

Contributions to the understanding of gait control

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This thesis is based on the following articles (referenced P1-P10):

- P1. Simonsen EB, Dyhre-Poulsen P. Amplitude of the soleus H reflex during walking and running. *Journal of Physiology* 1999;515:929-939.
- P2. Simonsen EB, Dyhre-Poulsen P, Alkjaer T, Aagaard P, Magnusson SP. Inter-individual differences in H reflex modulation during normal walking. *Experimental Brain Research*, 2002;142(1):108-115.
- P3. Simonsen EB, Dyhre-Poulsen P. Test-retest reliability of the soleus H-reflex excitability measured during human walking. *Human Movement Science* 2010;30(2):333-40.
- P4. Simonsen EB, Moesby LM, Hansen LD, Comins J, Alkjaer T. Redistribution of joint moments during walking in patients with drop-foot. *Clinical Biomechanics* 2010;25(9):949-52.
- P5. Simonsen EB, Svendsen MB, Nørreslet A, Baldivinsson HK, Heilskov-Hansen T, Larsen PK, Alkjaer T, Henriksen M. Walking on high heels changes the dynamics and muscle activity of human walking significantly. *Journal of Applied Biomechanics* 2012;28(1):20-28.
- P6. Simonsen EB, Alkjaer T. The variability problem of normal human walking. *Medical Engineering and Physics* 2012;34(2):219-224.
- P7. Simonsen EB, Cappelen KL, í Skorini R, Larsen PK, Alkjaer T, Dyhre-Poulsen P. Explanations pertaining to the hip joint flexor moment during the stance phase of human walking. *Journal of Applied Biomechanics* 2012;28(5):542-50.
- P8. Simonsen E B, Tegner H, Alkjaer T, Larsen P K, Kristensen J H, Jensen B R, Remvig L, Juul-Kristensen B. Gait analysis of adults with generalized joint hyper mobility. *Clinical Biomechanics* 2012;27(6):573-577.
- P9. Simonsen EB, Alkjaer T, Raffalt PC. Reflex response and control of the human soleus and gastrocnemius muscles during walking and running at increasing velocity. *Experimental Brain Research* 2012;219(2):163-174.
- P10. Simonsen EB, Alkjaer T, Raffalt PC. Influence of stimulus intensity on the soleus H-reflex amplitude and modulation during locomotion. *Journal of Electromyography and Kinesiology* 2013;23:438-442.

INTRODUCTION

Walking is likely to be the most important skill of the human species. Loss of the ability to walk has been lethal during most of human history and today it is considered a severe handicap and loss of life quality. Walking is assumed to have been a decisive factor in the development of the superior brain and the evolutionary success of homo sapiens. It is therefore a scientific challenge to describe and understand the basic mechanisms underlying this movement pattern.

Human gait, i.e. walking and running, was almost fully developed already 3.6 million years ago. This is known from footprints found in Laetoli, Tanzania (Fig. 1). The footprints were discovered in 1978 by Louis and Mary Leaky and are considered the first evidence of bipedalism in hominids. A volcano erupted and spread out ash, which a light rain fall turned into a substance similar to wet cement. At least two hominids walked over this surface leaving their footprints, which shortly after were covered and preserved by more ash. These footprints show that the foot must have had the same anatomy as a present human foot with a rounded heel and a straight big toe in contrast to the grasping big toe of an ape. The footprints illustrate the scenario of an adult walking next to a child, probably led by hand.

The only hominids known to have been living at that time and location is *Australopithecus afarensis*, commonly known as Lucy. This skeleton (A.L. 288-1) was recovered in 1974 by Johanson and Taib [1] in Hadar, Ethiopia [2] (Fig. 2). *A. afarensis* lived between 3.9 and 2.9 million years ago and is believed to be closely related to the genus *Homo*, which includes the modern human species *Homo sapiens*. *A. afarensis* may have been a direct ancestor or a close relative of an unknown ancestor to *Homo sapiens*.

