters per minute. min⁻¹ week, average weekly training the last 3 months in minutes. *p < 0.05 significantly different from male value. **p < 0.01 significantly different from male value. §§p < 0.01 significantly different from 16 to 18 years value.

(Biophysic GmbH, Leipzig, Germany) was used for all VO_2 measurements, with measurements every 10 s. Before testing the O_2 -analyzer were calibrated with ambient air and certified calibration gases (16% O_2 /4% CO_2), while the flow sensors were calibrated with a 3-L calibration syringe (Biophysic GmbH, Leipzig, Germany) before each test. The treadmill used was a Woodway PPS 55 sport (Waukesha, WI, United States), calibrated for speed and incline. HR were registered by the participants own heart rate monitors or by Polar s610 HR monitors (Kempele, Finland).

After at least 1 h of rest, a 5.64 km TT_{DP} test was performed in a paved roller ski course track of 940 m. The TT procedures have been previously presented in Sunde et al. (2019). Only the DP technique was allowed throughout the test. The TT was organized with individual starts, and 30 s starting intervals. Drafting was not allowed. The subjects used their own roller-skis for classic skiing and poles and were instructed to use wheel type 2 for the time trial test. All subjects used the same pair of roller skis at PRE, POST1, and POST2. Differences in temperature and humidity may influence the rolling resistance of the roller skis, and thus the results of this test. Therefore, we used the same procedures for calculating a correction factor described previously in Sunde et al. (2019).

The second day of testing consisted first of sub-maximal VO_2 and $[\text{La}^-]_{\text{b}}$ measurements in DP, in order to determine C_{DP} and LT. This was, after 5 min of active recovery, followed by a ramp protocol to exhaustion to determine $\text{DP-VO}_{2\text{peak}}$. After 1 h of rest, the second day of testing ended with two maximal strength tests in half-squat and pull-down.

The DP tests were performed on a motorized treadmill specialized for cross-country skiing (Rodby RL 2700E, Rodby Innovation, Vänge, Sweden). Every participant performed one 30-min workout for familiarization to the DP treadmill before testing, as previously used in Sunde et al. (2019). All participants used the same pair of roller skis at all DP tests during the study period (Swenor Fiberglass, Sarpsborg, Norway) with the same binding system (NNN, Rottefella, Klokkearstua, Norway). The subjects were allowed to use their own poles and additional skiing equipment, which was the same in all three test sessions. During treadmill testing, the participants were attached to a safety harness, connected to the roof, to avoid falling. Three to six 4-min work periods, with registration of VO_2 and HR measurements the last minute, were conducted for calculating C_{DP} at LT intensity and LT. Work periods were only separated by 1-min for measurements of $[\text{La}^-]_{\text{b}}$. Whole blood lactate values were measured by a Lactate Scout+ (SensLab GmbH, Leipzig, ray Inc., Kyoto, Japan). The subjects started the first work period at a work intensity assumed to be 50–70% of their $\text{DP-VO}_{2\text{peak}}$. This corresponded to 10–11.5 $\text{km} \cdot \text{h}^{-1}$ and 4% inclination for males and 6–8 $\text{km} \cdot \text{h}^{-1}$ and 4% inclination for females. In the following work periods, the speed increased by 1–3 $\text{km} \cdot \text{h}^{-1}$, and the test terminated after $[\text{La}^-]_{\text{b}}$ levels exceeding the subjects' LT. Warm up lactate value (i.e., the lowest measured lactate value) + 2.3 $\text{mmol} \cdot \text{L}^{-1}$ were used to define LT. This is in accordance with the protocol from Helgerud et al. (1990) and described and discussed in detail in Støren et al. (2014) and Sunde et al. (2019).

After 5-min of active rest, the subjects performed the RAMP protocol to exhaustion for determining $\text{DP-VO}_{2\text{peak}}$. The starting intensity was set to 6% inclination and 7 $\text{km} \cdot \text{h}^{-1}$ for both genders. The inclination was constant through the whole test, while speed increased by 1 $\text{km} \cdot \text{h}^{-1}$ every 60 s. All participants received motivational feedback throughout the test. The test terminated when the skiers slowly moved backward, despite intense motivational feedback, and reached a pre-defined mark 1 m behind the subjects starting position on the treadmill. TTE was registered and the $\text{DP-VO}_{2\text{peak}}$ was defined as the mean of the two highest subsequent VO_2 -measurements. Maximal aerobic speed (MAS) in double poling were calculated in the same way as presented in Sunde et al. (2019) and Johansen et al. (2020), i.e., $\text{DP-VO}_{2\text{peak}}/C_{\text{DP}}$.

A 60-min rest period were given prior to the tests of 1RM and maximal power output in half-squat (Smith-machine, PreCore, Woodinville, WA, United States) and pull-down (Gym 2000, Vikersund, Norway). Pilot testing in Støren et al. (2008) showed no deterioration in 1RM half-squat 30 min after maximal aerobic tests, thus we considered 60-min to be more than sufficient to give valid maximal strength results. The strength tests protocol is identical to the protocol used in Sunde et al. (2019). Both strength tests started with 10 reps at approximately 50% of 1RM. After this, the following sets were performed at approximately 60% (5 reps), 70% (3 reps), and 80% (2 reps), only separated by 3 min rest periods. All repetitions were performed with a slow eccentric phase with a complete stop of movement in the lowest position (half-squat) or the highest position (pull-down) of approximately 1 s. This was followed by a maximal mobilization in the concentric phase. The MuscleLab system (Ergotest Innovation, Porsgrunn, Norway) calculated power output by measurements of lifting time and distance of work. After the sub-maximal series, the participants performed at least 1 rep at their estimated 1RM. From there on: 1 rep, and load increments of 2.5–10 kg from the subsequent lift, were conducted until 1RM was reached.

Training Registration

The participants were instructed to train according to their own training plans worked out by themselves or by their coaches throughout the study period, without any influence or interventional instructions from the research personnel. All participants recorded training data in digital training diaries, i.e., in an online diary from the Norwegian Olympic Federation, or in Polar Flow. The athletes had all used digital training diaries for at least 1 year prior to the study. Every training session and competition was recorded and controlled by the same research personnel throughout the study period, and 3-months prior to PRE. The two training periods between PRE to POST1 and POST1 to POST2 were defined as 1st training period (P_1) and 2nd training period (P_2). In order to investigate potential changes in training inside P_1 and P_2 , the periods have been further divided into a total of four periods where appropriate (P_{1A} , P_{1B} , P_{2A} , and P_{2B}).

All training data were systemized based on training modality and training intensity. Training modality was either endurance,

strength, speed/jump or other, and activity was running, roller-skiing, cross-country skiing or cycling. Roller-skiing and cross-country skiing on snow were defined as ski-specific training, while running and cycling was defined as unspecific training. Endurance training intensity were monitored as HR “time in zone,” and categorized into three intensity zones: (1) low-intensity training (LIT; $\leq 81\%$ of HRmax), (2) moderate-intensity training (MIT; $82\text{--}87\%$ of HRmax), and (3) high-intensity training (HIT; $\geq 88\%$ of HRmax). All endurance training and competitions were performed with the skiers’ personal heart rate monitors. This is in accordance with the procedures used in Støren et al. (2008) and Sunde et al. (2010).

Strength training consisted mainly of maximal strength training and/or general strength training. Maximal strength training was targeting large muscle groups, i.e., 1–6 repetitions in, i.e., half squat, pull-down or deadlift. General strength training was performed with 10–30 repetitions and with a main purpose of increase stability and general strength in the upper-body and trunk. The duration of strength training sessions where quantified as the time between the first set of the first exercise and last set of the last exercise, including rest periods between sets and exercises. Additional warm-up and cool-down were registered as LIT, while stretching where included in “other training.” Jump training (i.e., 1–6 box-jumps or jump exercises in stairs) was quantified in the same manner as strength training. Speed training during LIT- or MIT-sessions was mainly performed during ski-specific training. The number of sprints were multiplied by 1.5 min since the period after each sprint was performed at a very low intensity. The monitoring of strength-, speed-, and jump training is in accordance with the quantification procedures used in Sandbakk et al. (2016).

DNA Sampling and Genotyping

Venous blood was drawn when the participants first attended to the laboratory before the physiological testing procedures at the first testing session (April/May). The EDTA tubes were stored at -20°C . Before the DNA extraction, the samples were thawed at room temperature. DNeasy Blood & Tissue Kit (Qiagen, MD, United States) was used to extract the DNA from 100 μl of blood following the manufacturer’s instructions.

ACE I/D polymorphism, rs4343 polymorphism in the *ACE* gene was genotyped as it might be the best proxy to I/D polymorphism (Abdollahi et al., 2008), than analyzed to determine the I/D genotype. Genotyping for all polymorphisms was performed using TaqMan[®] SNP Genotyping Assay. Assay IDs were as follows: C__11942562_20 for *ACE* rs4343; C__590093_1 for *ACTN3* R577X; C__30469648_10 for *ACSL1* rs6552828; C__1643192_20 for the *PPARGC1A* rs8192678; C__1839698_20 for *IL6* rs1474347; C__1129864_10 for *PPARG* rs1801282 and C__2985251_20 for *PPARA* rs4253778 polymorphism (Thermo Fisher Scientific, MA, United States). StepOnePlus[™] Real-Time PCR System (Applied Biosystems[®], CA, United States) was used to carry out the qPCR. Genotype calling was performed by StepOne Software v2.0. 15 μl of final reaction volume contained 8.44 μl Genotyping Master Mix, 0.42 μl Assay mix (40 \times), 6.33 μl double distilled H₂O and ~ 100 ng of DNA template. Cycling conditions were as follows:

30 s at 60°C was followed by initial denaturation step for 10 min at 95°C ; then, 40 cycles of denaturation at 95°C for 15 s were followed by annealing at 60°C for 1 min in cycling stage, finishing with the final post-read step for 30 s at 60°C .

