The purpose of this abstract is to provide an overview over my career activities in the areas of muscle and sport biomechanics. I started in the area of sport biomechanics as an undergraduate student at the Federal Technical Institute in Zurich with the intention of becoming a track and field coach. During my graduate studies, I realized that the science of human motion was more fascinating to me than the possibility to coach athletes, and so I pursued a career that led me to do work on the cellular and molecular mechanisms of muscle contraction. For the past decade, I have tried to apply the knowledge gained on the molecular and cellular level to practical problems in sport and rehabilitation. One of the lessons learnt in these endeavours was that intuition is good in science, but reliance on intuition alone often leads to incorrect conclusions. Therefore, checking your intuition at all times is essential. Another lesson I learnt was that, particularly in sport science, the dramatic breakthroughs in technique and material development (Fosbury flop, skate skiing, etc.) often come from athletes and coaches rather than scientists, thus working with athletes and coaches, rather than merely using them as subjects of your studies is essential.

**KEY WORDS:** sport biomechanics, muscle mechanics, mechanisms of muscle contraction, muscle adaptation, eccentric contraction, cellular and molecular biomechanics, running, cycling, long jumping, cross-country skiing.

**INTRODUCTION:** I had the great pleasure of meeting Geoffrey Harry George Dyson when I was a graduate student with Jim Hay at the University of Iowa. He gave a seminar around 1983 of which, I must admit to my shame, I remember little. And as so often happens in life, we are experiencing historical events, and only realize in hindsight the importance of them. Only much later did I learn that Geoffrey Dyson was a famous track coach for the British and the Canadian athletics team, establishing a coaching culture in these two countries that was unparalleled. He led the British Olympic Athletic Team in 1952, 1956 and 1960. In the 1948 games, his future wife, Maureen Gardner, won the silver medal in the 80m hurdles behind the woman who became the track athlete of the century; Francina (Fanny) Elsje Blankers-Koen. He also coached a young man who went on to become the Common Wealth Pole Vault Champion in 1954 and 1958,
Geoff Elliott, who I met at the University of Calgary. Because of our common track background, Geoff and I became instantaneous friends.

I started to study biomechanics with the goal of becoming a track and field coach. My greatest ambition at the time was to coach the Swiss National Athletics Team, and my studies at the University of Iowa would be my ticket for that job. In Iowa, Jim Hay and his students were part of a project aimed at preparing the long jumpers and triple jumpers of the United States for the upcoming 1984 Los Angeles Summer Olympics. We worked with Carl Lewis and Larry Myricks who ended up 1st and 4th in the long jump, Angela Thacker and Jackie Joyner-Kersee (4th and 5th in the long jump), and Mike Conley and Al Joyner (1st and 3rd in the triple jump). What a privilege it was to work with some of the world’s best athletes, and I was on the best way of becoming a knowledgeable track and field coach.

However, it must have been in 1982 or 1983, just after we had filmed and analysed all long jumpers at that year’s Pepsi meet in Los Angeles. Carl Lewis had all the prerequisites to break the world record, but he had not done so (and as it turns out – never would). Jim Hay asked me: “what do you think it would take for Carl to break the world record”, and my reply was: “I wonder how far somebody can jump given Carl’s speed and strength”. It seemed that I was not interested in the athlete or the world record anymore, but was fascinated by the problem of how to maximize jumping distance given a set of musculoskeletal input parameters. And without fully realizing it at the time, I had become a scientist and my coaching ambitions were largely gone.

SPORT BIOMECHANICS:
My sport science career started at the ETH in Zurich under the tutelage of Jachen Denoth. Jachen was a professor for biomechanics supervising my diploma research work on the footfall patterns of runners on different surfaces. The thoroughness of Jachen’s approach, and the ever present theoretical underpinning for his research, remain an inspiration to this day. At the University of Iowa, we worked primarily on swimming technique and track and field. From Jim Hay, I learnt how to identify scientific problems and how to approach them in a systematic manner. His deterministic models of sport performance, as illustrated for example in his long jump research accounting for each mechanical variable that determines ultimate performance, were an inspiration and served as a tool for much of my own research.