It has been discussed for many years whether bipedalism evolved prior to the large brain volume, which characterizes modern man, but if the footprints after *A. afarensis* can be taken as a proof of bipedal walking with straight legs, this shows that bipedal locomotion came first and then the large brain volume. Several biomechanical studies have sought to prove that Lucy would walk like a modern human being rather than a chimpanzee with flexed knee and hip joints, but the biomechanical studies of Nagano et al. [3] and Raichlen et al. [4] are by far the most convincing evidence for this.

Lucy was about 1.10 m tall and weighed about 30 kg [3] (Fig. 2). So her gait pattern has to be compared to an



Figure 1
Footprints found in Tanzania from *Australopithecus aferensis* are 3.6 million years old.

A child had walked besides an adult.

eight-year-old human child. In the study of Nagano et al. [3] a 3D computer simulation model was constructed based on scannings of the existing bones or partial bones (Fig. 2). Fifty-two muscles were attached to the lower extremities and the model was "trained" to walk based on forward dynamics simulations and an optimization algorithm set to minimize energy expenditure (Fig. 3). The simulation was successful and revealed a walking pattern very similar to bipedal walking as we know it today. This resemblance was evaluated by periods of muscle activity during the gait cycle and by gross metabolic energy expenditure calculated on the computer model and compared to experimental data. Lucy was less economical than modern adult humans, but had an energy cost comparable to modern humans with the same body mass (8-9-year-old children) (Fig. 3). Walking on almost fully extended knee joints is considered the reason why modern bipedal human walking is by far the most economical way of loco-

motion on the planet [4]. It is not possible to measure mechanical efficiency during walking and running, because there is no accurate way to measure or calculate the mechanical work. However, oxygen consumption can be measured and expressed relative to body mass at a given velocity. Human walking has in this connection been shown to be superior to all other mammals and apes [5] and it is a possibility that humans used walking for hunting by following animals for days until the animals exhausted completely. Another common explanation for the evolution of bipedal walking is that the upper extremities were freed for other purposes such as carrying infants or handling tools. The human child cannot follow the adult for extended distances until it is several years old. Therefore, child transportation is considered essential for evolution and survival [5]. The first Homo species to leave Africa was *Homo erectus*, which is considered to be the immediate ancestor of modern humans [6]



Figure 2
The skeleton of Lucy.

Lucy compared to homo sapiens.

[7]. With the exception of Antarctica, Homo sapiens proceeded to inhabit the whole planet, Europe and Asia 125,000-60,000 years ago, Australia 40,000 years ago and America around 15,000 years ago (Wikipedia) [8]. And all these continents were reached by walking. About 12,000 years ago humans invented agriculture by using tools and this was the basis for an explosive development, which increased the human species from only a few hundred thousand to seven billion individuals.

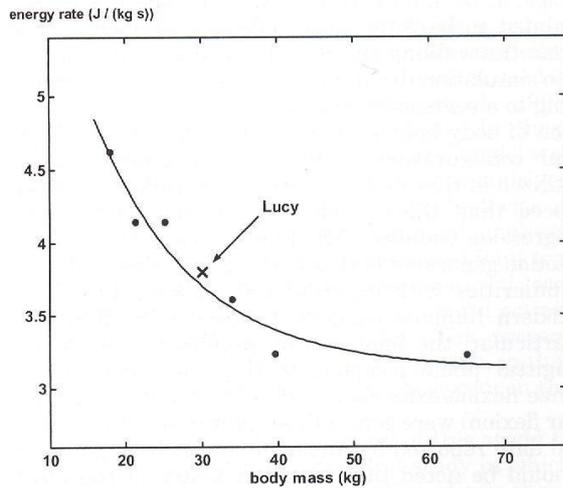


Figure 3
The computer simulation model of Lucy walked with a calculated energy consumption corresponding to that of a human child with a bodymass of app. 30 kg (Nagano et al., 2005)

Human walking is characterized by heel strike with a dorsiflexed ankle joint and no other species exhibit such a walking pattern. Even bipedal animals all demonstrate digitigrade walking where the forefoot is put to the ground at touchdown. The human heel is rounded and covered by a heel pad consisting of chambers made of connective tissue and filled with fat. The role of this pad is mechanical damping at heel strike [9,10]). After heel strike, rotation takes place around the contact point on the heel until the whole foot is in contact with the ground – a small controlled plantar flexion also takes place during this action. Then the leg rotates as an inverted pendulum until the heel starts to lift off from the ground and the final plantar flexion continues until toeoff (Fig. 4). During this process the center of pressure (cop) moves under the planta from the lateral side of the heel to the first metatarsal joint. Cop is the point of application of the ground reaction forces.