Statistical Analyses

Normality tests and Q-Q plots were used to evaluate normal distribution for main variables (TT_{DP}, RUN-VO_{2max} and MAS). In all cases, a normal distribution was observed, thus parametric statistics were used. Values were expressed as mean \pm SD, and inter-individual variability in training and physiological variables were expressed as coefficient of variance (CV). To evaluate potential changes in physiological response and training characteristics for the total group, within sexes and within age groups, a Univariate General Linear Model (GLM) test with Tukey *Post Hoc*-tests was used. To examine potential differences between sexes and age groups in physiological response and training characteristics during the study period, GLM Univariate with pairwise comparisons and independent sample *t*-tests were conducted. For correlations between baseline values, and between differences between different test points (delta correlations), correlation coefficients *r* was used from Pearson’s bivariate tests. Correlation coefficients were evaluated in accordance with Hopkins (2000), which are presented in detail previously (Sunde et al., 2019). Since the participants represented both female and male skiers, also partial correlations were conducted corrected for sex and age.

One-way ANOVA with Tukey *Post Hoc*-tests was used to assess the associations between the genotypes and physiological and performance variables at baseline. To assess the effects of the alleles on these variables, a two-tailed independent sample *t*-test was applied. In order to test for the Hardy-Weinberg equilibrium (HWE) for all polymorphisms and to compare the genotype frequencies to those of other studies, Pearson’s Chi-square test (χ^2) was used. When analyzing effects of different genotypes on physiological parameters, all female values from the physiological tests were multiplied according to the average gender difference between males and females in the present study. This was conducted to avoid bias effects of different gender representation for the different candidate genes and genotypes. In order to promote comparability between candidate gene studies, effect size (Cohen’s *d*) was calculated using Microsoft[®] Excel[®] (Redmond, WA, United States) for the gender corrected variables across the genotypes (**Supplementary Table 6**). The effect size was interpreted as follows: below 0.50 – small effect, 0.5 and above – moderate effect, 0.8 and above – large effect (Cohen, 1988). As the participants were following individual training programs, genetic analyzes of trainability were not performed. For all statistical analyzes performed, the statistical package for social science version 26 (SPSS, IBM, Chicago, IL, United States) was used. A *p* value < 0.05 was accepted as statistically significant in all tests (two-tailed).

Power calculations prior to the study revealed that with a between-group difference in the selected physiological variables of 5%, and with a common standard deviation of the same size, a sample size of 12 to 16 subjects were needed in each age- and gender group in order accomplish a significant level of 0.05 and

a power of 80%. Regarding the genetic variables, the material is under-powered in order to accomplish full genetic analyses. Multivariate ANOVA analyzes between the different genotypes and the different physiological variables were thus not performed. However, the material was still interesting in order to see if there were substantial differences in physiological variables related to single genes. Also, the material was sufficient to investigate if the cohort of skiers differentiated from a general population from the same geographical area in genotype and allele frequencies.

RESULTS

Training Characteristics

The skiers training was registered for 23.4 ± 2.2 weeks from PRE to POST2. From PRE to POST1 the skiers trained for 12.7 ± 1.7 weeks, and for 10.7 ± 1.4 weeks from POST1 to POST2. In total, 8460 training sessions were registered, with 5957 inside the 6-months study period. The remaining sessions registered were conducted in the 3 months before PRE. This corresponded to an average of 205 ± 48 sessions per skier during the study period, and 292 ± 72 sessions per skier when the training period before PRE were included.

Training characteristics for the whole group in P_1 and P_2 are presented in **Table 2**, while the sub-periods (P_{1A} , P_{1B} , P_{2A} , and P_{2B}) are presented in **Supplementary Table 3**. The mean total training volume in P_1 was 701.5 ± 169.8 min \cdot week $^{-1}$ and increased significantly to 753.2 ± 137.6 min \cdot week $^{-1}$ in P_2 ($p < 0.05$). Total endurance training accounted for 86.9 ± 6.6 and

$84.4 \pm 7.1\%$ of total training volume in P_1 and P_2 , respectively. The relative intensity distribution in the endurance training was 90.0 ± 4.3 , 4.8 ± 2.2 , and $5.2 \pm 3.0\%$ in LIT, MIT, and HIT, respectively, in P_1 . In P_2 , LIT, MIT, and HIT represented 89.6 ± 3.2 , 4.8 ± 2.2 , and $5.7 \pm 2.4\%$, respectively. The relative intensity distribution did not change significantly throughout the 6-months training period. Ski-specific training accounted for 49.7 ± 13.6 and $55.7 \pm 10.5\%$ of total endurance training in P_1 and P_2 , respectively. Total ski-specific training and ski-specific LIT increased significantly from P_1 to P_2 ($p < 0.01$), while ski-specific MIT and HIT remained unchanged. In total, 65.2 ± 18.0 and $62.4 \pm 17.7\%$ of ski-specific training was performed as classic skiing, while the remaining 34.8 ± 17.3 and $37.6 \pm 17.7\%$ was performed as freestyle-skiing in P_1 and P_2 , respectively. Most of the remaining volume of total endurance training were performed either as running ($40.1 \pm 9.8\%$ in P_1 , $38.6 \pm 9.0\%$ in P_2) or as cycling ($9.9 \pm 14.7\%$ in P_1 , $5.6 \pm 7.0\%$ in P_2).

Strength training was performed regularly with 1–3 sessions per week throughout the study period. In P_1 , strength training accounted for $8.8 \pm 4.0\%$ of the total training volume while in P_2 , $10.3 \pm 3.8\%$ of total training volume was strength training. The amount of strength training increased significantly from P_1 to P_2 ($p < 0.01$). Speed/jump and other training stayed unchanged throughout the whole training period while accounting for 1.2 ± 1.3 and $3.1 \pm 4.8\%$ in P_1 and 1.3 ± 1.4 and $4.0 \pm 4.1\%$ in P_2 , respectively.

Physiological Adaptations

Results in physiological and performance variables at the three testing sessions (PRE, POST1, and POST2) are presented in **Table 3**. No significant changes were observed in physiological and performance variables in the whole group from PRE to POST1, from POST1 to POST2, except for RER_{RUN} ($p < 0.05$), or PRE to POST2.

Correlations between physiological and performance variables at baseline and between delta values in physiological, performance and training variables is presented in **Tables 4–6**. Strong correlations were observed between TT_{DP} and DP-VO_{2peak} ($r = -0.79$, $p < 0.01$), MAS ($r = -0.79$, $p < 0.01$), LT_v ($r = -0.82$, $p < 0.01$), RUN-VO_{2max} ($r = -0.68$, $p < 0.01$), and 1RM pull-down ($r = -0.64$, $p < 0.01$) at baseline for the whole group. Corrected for gender, strong significant correlations were still apparent between TT_{DP} and DP-VO_{2peak} ($r = -0.63$, $p < 0.01$), MAS ($r = -0.58$, $p < 0.01$), and LT_v ($r = -0.64$, $p < 0.01$) at baseline. Corrected for age-groups, the similar strong correlations as seen for the whole group were almost at same level between TT_{DP} and RUN-VO_{2max} ($r = -0.68$, $p < 0.01$), LT_v ($r = -0.77$, $p < 0.01$), DP-VO_{2peak} ($r = -0.76$, $p < 0.01$), MAS ($r = -0.75$, $p < 0.01$), and 1RM pull-down ($r = -0.52$, $p < 0.01$). A strong correlation was also apparent between MAS and LT_v, both independent ($r = 0.93$, $p < 0.01$) and dependent ($r = 0.85$, $p < 0.01$ and $r = 0.89$, $p < 0.01$) of gender and age, respectively.

No delta correlations were observed between Δ TT_{DP} and any delta values of the physiological or training variables (**Tables 5, 6**). Δ MAS revealed strong significant correlations to Δ LT_v ($r = 0.57$, $p < 0.01$) and Δ C_{DP} ($r = -0.85$, $p < 0.01$). Δ ski specific

TABLE 2 | Training characteristics during the 6 months study period ($n = 29$).

Variable	P_1 (May to July)	P_2 (August to October)
Duration (weeks)	12.7 ± 1.7	10.7 ± 1.4
Training (min \cdot week$^{-1}$)		
Total training volume	701.5 ± 169.8	$753.2 \pm 137.6^*$
Endurance training		
LIT	548.7 ± 148.2	569.1 ± 116.9
MIT	29.4 ± 11.4	30.4 ± 14.7
HIT	31.8 ± 15.7	36.0 ± 17.2
Total	609.8 ± 154.1	635.5 ± 126.3
Training mode		
Ski specific	303.1 ± 120.1	$353.8 \pm 105.4^{**}$
LIT _{ski}	270.2 ± 108.0	$313.6 \pm 91.0^{**}$
MIT _{ski}	15.7 ± 8.4	19.4 ± 12.4
HIT _{ski}	14.0 ± 11.7	17.5 ± 10.6
Running	244.5 ± 77.6	245.4 ± 71.8
Cycling	60.5 ± 95.5	35.3 ± 46.2
Strength training	61.7 ± 30.5	$77.8 \pm 31.4^{**}$
Speed/jump training	8.2 ± 8.4	9.6 ± 10.4
Other	21.7 ± 41.8	30.5 ± 33.9

Values are mean and SD with coefficient of variance in percentage. min \cdot week $^{-1}$, minutes per week. P_1 , first training period from May to July. P_2 , second training period from August to October. LIT, low-intensity training. MIT, moderate-intensity training. HIT, high-intensity training. * $p < 0.05$ significantly different from P_1 value. ** $p < 0.01$ significantly different from P_1 value.

TABLE 3 | Physiological and performance characteristics during the study period ($n = 29$).