Jim Hay was also a highly intuitive person who dared to think differently in ways few do. For example, he realized that long jumpers create a natural forward (somersaulting) angular momentum at the take-off to the long jump. He hypothesized that it might be easier for a long jumper to give in to this natural tendency and perform a somersault while long-jumping, rather than fighting the angular momentum as jumpers typically do so they can keep the upper body upright and achieve decent landing positions. Experiments and theoretical simulations on the somersault long-jump technique indicated that this form of jumping might lead to better performance. However, the technique was disallowed by the international Track and Field Association because it was considered too dangerous, especially for young jumpers and children who were trying to imitate it before they reached the jump distances required for it to become useful and safe.

FROM MEDALS TO MUSCLES AND MOLECULES:
Following my doctoral studies with Jim Hay, I felt that in order to understand sport performance I needed to understand the muscles powering human movement, and the constraints imposed by the neural and skeletal system in accessing the full extent of the mechanical possibilities of the muscles. I realized that although we had studied athletes who won Olympic medals, I did not understand why they could do that, nor how the muscles worked who could achieve those performances. Therefore, I started a series of experiments evaluating the mechanical properties of human skeletal muscles, and then evaluated how muscle properties changed in athletes as they were performing specialized training over years of competing.

While studying human muscle properties, two things happened: first, I realized that athletes in many sports used techniques that seemed mechanically incorrect, or I should say, they appeared mechanically sub-optimal, and second, I realized that many of the human muscle properties we had observed could not be explained with current thinking on the mechanisms of muscle contraction and force production.
Regarding the first problem (sub-optimal techniques), I questioned why world class shot putters released the shot an angle of about 37-38° when clearly the optimal angle of release (assuming a release height of about 2.40 m) would not be closer to 42°. Or, I asked why cyclists exert forces on the pedal in the power phase that do not contribute to the work performed on the cycle-rider system? Also, why do cross-country skiers revert to a gait pattern in skate skiing at high speeds when this gait pattern was rejected at an intermediate speed in favour of a more optimal gait? And furthermore, why do track sprint cyclists pedal at a frequency of about 150 revolutions per minute when laboratory experiments clearly show that pedalling between 100-120 revolutions per minute produces the greatest power output. As it turns out, these questions can be answered readily by understanding muscle properties and the musculoskeletal system. I will discuss some of these examples more extensively below.

Regarding the second problem (unexplained muscle properties), we found that eccentric contractions and associated history-dependent properties of skeletal muscles could not be explained within the framework of the traditional theories of muscle contraction: the sliding filament and cross-bridge theories. It became obvious that in order to understand muscle contraction, we had to start performing experiments on the single fibre, single myofibril, and isolated sarcomere level. Work in these preparations led us to the conclusion that active force was not only produced and controlled by the contractile proteins actin and myosin, but was also crucially regulated by the structural protein titin. We referred to this as the three filament model of sarcomeres. We determined that titin regulates force by changing its stiffness in an activation and force-dependent manner. These stiffness changes were achieved by binding calcium to titin upon activation, and by titin binding to actin, thereby shortening titin’s spring length and making it stiffer than in the non-activated state. At last, I had a molecular model of muscle contraction that allowed for explanations of all mechanical muscle properties we had observed in human muscle testing.

FROM MOLECULES BACK TO MEDALS: Armed with a new understanding of how muscles contract, I felt ready to tackle applied problems again. These applied problems revolved around understanding of musculoskeletal injuries and diseases, primarily knee joint osteoarthritis and cerebral palsy, but were also concerned with practical problems in sport. Below, I will briefly discuss three such applications.