In the study of Raichlen et al. [4] the footprints found in Laetoli were scanned in 3D and compared to human subjects setting footprints in wet sand. In addition to normal walking, the subjects were asked to walk with their knee and hip joint flexed, resembling a chimpanzee walking on two legs. The latter walking style produced very little pressure under the heel and the rearfoot and high pressure on the forefoot. This was different from the footprints of Laetoli and the experimentally produced human footprints, which showed an equally distributed pressure under the rearfoot and the forefoot. The results are considered further evidence that A. afarensis had developed economical bipedal locomotion on straight legs 3.6 million years ago [4].

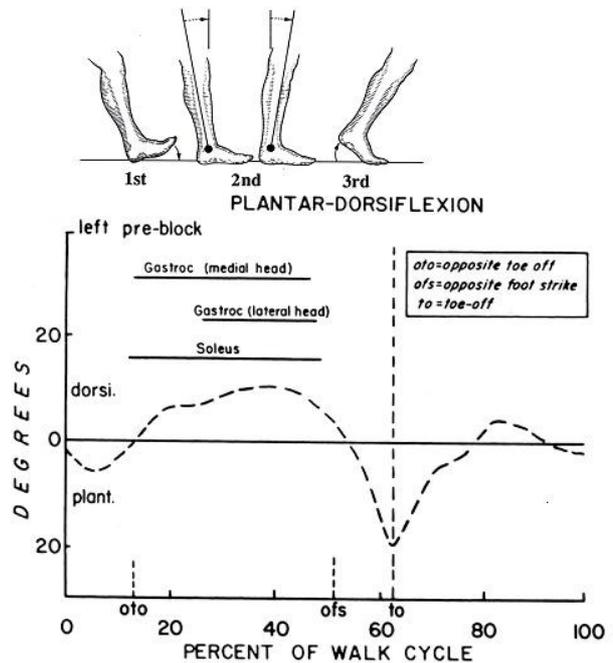


Figure 4
The human heel strikes the ground first and the leg rotates as an inverted pendulum during walking.

Small animals move with flexed joints in the legs (e.g. mice), while large animals (e.g. elephants) show almost extended straight legs during locomotion. This is believed to be due to bone-on-bone forces in the knee joint. Flexed knees imply that the external forces act at a longer moment arm with respect to the joint, which demands great muscle forces to produce corresponding joint moments acting at short moment arms and thereby very high bone-on-bone forces. With an extended knee joint the moment arms of the external forces are reduced significantly by a factor 5-10 resulting in also lower bone-on-bone forces. In small animals the bone-on-bone forces are never high enough to damage the bones or the articular surfaces, but in large and heavy animals measures have to be taken to reduce these forces. This is, among other things, accomplished by straight legs [11]. Accordingly, the elephant never trots or gallops, as this could potentially damage the bones.

The human being is neither a small nor large animal, regarding body mass. Therefore, it is believed that the straight legs of the human function as energy conservation rather than a mechanism to reduce bone-on-bone forces. However, the knee joints are not fully extended during human walking. Rather, the knee joint is flexed some 20 deg. and extended again during the first half of the stance phase and in the rest of stance it is flexed even more until toeoff (Fig. 5). Moreover, the dynamics of the knee joint vary to a great extent. Normal healthy people walking at the same speed exhibit large differences between individuals especially regarding the knee joint moment [12,13,14].

During running the body center of mass is lowest in the middle of the stance phase when the two knee joints pass each other. At toeoff the center of mass is at the highest level [15,16,17]. As the horizontal velocity follows the same pattern, the potential and the kinetic energy of the body are in phase with each other during running. Moreover, as a consequence, the extensor muscles about the ankle and the knee joint contract eccentrically during

the first half of the stance phase and concentrically during the second half and the three joints extend simultaneously [18].