Variable	PRE		POST1		POST2 ^a	
BW (kg)	69.4 ± 9.3	(13.4)	69.0 ± 8.6	(12.5)	69.6 ± 8.3	(11.9)
TT_{DP}						
seconds	875.1 ± 92.8	(10.6)	866.9 ± 91.4	(10.5)	845.9 ± 88.2	(10.4)
RUN-VO_{2max}						
mL · kg ⁻¹ · min ⁻¹	62.9 ± 8.0	(12.7)	64.7 ± 7.7	(11.9)	64.1 ± 8.8	(13.7)
L · min ⁻¹	4.38 ± 0.87	(19.9)	4.48 ± 0.85	(19.0)	4.47 ± 0.86	(19.2)
mL · kg ^{-0.67} · min ⁻¹	254.6 ± 36.1	(14.2)	261.4 ± 35.4	(13.5)	259.7 ± 38.8	(14.9)
HR	196.6 ± 10.6	(5.3)	195.5 ± 10.6	(5.4)	193.6 ± 10.9	(5.6)
RER	1.12 ± 0.03	(2.7)	1.11 ± 0.05	(4.5)	1.14 ± 0.04*	(3.5)
[La ⁻ _b]	10.1 ± 2.3	(22.8)	11.3 ± 2.6	(23.0)	10.0 ± 2.1	(21.0)
RPE	17.2 ± 1.7	(9.9)	17.9 ± 1.2	(6.7)	17.6 ± 1.4	(7.9)
DP-VO_{2peak}						
mL · kg ⁻¹ · min ⁻¹	54.3 ± 7.3	(13.4)	54.6 ± 7.2	(13.2)	55.5 ± 7.3	(13.2)
L · min ⁻¹	3.79 ± 0.79	(20.8)	3.80 ± 0.73	(19.2)	3.89 ± 0.74	(19.0)
mL · kg ^{-0.67} · min ⁻¹	220.0 ± 33.0	(15.0)	221.0 ± 31.7	(14.3)	225.2 ± 32.3	(14.3)
%RUN-VO _{2max}	86.5 ± 7.3	(8.4)	84.4 ± 5.8	(6.9)	86.9 ± 5.7	(6.6)
HR	190.8 ± 9.8	(5.1)	190.9 ± 9.9	(5.2)	190.8 ± 9.9	(5.2)
RER	1.10 ± 0.06	(5.4)	1.11 ± 0.05	(4.5)	1.13 ± 0.05	(4.4)
[La ⁻ _b]	9.2 ± 2.0	(21.8)	9.0 ± 1.9	(21.1)	9.0 ± 1.7	(18.9)
RPE	17.5 ± 1.2	(6.9)	17.6 ± 1.1	(6.3)	17.5 ± 1.4	(8.0)
TTE (s)	494.3 ± 125.4	(25.4)	524.0 ± 127.9	(24.4)	542.9 ± 124.0	(22.8)
C_{DP} at LT						
mL · kg ⁻¹ · m ⁻¹	0.198 ± 0.021	(10.6)	0.193 ± 0.019	(9.8)	0.193 ± 0.020	(10.4)
mL · kg ^{-0.67} · m ⁻¹	0.800 ± 0.078	(9.8)	0.779 ± 0.070	(9.0)	0.780 ± 0.066	(8.5)
MAS						
m · min ⁻¹	278.1 ± 52.6	(18.9)	285.4 ± 45.1	(15.8)	290.3 ± 44.2	(15.2)
km · h ⁻¹	16.7 ± 3.2	(19.2)	17.1 ± 2.7	(15.8)	17.4 ± 2.7	(15.5)
LT						
%DP-VO _{2peak}	82.3 ± 6.5	(7.9)	82.4 ± 6.3	(7.6)	81.6 ± 5.6	(6.9)
HR	175.4 ± 11.5	(6.6)	173.2 ± 11.9	(6.9)	172.3 ± 11.9	(6.9)
VO ₂	44.6 ± 6.6	(14.8)	44.9 ± 6.4	(14.3)	45.3 ± 6.8	(3.9)
[La ⁻ _b]	4.6 ± 0.6	(13.0)	4.7 ± 0.7	(14.9)	4.5 ± 0.6	(13.3)
Speed (km · h ⁻¹)	13.7 ± 2.5	(18.7)	14.1 ± 2.2	(15.6)	14.2 ± 2.1	(14.8)
Strength						
1RM half squat (kg)	120.8 ± 21.9	(18.1)	129.7 ± 24.2	(18.7)	131.1 ± 23.3	(17.8)
1RM pull-down (kg)	87.4 ± 16.5	(18.9)	87.9 ± 15.6	(17.7)	89.8 ± 16.2	(18.0)
Maximal power						
Half squat (w)	808.6 ± 207.6	(25.7)	816.6 ± 177.4	(21.7)	831.8 ± 180.7	(21.7)
Pull-down (w)	473.9 ± 152.8	(32.2)	469.7 ± 119.1	(25.4)	490.3 ± 124.0	(25.3)
SJ (cm)	28.0 ± 5.1	(18.2)	26.8 ± 4.7	(17.5)	27.2 ± 4.8	(17.6)
CMJ (cm)	31.5 ± 5.5	(17.5)	31.6 ± 4.2	(13.3)	30.7 ± 5.0	(16.3)
CMJas (cm)	35.9 ± 5.5	(15.3)	35.0 ± 4.9	(14.0)	33.6 ± 5.2	(15.5)

Values are mean and SD with coefficient of variance in percentage in parenthesis. ^ano effect size for delta physiological variables from PRE to POST2 over 0.5. BW, body-weight. Kg, kilograms. TT_{DP}, double poling time trial. RUN-VO_{2max}, maximal oxygen uptake in running. mL · kg⁻¹ · min⁻¹, milliliters per kilogram bodyweight per minute. L · min⁻¹, liters per minute. mL · kg^{-0.67} · min⁻¹, milliliters per kilogram raised to the power of -0.67 per minute. HR, heart rate. RER, respiratory exchange ratio. [La⁻_b], blood lactate concentration. RPE, rate of perceived exertion. %RUN-VO_{2max}, fractional utilization of RUN-VO_{2max} at DP-VO_{2peak}. TTE, time to exhaustion. C_{DP}, oxygen cost of double poling at lactate threshold. mL · kg⁻¹ · m⁻¹, milliliters per kilogram per meter. mL · kg^{-0.67} · m⁻¹, milliliters per kilogram raised to the power of -0.67 per meter. MAS, maximal aerobic speed. LT, lactate threshold. VO₂, oxygen uptake. Km, kilometers. H, hours. 1RM, one repetition maximum. W, watt. SJ, squat jump. CMJ, counter movement jump. CMJas, counter movement jump with armswing. Cm, centimeters. * $p < 0.05$ significantly different from POST1 value.

training and Δ LIT_{ski} showed low significant correlations to Δ LT_v ($r = 0.48$, $p < 0.01$ and $r = 0.45$, $p < 0.05$, respectively), while Δ LIT_{ski} showed a low significant correlation to Δ C_{DP} ($r = -0.41$, $p < 0.05$).

Sex Differences

Male skiers trained significantly higher volumes than females 3 months before pre-tests ($p < 0.05$). Additionally, no statistical difference was observed in LIT, MIT, HIT, total endurance

TABLE 4 | Baseline correlations between performance and physiological variables (*n* = 29).

Variable	TT _{DP}	VO _{2max} (mL · kg ^{-0.67} · min ⁻¹)	MAS
Age	-0.09 (0.23)	0.15 (0.25)	0.07 (-0.28)
BW	-0.41* (-0.01)	0.43* (-0.02)	0.40* (-0.03)
TT_{DP}			
seconds	-	-0.73** (-0.39)	-0.79** (-0.58**)
RUN-VO_{2max}			
mL · kg ⁻¹ · min ⁻¹	-0.68** (-0.33)	0.96** (0.92**)	0.69** (0.34)
L · min ⁻¹	-0.71** (-0.35)	0.92** (0.77**)	0.72** (0.27)
mL · kg ^{-0.67} · min ⁻¹	-0.73** (-0.39)	-	0.75** (0.37)
HR	-0.07 (-0.07)	-0.02 (-0.003)	-0.03 (-0.01)
RER	-0.14 (-0.001)	-0.01 (-0.34)	0.08 (-0.15)
[La ⁻ _b]	0.26 (0.24)	0.08 (0.27)	-0.22 (-0.23)
RPE	-0.36 (-0.45*)	0.06 (0.03)	0.16 (0.21)
DP-VO_{2peak}			
mL · kg ⁻¹ · min ⁻¹	-0.79** (-0.63**)	0.75** (0.44*)	0.81** (0.65**)
L · min ⁻¹	-0.78** (-0.57**)	0.77** (0.34)	0.79** (0.48*)
mL · kg ^{-0.67} · min ⁻¹	-0.83** (-0.69**)	0.80** (0.46*)	0.85** (0.68**)
%RUN-VO _{2max}	-0.24 (-0.32)	-0.20 (-0.46*)	0.24 (0.32)
HR	-0.06 (0.08)	-0.001 (-0.12)	0.09 (0.03)
RER	0.18 (0.49*)	0.11 (-0.09)	-0.03 (-0.29)
[La ⁻ _b]	0.08 (0.21)	0.09 (-0.10)	0.11 (-0.04)
RPE	-0.01 (-0.16)	-0.03 (0.14)	-0.04 (0.13)
TTE (s)	-0.84** (-0.72**)	0.78** (0.43*)	0.93** (0.85**)
C_{DP} at LT			
mL · kg ⁻¹ · m ⁻¹	0.41* (0.17)	-0.40* (-0.07)	-0.69** (-0.63**)
mL · kg ^{-0.67} · m ⁻¹	0.27 (0.17)	-0.23 (-0.08)	-0.56** (-0.62**)
MAS			
m · min ⁻¹	-0.79** (-0.58**)	0.75** (0.37)	-
km · h ⁻¹	-0.79** (-0.58**)	0.75** (0.37)	-
LT			
%DP-VO _{2peak}	-0.05 (-0.13)	-0.03 (0.17)	-0.24 (-0.19)
HR	0.08 (0.01)	-0.25 (-0.19)	-0.22 (-0.11)
VO ₂	-0.72** (-0.56**)	0.66** (0.46*)	0.59** (0.37)
[La ⁻ _b]	0.25 (0.51**)	-0.06 (-0.26)	-0.23 (-0.51**)
Speed (km · h ⁻¹)	-0.82** (-0.64**)	0.77** (0.48*)	0.91** (0.84**)
Strength			
1RM half squat	-0.49** (-0.15)	0.59** (0.33)	0.55** (0.29)
1RM pull-down	-0.64** (-0.27)	0.61** (0.07)	0.60** (0.13)
Power half squat	-0.48** (-0.12)	0.54** (0.10)	0.49** (0.05)
Power pull-down	-0.53** (-0.27)	0.50** (-0.14)	0.54** (0.07)

Values are correlation coefficients *r* and partial correlation coefficients corrected for sex in parenthesis. BW, body-weight. Kg, kilograms. TT_{DP}, double poling time trial. RUN-VO_{2max}, maximal oxygen uptake in running. mL · kg · min⁻¹, milliliters per kilogram bodyweight per minute. L · min⁻¹, liters per minute. mL · kg^{-0.67} · min⁻¹, milliliters per kilogram raised to the power of -0.67 per minute. HR, heart rate. RER, respiratory exchange ratio. [La⁻_b], blood lactate concentration. RPE, rate of perceived exertion. %RUN-VO_{2max}, fractional utilization of RUN-VO_{2max} at DP-VO_{2peak}. TTE, time to exhaustion. C_{DP}, oxygen cost of double poling at lactate threshold. mL · kg⁻¹ · m⁻¹, milliliters per kilogram per meter. mL · kg^{-0.67} · m⁻¹, milliliters per kilogram raised to the power of -0.67 per meter. MAS, maximal aerobic speed. LT, lactate threshold. VO₂, oxygen uptake. Km, kilometers. H, hours. 1RM, one repetition maximum. **p* < 0.05 significant correlation. ***p* < 0.01 significant correlation.

training, ski-specific training, running, strength training or other training between males and females in either *P*₁ or *P*₂. Males trained significantly more cycling in *P*₂ (*p* < 0.05), and females trained significantly higher volumes of speed/jump training, both in *P*₁ (*p* < 0.01) and *P*₂ (*p* < 0.05). No statistical difference was observed in training progression throughout the 6-months period between males and females, except for other training (*p* < 0.05). Differences in training characteristics

between males and females are shown in **Figures 1A,B** and **Supplementary Table 4**.