Sarcomerogenesis: Sarcomerogenesis refers to the ability of muscles to add sarcomeres to the end of myofibrils, thereby increasing the length of myofibrils, fibres and muscles. In many power sports, coaches and athletes are eager to increase the number of serial sarcomeres in myofibrils and fibres, because more sarcomeres allow for faster muscle contraction speeds and greater power output. It is well known from animal studies that chronic (about 3-4 weeks) stretching or shortening of a muscle results in an increase/decrease of serial sarcomeres. However, it has never been shown unequivocally if this can also be done in human athletes. We demonstrated that the rectus femoris muscle (RF) of runners operated on the ascending limb and RF of cyclists on the descending limb of the force-length relationship, consistent with the everyday use of that muscle in running and cycling, and consistent with the notion of serial sarcomere adaptation with chronic training. This result provided evidence that mechanical properties of muscles, like physiological properties, adapt to the requirements of chronic exercise, and therefore, that muscle mechanical properties change to optimize performance.

Force direction control: When running or walking, we exert specific ground reaction forces. The magnitude of these forces and their time history have been recorded thousands of times. However, the instantaneous direction of the ground reaction forces is studied much less, and how the direction of the ground reaction force is controlled has received comparably little attention. However, a given muscle when activated will produce a ground reaction force of determined direction for the limb in a given position. Therefore, if we require force to be in a given direction in a sports movement, we may constrain which muscles can contribute to what extent. In cycling, for example, coaches have advised athletes to exert force only in the direction perpendicular to the crank at all

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times, as forces parallel to the crank do not contribute to the work and power production of cycling. However, even the best cyclists neglect this well-meant recommendation that, on the surface, seems well-grounded on mechanical principles. We performed a study where we asked cyclists to exert the greatest force they could on the pedal during the power phase of cycling, and then repeated the test by telling them again to exert the greatest force possible but it had to be perpendicular to the direction of the crank. When comparing the force component perpendicular to the crank for both situations, it turned out that the force perpendicular to the crank was significantly greater when cyclists were not constrained by force direction, and the muscle synergies were completely different for the two situations. This result indicates that although it is mechanically correct that only the force perpendicular to the crank produces work, the human musculoskeletal system is built such that pushing only perpendicular to the crank does not allow for all muscles to fully participate in the cycling motion, and thus is not good strategy when attempting to maximize performance. Understanding the control of force direction, and how muscles contribute to the force direction, makes us understand why elite cyclists apply force to the crank the way they do.

Force-power-efficiency-velocity relationships: In cross-country skate skiing, athletes use the so-called two-skate technique at slow speeds, the one-skate technique at intermediate speeds, and then return to the two-skate technique at very high, sprinting speeds. Cross-country skiers produce propulsion with all four limbs, and thus can be compared in their gait patterns to four-legged animals, for example, a horse. We asked the question: why do cross-country skiers revert to the two-skate technique when this gait pattern was rejected at some intermediate speed. This behaviour seemed equivalent to a horse switching from a gallop to a trot at a very fast speed, a switch no horse would ever make. The solution again lies in the mechanics of the muscles, more specifically the force-power-efficiency-velocity relationship of skeletal muscles. In the one-skate technique, skiers rely primarily on the arms and poles for propulsion, while in the two-skate technique they rely primarily on the legs and skis. Furthermore, the time of contact with the ground remains virtually unaltered for the skis but becomes continuously smaller for the poles with increasing speeds of skiing. When measuring the power-velocity and efficiency-velocity relationships for the arm action in skate skiing, it turned out that these relationships were optimal at some intermediate speeds, thereby favouring propulsion with the arms, while these relationships were not favourable at slow and fast speeds of skiing. Since the ground contact time is virtually unaltered for the skis, the leg propulsion is much less dependent on the speed of skiing than the arm propulsion creating a situation where arm propulsion is efficient and effective at some intermediate speed but not at very slow or very fast speeds.

CONCLUSION: An understanding of muscle mechanics and adaptations of muscles to chronic training might help optimize sport performance. Unfortunately, there is little muscle mechanics research applied to athletes and sport performance. I believe there are excellent opportunities for young scientists in sport biomechanics to contribute effectively to this field by incorporating muscle mechanics into their arsenal of knowledge.

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