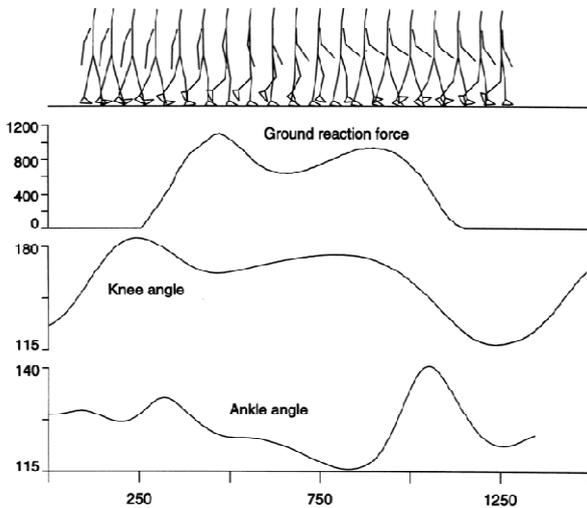


Figure 5
In the first half of the stance phase the knee joint is flexed and extended and in the last part of stance the ankle joint is plantar flexed.

During walking the body center of mass is lowest at heel strike and highest in the middle of the stance phase and accordingly the potential and the kinetic energy are out of phase with each other during walking. Another characteristic of walking is that the knee joint extends in the first half of the stance phase while the ankle joint extends (plantar flexion) late in the stance phase (Fig. 5). This is an effective way of minimizing the vertical oscillations of the body during walking.

The hip joint extends during most of the stance phase, and the net hip joint moment is extensor dominated in the first half of the stance phase, but flexor dominated during the last half or even more, which seem to work against the forward propelling of the body (Fig. 6). This pattern is seen both during walking and running.

The knee joint moment normally shows two extensor peaks during the stance phase of walking (Fig. 6). During the first, the quadriceps muscle is active, but during the last peak the knee joint extensors are normally silent. Moreover, the knee joint is flexed in the last part of the stance phase, so the extensor moment should be due to eccentric muscle contractions.

A primary purpose of the present thesis was to try to explain the origin and the function of the net joint moments observed during human walking.

It is anticipated that walking is controlled by a central pattern generator located at the spinal level and that the rhythmical muscle activity provides the leg with sufficient force and stiffness to support the body mass and propel the body forward at the desired speed [19]. However, it has also been shown that the brain plays an important role in regulating the motor output during walking [20].

However, to what extent sensory input to the spinal cord contributes to the final motor output [21] is an open question. Therefore, the second purpose of the present thesis was to investigate the possible role of afferent input from the muscle spindles during walking and running.

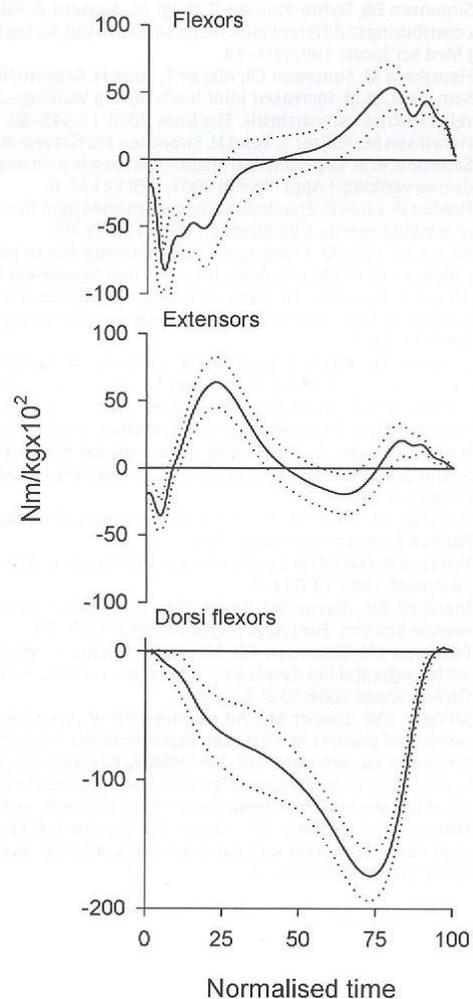


Figure 6
Typical net joint moments in the leg during the stance phase of walking. Muscular dominance is indicated. For example a positive knee joint moment means extensor dominance.