Significant sex differences in physiological and performance variables were observed at PRE-tests. Results from physiological and performance tests are presented in **Supplementary Table 1**. Males had on average 14.7% (*p* < 0.01, effect size = 2.28) better TT_{DP} performance, 19.3% (*p* < 0.01, effect size = 1.91) higher RUN-VO_{2max} (mL · kg⁻¹ · min⁻¹), 19.3% (*p* < 0.01,

TABLE 5 | Delta correlations between physiological and performance variables and training ($n = 29$).

Variables	RUN-VO _{2max}	DP-VO _{2peak}	C _{DP}	MAS	LT _v	TT _{DP}
Total training	0.11	-0.01	-0.25	0.19	0.35	-0.13
Ski specific training	0.08	-0.03	-0.34	0.28	0.48**	-0.06
LIT _{ski}	0.07	-0.11	-0.41*	0.29	0.45*	-0.05
Strength training	0.15	-0.08	-0.30	0.16	0.36	-0.32

Values are correlation coefficient r for delta physiological values from POST1 to POST2, and delta training values that showed significant differences from 1st training period to 2nd training period. RUN-VO_{2max}, maximal oxygen uptake in running in milliliters per kilogram body weight raised to the power of -0.67 per minute. DP-VO_{2peak}, peak oxygen uptake in double poling in milliliters per kilogram body weight raised to the power of -0.67 per minute. C_{DP}, oxygen cost of double poling in milliliters per kilogram bodyweight per meter. MAS, maximal aerobic speed. LT_v, velocity at lactate threshold. TT_{DP}, double poling time trial. LIT_{ski}, ski-specific low intensity training. * $p < 0.05$ significant correlation. ** $p < 0.01$ significant correlation.

effect size = 1.72) higher DP-VO_{2peak} ($\text{mL} \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$), 9.1% ($p < 0.01$, effect size = 0.97) better C_{DP} ($\text{mL} \cdot \text{kg}^{-1} \cdot \text{m}$), 30.2% ($p < 0.01$, effect size = 2.04) higher LT_v and a 32.3% ($p < 0.01$, effect size = 2.16) higher MAS than females at baseline. In addition, males were 21.3% ($p < 0.01$, effect size = 1.22) and 30.5% ($p < 0.01$, effect size = 1.86) stronger than females in half squat and pull-down, respectively, and displayed 34.7% ($p < 0.01$, effect size = 1.37) and 45.9% ($p < 0.01$, effect size = 1.37) higher power values in half squat and pull-down, respectively. No significant gender differences were apparent in HR, RER, $[\text{La}^-]_b$ or RPE in running or double-poling, %RUN-VO_{2max} or LT%, at baseline (all effect sizes < 0.7).

No sex differences were observed in physiological or performance adaptations from PRE to POST2, except for $[\text{La}^-]_b$ in RUN-VO_{2max} ($p < 0.05$, effect size = 0.93). From PRE to POST1, only RER_{RUN} ($p < 0.05$, effect size = 0.88), C_{DP} ($p < 0.05$, effect size = 0.77), and LT% ($p < 0.05$, effect size = 0.91) changed significantly different between males and females. However, no gender differences were observed in physiological or performance adaptations from POST1 to POST2. Training adaptations for males and females in key physiological variables are presented in **Figure 2**.

Age-Group Differences

No age differences were observed in total training volume 3-months before PRE. Total MIT volume was significantly higher in the ≥ 19 years group ($p < 0.05$) in both P_1 and P_2 , while other training volume was significantly lower in the same group compared to the 16–18 years group. Speed/jump and strength training was significantly lower in the ≥ 19 years group in P_2 ($p < 0.05$ and $p < 0.01$, respectively), while no difference was apparent in P_1 . No training differences between age groups were displayed in total training volume, LIT, HIT, ski-specific training, running, or cycling during the whole training period. No age group differences were observed in delta training values throughout the whole period. Training characteristics

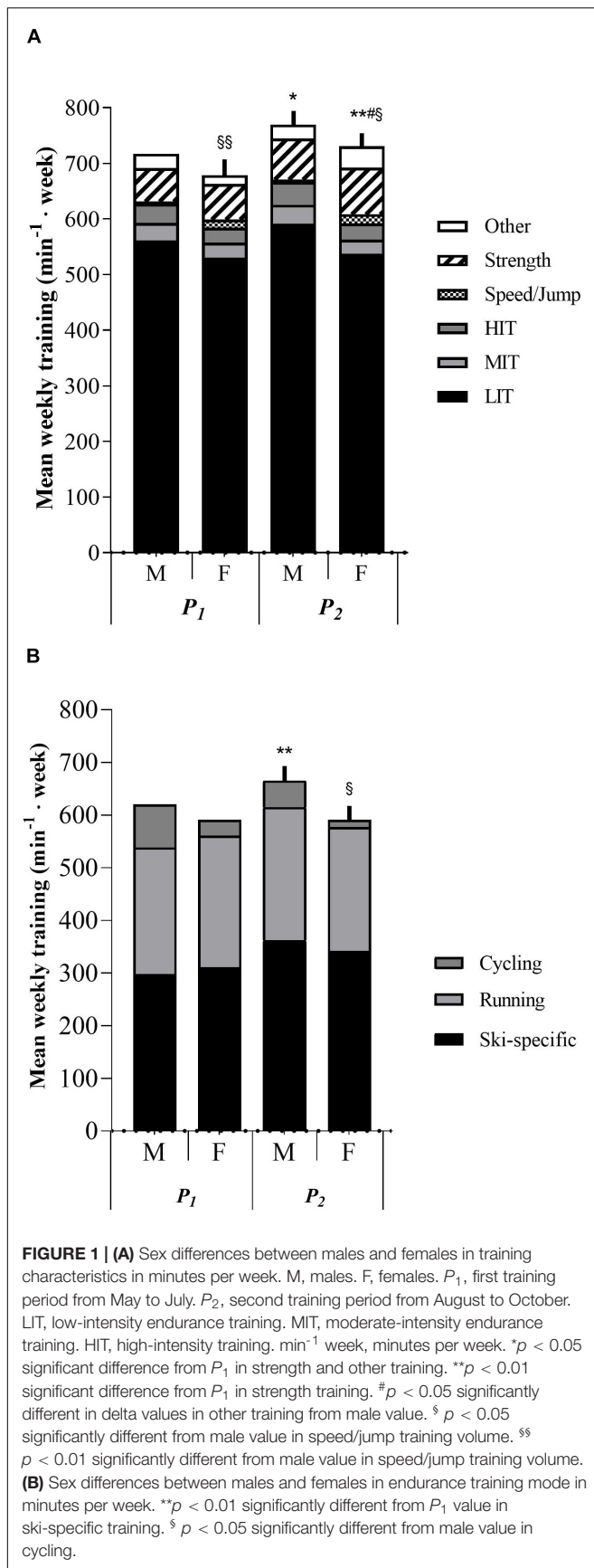
TABLE 6 | Delta correlations between performance and physiological variables ($n = 29$).

Variable	ΔTT_{DP} $\Delta \text{ PRE-POST2}$	$\Delta \text{RUN-VO}_{2max}$ $\Delta \text{ PRE-POST2}$	ΔMAS $\Delta \text{ PRE-POST2}$
ΔBW	0.34	-0.24	-0.31
ΔTT_{DP} seconds	–	-0.05	-0.09
$\Delta \text{RUN-VO}_{2max}$ $\text{mL} \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$	-0.11	0.99**	-0.21
$\text{L} \cdot \text{min}^{-1}$	0.08	0.93**	-0.20
$\text{mL} \cdot \text{kg}^{-0.67} \cdot \text{min}^{-1}$	-0.05	–	-0.21
HR	-0.11	0.19	-0.39*
$\Delta \text{DP-VO}_{2peak}$ $\text{mL} \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$	-0.19	0.02	-0.08
$\text{L} \cdot \text{min}^{-1}$	0.03	-0.11	-0.11
$\text{mL} \cdot \text{kg}^{-0.67} \cdot \text{min}^{-1}$	-0.12	-0.03	-0.10
%RUN-VO _{2max}	-0.08	-0.72**	0.16
HF	0.10	-0.25	-0.15
TTE (s)	-0.25	0.30	-0.02
ΔC_{DP} at LT $\text{mL} \cdot \text{kg}^{-1} \cdot \text{m}^{-1}$	-0.02	0.19	-0.85**
$\text{mL} \cdot \text{kg}^{-0.67} \cdot \text{m}^{-1}$	0.01	0.16	-0.79**
ΔMAS $\text{m} \cdot \text{min}^{-1}$	-0.09	-0.21	–
$\text{km} \cdot \text{h}^{-1}$	-0.09	-0.21	–
ΔLT %DP-VO _{2peak}	-0.09	0.24	-0.53**
HF	0.12	-0.09	-0.46*
VO ₂	-0.16	0.23	-0.49**
$[\text{La}^-]_b$	0.004	-0.10	-0.17
Speed ($\text{km} \cdot \text{h}^{-1}$)	-0.16	0.05	0.57**
$\Delta \text{Strength}$ Half squat	-0.20	-0.23	-0.01
Pull-down	-0.28	0.10	-0.20
ΔPower Half squat	0.30	-0.15	-0.17
Pull-down	0.05	0.13	-0.28
SJ	-0.24	0.42*	0.22
CMJ	-0.12	0.13	-0.12
CMJas	-0.11	-0.12	0.20

Values are correlation coefficients r . ΔBW , change in body-weight. Kg, kilograms. ΔTT_{DP} , change in double poling time trial. $\Delta \text{RUN-VO}_{2max}$, change in maximal oxygen uptake in running. $\text{mL} \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$, milliliters per kilogram bodyweight per minute. $\text{L} \cdot \text{min}^{-1}$, liters per minute. $\text{mL} \cdot \text{kg}^{-0.67} \cdot \text{min}^{-1}$, milliliters per kilogram raised to the power of -0.67 per minute. HR, heart rate. RER, respiratory exchange ratio. $[\text{La}^-]_b$, blood lactate concentration. RPE, rate of perceived exertion. $\Delta \text{DP-VO}_{2peak}$, change in peak oxygen uptake in double poling. %RUN-VO_{2max}, fractional utilization of RUN-VO_{2max} at DP-VO_{2peak}. TTE, time to exhaustion. ΔC_{DP} , change in oxygen cost of double poling at lactate threshold. ΔMAS , change in maximal aerobic speed. ΔLT , change in lactate threshold. VO₂, oxygen uptake. Km, kilometers. H, hours. 1RM, one repetition maximum. SJ, squat jump. CMJ, counter-movement jump. CMJas, counter-movement jump with armswing. * $p < 0.05$ significant delta correlation. ** $p < 0.01$ significant delta correlation.

for the two age groups are presented in **Figures 3A,B** and **Supplementary Table 5**.

Results from physiological and performance tests among age-groups are presented in **Supplementary Table 2**. At PRE



the ≥19 years group had a 9.6% ($p < 0.01$) better TT_{DP} performance, 12.0% ($p < 0.05$) higher DP-VO_{2peak} (mL · kg⁻¹ · min⁻¹), 7.3% ($p < 0.05$) better C_{DP}, 23.4% ($p < 0.01$) higher LT_v and 21.6% ($p < 0.01$) higher MAS than the younger skiers. In addition, the oldest skiers were significantly stronger in half squat (15.9%, $p < 0.05$) and pull-down (26.5%, $p < 0.01$), and had higher maximal power values both in half squat (35.1%, $p < 0.01$) and pull-down (41.5%, $p < 0.01$). No differences were observed between age groups in RUN-VO_{2max} (mL · kg⁻¹ · min⁻¹), RER, [La⁻]_b, %RUN-VO_{2max} or LT_v.

No differences in delta values was observed between age groups from PRE to POST2, except for BW ($p < 0.05$, effect size = 0.94), [La⁻]_b in running ($p < 0.05$, effect size = 0.92), LT_v ($p < 0.05$, effect size = 0.87) and power in half squat ($p < 0.05$, effect size = 0.88). Additionally, differences in delta values were observed in RUN-VO_{2max} (mL · kg⁻¹ · min⁻¹, $p < 0.05$, effect size = 0.87) and power in half squat ($p < 0.01$, effect size = 1.22) from PRE to POST1. No differences were observed in physiological and performance adaptations from POST1 to POST2. Training adaptations in key variables for the two age-groups are presented in **Figure 2**.

Impact of the Selected Genes

All polymorphisms were successfully genotyped, and were at Hardy-Weinberg equilibrium ($p > 0.05$). Genotype frequencies are displayed in **Table 7**. Minor allele frequencies (MAF) for the genotyped polymorphisms were as follows: 53% for ACTN3, 41% for ACE and IL6, 40% for ACSL1, 38% for PPARGC1A, 19% for PPARA and 9% for PPARG polymorphism.

Key physiological and performance results among genotypes in ACTN3 and ACE at baseline is presented in **Table 8**. All genotype and allele data is presented in **Supplementary Table 6**. There were no differences in physiological and performance results between the three ACTN3 genotypes when analyzing the 29 included skiers. The same picture was shown when analyzing all successfully genotyped participants ($n = 40$), except for a significantly higher DP-VO_{2peak} in the RX genotype compared to the RR genotype (**Supplementary Table 8**). When testing X allele carriers compared to the RR genotype, DP-VO_{2peak} (mL · kg⁻¹ · min⁻¹), both independent of- and corrected for gender, was, respectively, 12.4 and 8.8% higher ($p < 0.05$, effect sizes > 0.80).

For the ACE I/D genotypes, individuals with the DD genotype displayed an 18.4% better C_{DP} (mL · kg^{-0.67} · m⁻¹) compared to those with the II genotype ($p < 0.01$, effect size = 1.42). However, corrected for gender this difference was no longer significant. Individuals with DD genotype also displayed significantly higher values in 1RM pull-down from the II counterparts, both dependent (34%, $p = 0.05$, effect size = 1.67) and independent (23.4%, $p < 0.05$, effect size = 2.66) of gender (**Table 8**). Although the same picture was apparent, all significant associations disappeared when analyzing all 40 successfully genotyped participants (**Supplementary Table 8**). When comparing II genotypes to D carriers we detected a 9.2% higher RUN-VO_{2max} (mL · kg⁻¹ · min⁻¹), when corrected for

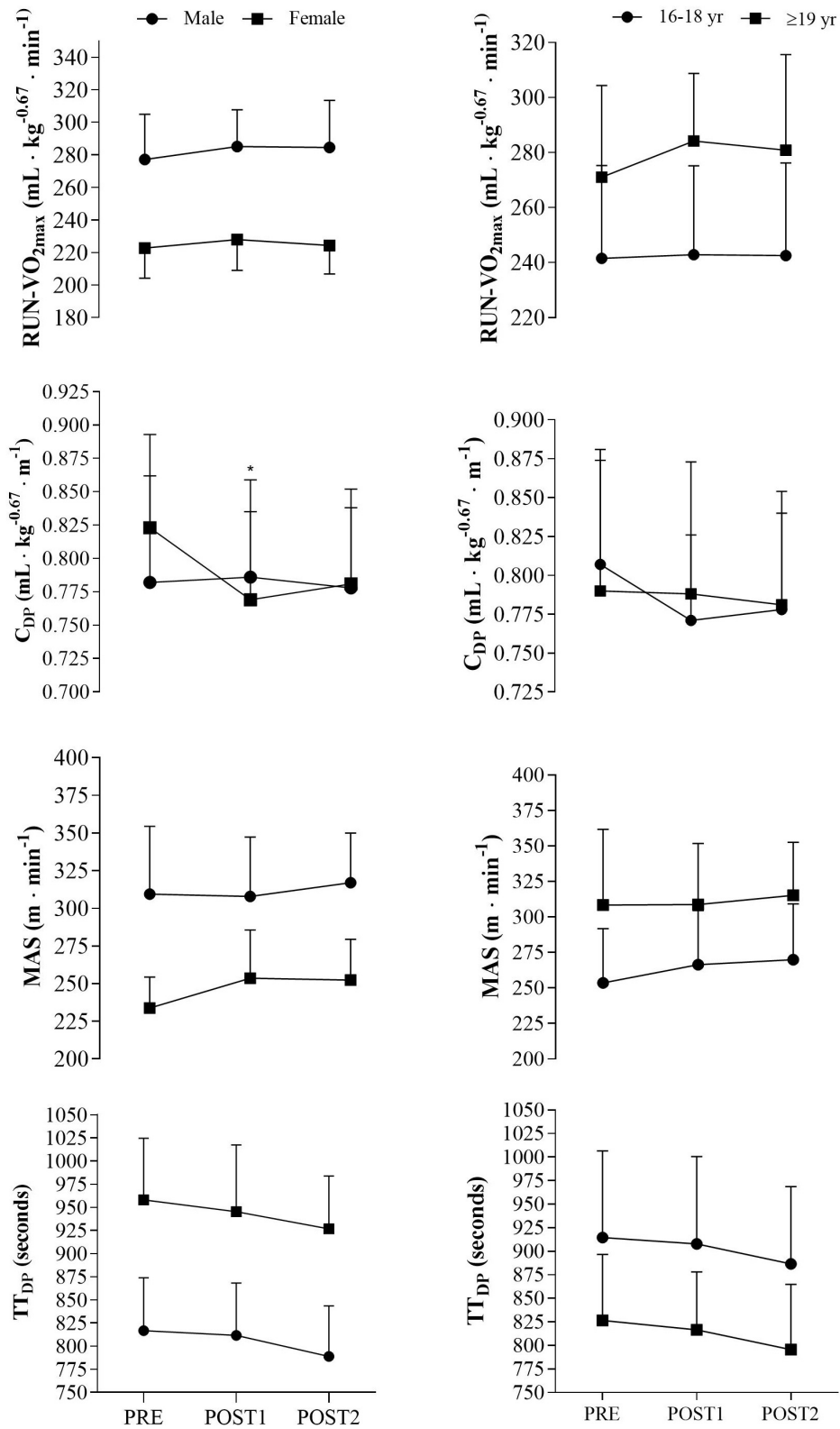
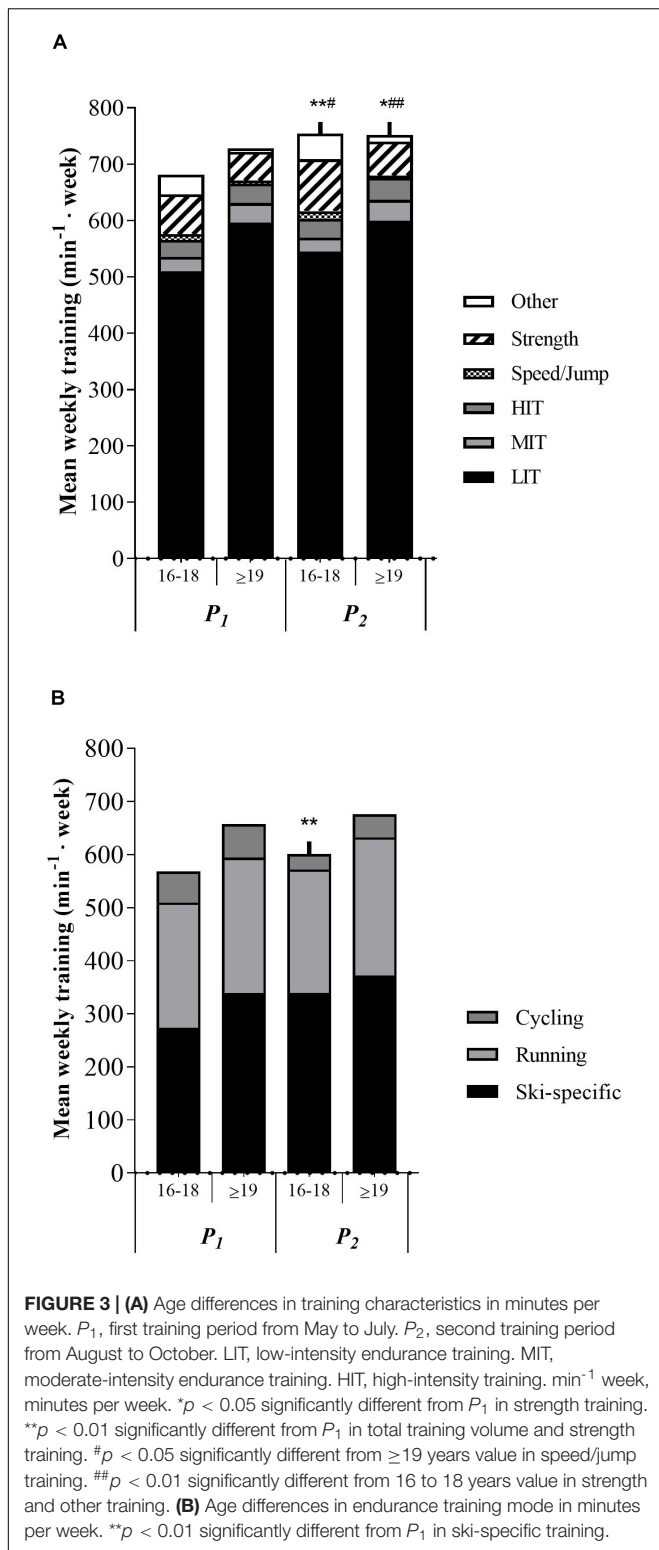