METHODS

Basically human gait was analyzed by biomechanical movement analysis and electromyography (EMG) in the studies of the present thesis. The movement analysis was in most cases performed by three-dimensional video analysis where the movements were recorded simultaneously by five digital video cameras operating at 50 frames per second while the subject walked over three force platforms embedded in the floor (Fig. 7). All signals were by the Ariel Performance Analysis System (APAS), and after digitization of reflective markers on the subjects (Fig. 8; Fig. 9), the movement data and the force platform data were input to software developed in Matlab.

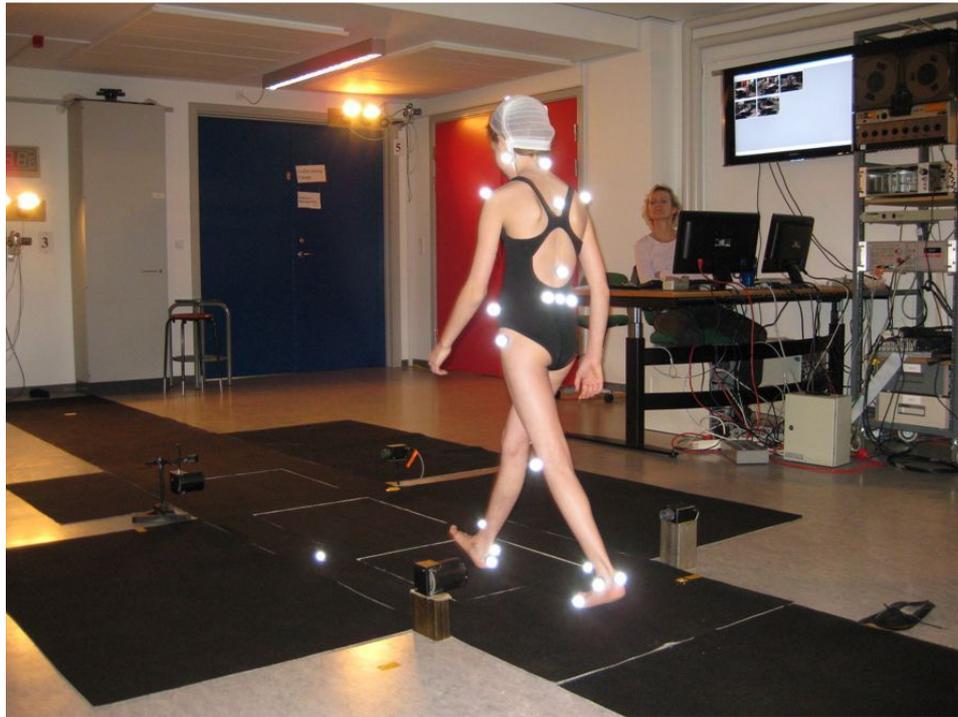


Figure 7

The gait lab at the Panum Institute with five video cameras and three force platforms. The markers seem disproportionately large due to the flash of the photo camera.



Figure 8

The spherical and reflective markers were placed at anatomical landmarks by adhesive tape.

Besides the APAS a Vicon system was used, consisting of six infrared cameras operating at 100 frames per second and two force platforms. The platforms were in both cases strain gauge based (AMTI ORG6-5-1) and measured three orthogonal ground reaction forces together with center of pressure (COP) in two directions (Fig. 10; Fig. 11).

When the movement data (3D coordinates) are combined with the ground reaction forces, net joint moments can be calculated by inverse dynamics. Joint moments expressed about anatomical axes for flexion/extension, abduction/adduction and internal/external rotation require that each body segment is



Figure 9

Markers were also placed to mark the location of the force platforms.

represented in space by at least three markers. With the APAS system and Matlab calculations the marker setup originally described by Vaughan et al. (1992) was used in P2, P5, P6, P7 and P8 (Fig. 12; Fig. 14).

In P4 the Helen Hayes marker setup (Kadaba et al., 1990) was used with the Vicon system (Fig. 16). This setup includes markers placed on wands, which amplifies the rotational movements. In both the Vicon and the APAS (Matlab) system 3D joint centres are calculated (Fig 13). In Matlab, anthropometric data provided by Vaughan et al. (1992) were used to calculate the joint centers while the anthropometry used by Vicon is unknown.