FIGURE 2 | Sex and age differences in key physiological and performance variables. RUN-VO_{2max}, maximal oxygen uptake in running. mL · kg^{-0.67} · min⁻¹, milliliters per kilogram raised to the power of -0.67 per minute. C_{DP}, oxygen cost of double poling at lactate threshold. mL · kg^{-0.67} · m⁻¹, milliliters per kilogram raised to the power of -0.67 per meter. MAS, maximal aerobic speed. m · min⁻¹, meter per minute. TT_{DP}, time trial performance in double poling. *p < 0.05 significant different from male delta value.



gender (*p* < 0.05, effect size = 1.14). Overall, D allele carriers were 27.2% stronger than individuals with the II genotype (*p* < 0.05), and the association remained significant when corrected for gender (17.4%, *p* < 0.01, effect size = 1.27).

TABLE 7 | Genotype distributions for selected genes (*n* = 29).

	<i>ACTN3</i>		<i>ACE</i>		<i>ACSL1</i>		<i>IL6</i>
RR	7 (24.1)	DD	9 (31.0)	GG	11 (37.9)	CC	7 (24.1)
RX	13 (44.8)	ID	16 (55.2)	GA	13 (44.8)	AC	20 (69.0)
XX	9 (31.0)	II	4 (13.8)	AA	5 (17.2)	AA	2 (6.9)

	<i>PPARGC1A</i>		<i>PPARG</i>		<i>PPARA</i>
CC	8 (27.6)	GG	24 (82.8)	GG	20 (69.0)
CT	20 (69.0)	CG	5 (17.2)	CG	7 (24.1)
TT	1 (3.4)	CC	0 (0.0)	CC	2 (6.9)

Values are presented as *n* with percentage genotype distribution in parenthesis. Genotypes are *ACTN3* R577X, *ACE* I/D, *ACSL1* rs6552828, *IL6* rs1474347, *PPARGC1A* rs819267, *PPARG* rs1801282, and *PPARA* rs4253778 polymorphisms.

There were no significant associations between genotypes of the *ACSL1* rs6552828 polymorphism and physiological variables. However, when corrected for gender, an 8.4% difference was observed in RUN-VO_{2max} (mL · kg⁻¹ · min⁻¹ and mL · kg^{-0.67} · min^{-0.67}; *p* < 0.05) between A allele carriers compared to the GG genotype. As to the *PPARGC1A* rs8192678, the highest RUN-VO_{2max} (mL · kg⁻¹ · min⁻¹, L · min⁻¹ and mL · kg^{-0.67} · min⁻¹) was exhibited by the only individual with TT. Significant differences were observed in RUN-VO_{2max} (*p* < 0.05), DP-VO_{2peak} (*p* < 0.05) and 1RM pull-down (*p* < 0.05) between genotypes and allele carriers in *PPARA* rs4253778, *IL6* rs1474347 and *PPARG* rs1801282 independent of gender. However, when corrected for gender, these differences disappeared.

DISCUSSION

Main Findings

This is the first study to investigate effects of age, sex, selected genes and training on physiological and performance characteristics and adaptations in well-trained cross-country skiers. Throughout the 6 months period, the skiers displayed no differences in relative distribution of training intensity, although the total training volume and relative amount of ski-specific training increased. This led to no significant differences in physiological and performance variables. Neither was there observed any differences between groups in training adaptations throughout the 6 months training period. At baseline, the male skiers trained more than the female skiers did, but with approximately the same distribution regarding training modalities and intensity zones. We did not detect any major differences in physiological or performance variables based on genotypes.

Training Characteristics

The participants in the present study were all well-trained and competitive skiers, although not international elite athletes. All skiers competed at national events, and some skiers competed at Scandinavian or international long-distance events (i.e., Vasaloppet and Marcialonga). Thus, all athletes planned

TABLE 8 | Physiological baseline results divided by *ACTN3* and *ACE* genotypes.

Genotype (N)	ACTN3		
	RR (7)	RX (13)	XX (9)
Independent of gender			
RUN-VO _{2max}	237.9 ± 43.9	259.2 ± 36.2	261.1 ± 28.7
DP-VO _{2peak}	201.5 ± 32.2	226.1 ± 36.9	225.6 ± 24.6
C _{DP}	0.796 ± 0.047	0.779 ± 0.082	0.829 ± 0.066
1RM half squat	113.6 ± 19.5	120.2 ± 21.6	127.2 ± 24.5
1RM pull-down	89.3 ± 19.7	84.2 ± 16.7	90.6 ± 14.7
Corrected for gender			
RUN-VO _{2max}	267.1 ± 22.9	285.7 ± 25.2	273.6 ± 22.4
DP-VO _{2peak}	227.4 ± 21.5	249.3 ± 28.7	236.0 ± 10.9
C _{DP}	0.773 ± 0.042	0.760 ± 0.074	0.820 ± 0.064
1RM half squat	126.1 ± 14.7	131.7 ± 20.2	132.8 ± 24.7
1RM pull-down	102.6 ± 13.2	94.8 ± 16.5	95.1 ± 7.8
Genotype (N)	ACE		
	DD (9)	ID (16)	II (4)
Independent of gender			
RUN-VO _{2max}	254.8 ± 48.4	256.3 ± 29.5	247.6 ± 38.6
DP-VO _{2peak}	220.9 ± 44.0	222.6 ± 28.9	207.3 ± 24.3
C _{DP}	0.755 ± 0.070	0.812 ± 0.067	0.844 ± 0.051
1RM half squat	121.4 ± 27.8	122.7 ± 16.1	112.5 ± 30.7
1RM pull-down	92.2 ± 16.4*	89.4 ± 15.2	68.8 ± 11.1
Corrected for gender			
RUN-VO _{2max}	278.1 ± 29.0	273.9 ± 23.7	290.1 ± 13.1
DP-VO _{2peak}	240.8 ± 24.1	238.4 ± 27.0	244.2 ± 11.0
C _{DP}	0.738 ± 0.066	0.799 ± 0.065	0.811 ± 0.035
1RM half squat	131.3 ± 23.2	130.8 ± 17.9	128.5 ± 25.9
1RM pull-down	102.7 ± 9.8*	96.8 ± 14.8	83.2 ± 3.3

Values are mean ± SD. RUN-VO_{2max}, maximal oxygen uptake in running expressed in milliliters per kilogram bodyweight raised to the power of -0.67 per minute. DP-VO_{2peak}, peak oxygen uptake in double poling expressed in milliliters per kilogram bodyweight raised to the power of -0.67 per minute. C_{DP}, oxygen cost of double poling expressed in milliliters per kilogram bodyweight raised to the power of -0.67 per meter. 1RM, one repetition maximum expressed in kilograms. *p < 0.05 significantly different from ACE II genotype.

and performed their training with a goal of developing better performance capacity. Compared to training data from elite cross-country skiers (Losnegaard et al., 2013; Tønnessen et al., 2014; Sandbakk et al., 2016; Solli et al., 2017, 2018), most of the participants displayed lower training volumes. This may partly be explained by the fact that the skiers in the present study had to perform their daily training beside other work duties, studies or family obligations. The national level skiers in the study of Sandbakk et al. (2016) are thus more comparable to these participants. Secondly, approximately 50% of the skiers in the present study were still 16 to 18 years, and their total training volume was not statistically different from the older (≥19 years) skiers. This may be because the younger skiers were attending different skiing high schools, where training was an incorporated part of the school schedule. In previous studies, total training volume of younger skiers were lower than in older skiers

(Sandbakk et al., 2010, 2013, 2016; Losnegaard et al., 2013; Solli et al., 2017).

The relative distribution of training intensity in the present study was in line with general recommendations for cross-country ski training (Sandbakk and Holmberg, 2017). Cross-country skiers are generally recommended to train with high amounts of LIT and low to moderate amounts of MIT and HIT during the preparation period (May to October). In the study of Sandbakk et al. (2016) national-class cross-country skiers performed on average 90% of their total endurance training at <81% of HR_{max}, 4% at 82–87% HR_{max} and 6% at 88% of HR_{max} or higher from May to October. The skiers in the present study displayed, respectively 90, 5, and 5% at the same intensity zones from May to July, showing almost exactly the same intensity distribution from August to October (88, 5, and 6%, respectively). However, different training quantification methods were used in the present study compared to Losnegaard et al. (2013) and Sandbakk et al. (2016). In the present study, training was registered as “time in zone,” meaning the exact time in each intensity zone regardless of how the training may have been planned. In Losnegaard et al. (2013) and Sandbakk et al. (2016), the session-goal approach was used, meaning that average HR during either continuous workouts or interval bouts is used to determine the intensity distribution during sessions. This makes the training data difficult to compare with the results in the present study, at least in the higher intensity zones. Sylta et al. (2014) has suggested a conversion factor of 1:3 for comparison of “time-in-zone” training data to session-goal training data for HIT training. By use of this factor on training data from Losnegaard et al. (2013) and Sandbakk et al. (2016), the HIT training should be only a third of what was reported. The study of Tønnessen et al. (2014) shows more comparable “time in zone” data for MIT and HIT in Olympic-medal winning skiers as the skiers in the present study. However, their study showed higher volumes of both HIT and total training volume compared to the present study.

In the present study, the skiers displayed almost no progression in training volume or relative distribution of training intensity during the 6 months period. These findings are in contrast to the study of Sandbakk et al. (2016), where the national level skiers showed a linear increase in training volume from May to September, generally due to higher volumes of LIT. However, the elite international skiers in the studies of Sandbakk et al. (2016) and Losnegaard et al. (2013) showed progression more similar to the skiers in the present study from May to October, but with an increase in HIT and a decrease in LIT during the competitive season, i.e., November to April. The latter may also be the case for the skiers in the present study, but training during the competitive season was not investigated here.

The skiers in the present study performed on average 50% of their total endurance training on ski-specific training, mainly roller skiing. The other half was devoted for the most part to running. These volumes and relative distribution of ski-specific vs. unspecific training are in close agreement with previous studies on cross-country skiers, both non-elite and elite (Losnegaard et al., 2013; Tønnessen et al., 2014; Sandbakk et al.,

2016; Solli et al., 2017). Ski-specific training may target the ski-specific aerobic capacity, work economy and technical factors better than general endurance training (Johansen et al., 2020). The skiers added approximately 60 min per week of ski-specific training from P_1 to P_2 , while running was held relatively constant throughout the whole training period. This may be a result of a desire to elevate ski-specific capacities (i.e., work economy or technical factors) closer to the competitive season, in line with training characteristics from Losnegaard et al. (2013) and Sandbakk et al. (2016).

The relative distribution of strength and speed/jump training was comparable to the training volumes observed previously (Losnegaard et al., 2013; Tønnessen et al., 2014). This is in line with the increased focus on the upper- and lower body strength and speed in modern cross-country skiing (Sandbakk and Holmberg, 2017; Sunde et al., 2019).

Training Adaptations

The 6 months of training from May to October led to no significant improvements in physiological and performance variables for the skiers in the present study. Since the training volume and intensity distribution was almost constant throughout the study period, this was no surprise. It is still noteworthy that junior- and sub-elite cross-country skiers that train a total of approximately 300 h from May to October show no improvements in physiological factors and only minor improvements in performance. On the other hand, the training performed was sufficient to maintain physiological and performance variables throughout the study period.

Strong correlations ($p < 0.01$) were found at baseline between TT performance and MAS ($r = -0.79$), DP-VO_{2peak} ($r = -0.83$) and IRM pull-down ($r = -0.72$). When corrected for gender all these correlations were still significant. This is in line with other studies examining performance determining factors in endurance sports, i.e., running, cycling and cross-country skiing (Pate and Kriska, 1984; Ingjer, 1991; di Prampero, 2003; Støren et al., 2013; Sunde et al., 2019; Johansen et al., 2020). Several studies have also observed better performance after improved MAS (Støren et al., 2008, 2012; Sunde et al., 2010; Johansen et al., 2020) or improved maximal strength (Hoff et al., 2002; Støren et al., 2008; Sunde et al., 2010). However, no significant relationships between changes in TT_{DP} performance and changes in physiological variables were found in the present study.

The 3.3% non-significant improvement in TT performance in the present study is approximately half of that reported in Losnegaard et al. (2013). That study observed a 6% improvement from June to October in a 1000-meter TT in V2 skating in elite cross-country skiers, despite no improvements in VO_{2peak} in V2 skating. However, C in V2 skating was significantly improved suggesting that the improvement in performance was due to an improvement in MAS in that study. Losnegaard et al. (2013) also explained the better performance by increased anaerobic capacity, measured as ΣO₂-deficit. Anaerobic capacity was not measured directly in the present study. However, compared to the 1000 m TT used in Losnegaard et al. (2013) the anaerobic capacity should be of lesser importance in the 5.6 km TT used in the present study.

Overall aerobic capacity (RUN-VO_{2max}) and specific (DP-VO_{2peak}) aerobic capacity was not improved significantly from May to October in the present study. These findings are in line with studies investigating training patterns and development in VO_{2max} in well-trained or elite cross-country skiers maintaining similar training routines (volume and intensity distribution) over longer periods (Rusko, 1987; Ingjer, 1992; Jones, 1998; Gaskell et al., 1999; Losnegaard et al., 2013; Solli et al., 2017). Further improvements of extremely high VO_{2max} in elite endurance athletes have shown to be challenging. Compared to their elite counterparts, the skiers in the present study had approximately 20% lower aerobic capacities (Tønnessen et al., 2015; Sandbakk and Holmberg, 2017). This suggests that the potential for further improvements should be higher for the skiers in the present study, at least for the younger skiers. There is much evidence supporting that HIT may effectively improve VO_{2max}, both in recreational and elite endurance athletes (Nilsson et al., 2004; Støren et al., 2012; Sandbakk et al., 2013; Rønnestad et al., 2014, 2016; Johansen et al., 2020). However, these interventional studies include longer or shorter periods of higher amounts of HIT, and lower total training volume. Stöggl and Sperlich (2014) reported superior adaptations in well-trained endurance athletes after 9 weeks of polarized training (56% LIT, 3% MIT, and 26% HIT) and HIT (43% LIT, 0% MIT, and 57% HIT) in VO_{2max}, compared to training models with no training at HIT intensities and higher training volumes. This is well in line with the studies of Støren et al. (2012) and Gaskell et al. (1999), where endurance athletes experienced great improvements with a training program with higher amounts of HIT, with the same, or reduced total training volumes. Thus, we may speculate that more HIT training during pre-season may be crucial for further development of aerobic capacity in junior- and sub-elite cross-country skiers.

No statistically significant improvements in C_{DP} were observed. However, like most of the other physiological variables, a slightly better average C_{DP} was seen, although not significant. Losnegaard et al. (2013) reported improved C from June to October in elite cross-country skiers and this could be due to the increased ski-specific training. A significant correlation was also observed between change in total ski-specific training and ΔC_{DP} in the present study, suggesting that adaptation is specifically to the movement patterns used in training (Scrimgeour et al., 1986; McMillan et al., 2005; Johansen et al., 2020). Previous studies have reported improved C after MST in both running (Støren et al., 2008), cycling (Sunde et al., 2010) and cross-country skiing (Hoff et al., 2002; Østerås et al., 2002). However, this relationship was not observed for the whole group in the present study, since MST and thus C_{DP} did not change during the 6 month period.

Several previous studies have reported no training adaptations in LT in % of VO_{2max} after shorter or longer periods of endurance or strength training (Helgerud et al., 2001, 2007; Støren et al., 2008, 2012; Sunde et al., 2010; Rønnestad et al., 2014). This is in line with results in the present study, since the skiers had almost exactly the same LT% at all test points. The present study also showed a strong correlation at baseline between MAS and LT_v ($r = 0.93$, $p < 0.01$) indicating a close relationship, which have

previously been reported (Støren et al., 2014; Sunde et al., 2019). Consequently, to elevate LT_v skiers should aim to improve MAS (VO_{2max} and C).

Sex Differences

Males had higher training volumes than females preceding the baseline tests in the present study. However, from May to October no significant sex differences were observed in total training volume, relative intensity distribution, endurance training, ski-specific training, strength training or other training. These training characteristics are in line with the findings in elite cross-country skiers from Solli et al. (2018), where males tended to train more in total than females throughout a whole year (~90 h), although not significant. In Solli et al. (2018), strength and speed training was similar for males and females, as observed in the present study regarding strength training. However, in the present study the amount of speed and jump training was four times higher in females than males.

Males displayed significantly higher values than females in $RUN-VO_{2max}$ (19%), $DP-VO_{2peak}$ (19%), and MAS (32%), had better C_{DP} (9%) and TT_{DP} (15%) at baseline in the present study. These sex differences are in line with previous results (Sandbakk et al., 2014; Andersson et al., 2019; Sunde et al., 2019). Since MAS is the product of $DP-VO_{2peak}$ and C_{DP} it was no surprise that the sum of sex differences in these two variables equalled almost exactly the difference seen in MAS. The gender difference in TT_{DP} seemed to correspond to the 32% difference in MAS. This is further supported by the correlation between MAS and TT_{DP} ($r = -0.58, p < 0.01$) at baseline corrected for gender.

Interestingly, the sex differences in $DP-VO_{2peak}$ was the same as in $RUN-VO_{2max}$ in the present study. Sandbakk et al. (2014) and Hegge et al. (2016), found the sex differences to be larger with increased contribution of upper-body musculature, i.e., larger in $DP-VO_{2peak}$ than in $RUN-VO_{2max}$. Regarding 1RM strength variables, the gender differences were larger in 1RM pull-down (30%) compared to 1RM half-squat (21%) in the present study. These sex differences in 1RM strength are in line with previous results (Sandbakk et al., 2014; Sunde et al., 2019).

The sex differences at baseline in the present study were maintained in TT_{DP} , $RUN-VO_{2max}$, and $DP-VO_{2peak}$ from May to October due to no significant differences in training progression between males and females in this period. This may suggest that males and females do not differ in physiological and performance adaptations to a similar training pattern, which is in line with previous studies (Astorino et al., 2011; Støren et al., 2017; Varley-Campbell et al., 2018). However, sex difference in C_{DP} declined significantly from PRE to POST1, due to a significantly improved C_{DP} in females while the males maintained their pre-values. This may be explained by the lower training volumes in females 3-months prior to pre-test, resulting in a greater sex difference in C_{DP} at PRE. From May to July, males and females trained more similar, at least in terms of ski-specific training, and this may have reduced the initial gap. Another explanation for the improved C_{DP} observed in females, may be the relationship observed earlier between improved maximal strength and improved C in running, cycling and cross-country skiing (Hoff et al., 2002; Støren et al., 2008; Sunde et al., 2010). In

the present study, a significant correlation was observed between $\Delta 1RM$ pull-down and ΔC_{DP} ($r = -0.60, p < 0.05$) in the female skiers, which supports this explanation. However, further improvements in C_{DP} was not observed in females or males from August to October.

Age-Related Differences

To the best of our knowledge, no studies have investigated age-related differences in training characteristics and training adaptations between younger (junior athletes) and older skiers (senior athletes). In the present study, the age groups did not differ significantly in total training volume 3-months prior to pre-test. No differences were apparent in total training volume or in LIT, HIT, ski-specific training, running, cycling, strength or speed/jump training during the preparation period from May to October. The only difference between 16 and 18 years old compared to ≥ 19 years old was the amount of MIT, where the average difference were ~20 min per week. Compared to other studies examining either junior- or adult skiers, the 16–18 years old skiers in the present study show similar training volumes as seen in previous studies on junior athletes, however, with a slightly lower amount of MIT and HIT (Sandbakk et al., 2011, 2013). However, the older skiers had lower training volumes compared to age-matched adult elite cross-country skiers (Losnegaard et al., 2013; Tønnessen et al., 2014; Sandbakk et al., 2016; Solli et al., 2017).

From May to October, the young and adult skiers did not differ significantly in training progression. The oldest skiers displayed almost no progression in all training variables, throughout the study period. This is in accordance to earlier observations of training progression in adult elite cross-country skiers (Losnegaard et al., 2013; Sandbakk et al., 2016).

At baseline, the adult skiers were 15% heavier than the younger skiers. A significant age-related difference was also apparent in TT_{DP} (10.6%), which was followed by a 17.8% difference in MAS. Corrected for age, MAS showed a strong correlation to TT_{DP} at baseline ($r = -0.77, p < 0.01$). The difference in MAS was almost exactly the same as in LT_v , supporting that $DP-VO_{2peak}$ and C_{DP} are the main predictors for LT_v . The age difference in MAS is a consequence of the 10.7% difference in $DP-VO_{2peak}$ and the 7.9% difference in C_{DP} . The age difference in $RUN-VO_{2max}$ and $DP-VO_{2peak}$ may be attributed to incomplete development of the cardiac system and muscle mass in the younger skiers still in puberty (Rusko, 1992). Additionally, the lower number of years of training in the young skiers may be an explanation for the observed difference. The difference in C_{DP} may also be a result of less training years and experience in the younger skiers. In addition, the adult skiers had 21% higher 1RM pull-down than the younger skiers. Stronger skiers have shown to have higher peak forces in DP, lower DP frequency and shorter contact time (Sunde et al., 2019). However, all these age differences should be handled with great caution as they are most probably due to the sex differences in the two age groups. When analyzing age differences in males and females separately in the two groups, young and adult females differed in the same physiological and performance variables observed for the whole group, except for C_{DP} and strength variables. For the males, almost every

significant age-related difference disappeared, except for 1RM pull-down and $DP\text{-}VO_{2\text{peak}}$ in absolute values.

Effect of Selected Genes

We did not detect any major effects for the selected genes on physical and performance variables at baseline. Based on the low number of participants and the expected influence by single genes, this was not unexpected. However, we did find some minor effects.

In the present study the common *ACTN3* R577X, X allele carriers demonstrated higher $DP\text{-}VO_{2\text{peak}}$ than participants with the RR genotype at PRE. This is in accordance to Pimenta et al. (2013) that observed that soccer players with the XX genotype had the highest $VO_{2\text{max}}$. According to Yang et al. (2003) the X allele is overrepresented among endurance athletes, especially females. The importance of the advantageous allele is also likely dependent on the performance level (Eynon et al., 2012). However, others have not been able to confirm this (Papadimitriou et al., 2018). The X allele frequency in the present study was slightly higher (44 vs. 53%) among athletes than the general population from the same geographical area (Goleva-Fjellet et al., 2020). For the *ACE* gene, skiers with the II genotype exhibited higher $RUN\text{-}VO_{2\text{max}}$ compared with carriers of the D allele. However, participants with DD genotype demonstrated ~15% better C_{DP} and had ~28% higher 1RM pull-down compared to the II genotype. The observed superior C_{DP} among skiers with the DD genotype could be explained by gender differences in 1RM (Sunde et al., 2019). The I allele frequency among the cross-country skiers included in the present study was 14.6% higher than in a Norwegian cohort from the same geographic region (Goleva-Fjellet et al., 2020).

For the *ACSL1* rs6552828, the A allele carriers had 8.4% higher $RUN\text{-}VO_{2\text{max}}$ ($\text{mL} \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$ and $\text{mL} \cdot \text{kg}^{-0.67} \cdot \text{min}^{-1}$; $p < 0.05$) compared to the GG genotype. A relatively large effect of 6% on the training response of $VO_{2\text{max}}$ have been reported previously with the carriers and the common G allele exhibiting larger increase than the homozygotes of the less common A allele (Bouchard et al., 2011). The differences between the findings in the present study and the study of Bouchard et al. (2011) might be due to the different study population profiles, i.e., highly trained athletes vs. sedentary adults, respectively. The latter group have a larger potential of increasing their $VO_{2\text{max}}$ as a result of standardized exercise-training programs compared to athletes. The present study did not measure a significant increase in the $VO_{2\text{max}}$ throughout the testing period.

All associations between *PPARGC1A* rs8192678 and physiological and performance variables disappeared when correcting for gender. The C allele (Gly) have been suggested to be an elite status endurance allele favorable to athletic ability (Tharabenjasin et al., 2019; Petr et al., 2020). Homozygotes of the C allele are generally more responding aerobic training compared to the T allele (Ser) (Petr et al., 2018). In the present study, only a single male participant possessed the least favorable genotype for endurance performance, i.e., TT. Despite possessing an unfavorable genotype to endurance performance, he demonstrated the highest $RUN\text{-}VO_{2\text{max}}$ of all participants.

This points at carefulness when interpreting physiological performance based on single genes.

No significant associations were found for either of the following polymorphisms in the present study when corrected for gender: *PPARA* rs4253778, *IL6* rs1474347, and *PPARG* rs1801282. For muscle function and jumping capacity, this is well in line with previous findings in other sports, at least for the *PPARA* rs4253778 polymorphism (Stastny et al., 2019). However, Stastny et al. (2019) found significant associations to other muscle parameters, such as reactive muscle index.

Despite previous findings on the effects of the *ACE* I/D and the *ACTN3* R577X polymorphisms on athletic ability and trainability, the impact of these are not strong enough predictors to determine the athletic ability (Venezia and Roth, 2019). Results from the present study confirms that genotype frequencies for the two most investigated and replicated polymorphisms (i.e., *ACE* I/D and *ACTN3* R577X) among the cross-country skiers were similar to those from a large general Scandinavian cohort (Goleva-Fjellet et al., 2020). Furthermore, there was the case of the one skier that possessed the least favorable endurance genotype for the *PPARGC1A* SNP, but still demonstrated the highest $VO_{2\text{max}}$. These findings may indicate that possessing the optimal alleles of the different polymorphisms may be beneficial for endurance performance, but it is not critical for the athletic ability (Venezia and Roth, 2019; Petr et al., 2020). This may be especially true for athletes competing at a national level compared to world-class elite athletes (Eynon et al., 2012; Papadimitriou et al., 2016). However, the results from the present study should be treated with some caution due to the limited sample size. Some genotypes within the selected genes were either not present or only apparent in 1–2 participants, and may therefore influence our results. The material is thus prone to false negative results (type 2 errors), and we can only state that there were minor associations between some genotypes and physiological variables in our cohort of 29 skiers. This should be taken into account when interpreting the genetic results from the present study. Also, these athletes were already well trained and could be argued to not represent a good sample population to detect associations between genotype variants and physiological or performance characteristics.

Practical Implications

In the present study, maintaining the same training intensity distribution, and only increase total training volume was not sufficient to further improve aerobic capacity and cross-country skiing performance significantly throughout 6 months of training. This suggests that training programs with the same training intensity distribution, only differing in training volume, may not ensure optimal development of each individual skier independent of age and sex (Gaskill et al., 1999). For the individual well trained athlete, substantial changes in training volume and training intensity distribution could be necessary to facilitate further improvements, as observed in earlier studies (Gaskill et al., 1999; Støren et al., 2012; Bratland-Sanda et al., 2020). This is important knowledge for trainers of talented cross-country skiers that have faced stagnation.

An interesting finding in the present study is that our cohort of skiers did not differentiate genetically in two of the most

investigated polymorphisms in association to athletic ability compared to a general Scandinavian cohort from the same geographical area. This may suggest that one might be able to reach a high national level in cross-country skiing without having the optimal genotypes in selected genes, with sufficient and individualized training.

CONCLUSION

Sex and age did influence physiological and performance variables at baseline, but did not influence training adaptations. Since the skiers in the present study did not display major changes in training, it was no surprise that no adaptations occurred in physiological or performance variables either. The genotype variants of selected genes were not critical determinants for physiological and performance variables in national and sub-elite cross-country skiers in the present study.

DATA AVAILABILITY STATEMENT

Restrictions apply to the datasets: the datasets presented in this article are not readily available due to the Norwegian legislation regarding the publication of genetic data. Requests to access the datasets should be directed to the corresponding author.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by Regional Ethics Committee of South-Eastern

Norway, Telemark, Norway. Written informed consent to participate in this study was provided by the participants' legal guardian/next of kin.

AUTHOR CONTRIBUTIONS

J-MJ, SG-F, ØS, AS, MS, and JH all participated significantly in the planning and design of the study, as well as the data analyzing and the writing of the article. J-MJ, AS, ØS, SG-F, LG, LS, BF, and MS participated in the data collection. LG, LS, and BF also participated in the writing of the article. All authors read and approved the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fphys.2020.581339/full#supplementary-material>

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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