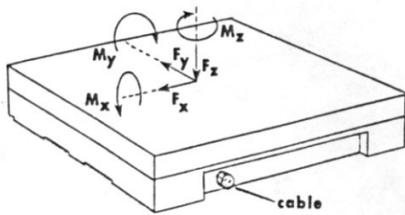


Figure 10
The force platform outputs three forces and three moments. M_x / F_z gives the center of pressure in the y -direction.

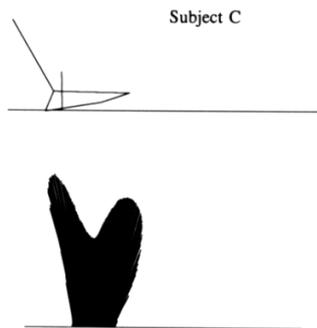
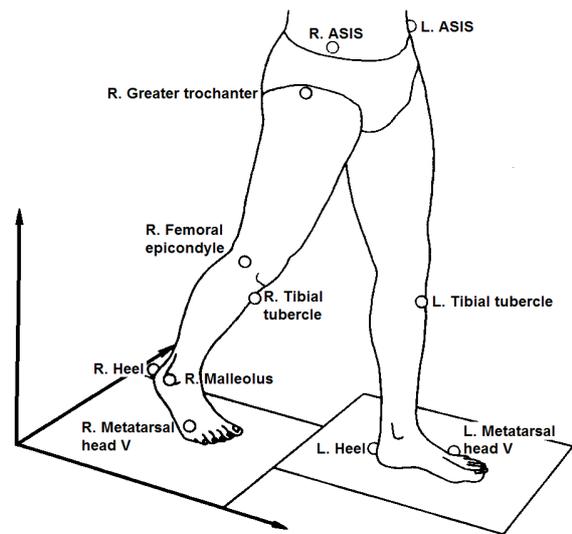


Figure 11
Center of pressure during walking

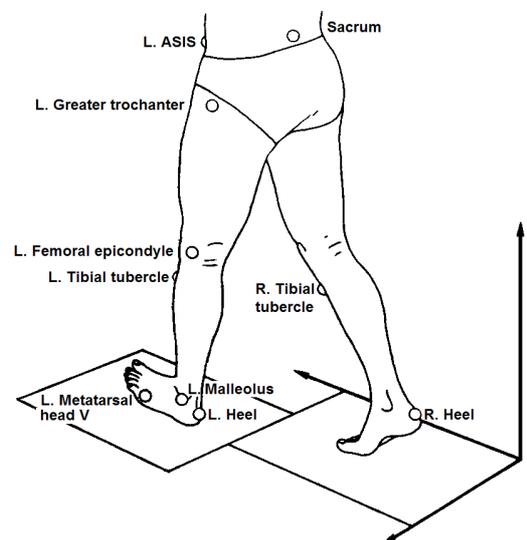


Figure 12
The marker setup described by Vaughan et al. [22].

Different software is likely to compute net joint moments differently to some extent. In the present thesis custom-written software in MatLab and commercial software (PlugInGait) from Vicon were used. The two approaches were compared by a specially designed experiment in which the two different marker setups were mounted simultaneously on the same subjects. Vicon digitized all markers and the 3D coordinates and the force plate data were exported to Matlab. Twelve gait cycles were averaged for each subject. The results showed a systematic and statistically significant difference in joint moments as the moments were consistently higher when calculated by Vicon's PlugInGait software. However, the shape (the time course pattern) of the moments were highly identical in all cases [24].

WALKING CONDITIONS.

Human walking was studied under different conditions in the papers of this thesis. Normal walking was studied in P1, P2, P3, P6, P8 and P9. The influence of a drop-foot was studied in P4, the influence of high-heeled shoes in P5, the influence of upper body position in P7 and finally consequences of joint hyper mobility in P8. During the contact phase of walking, no movement can take place in a single segment without causing movement in the connected chain of segments. Segment interaction is therefore of great interest and one way to study this phenomenon is to

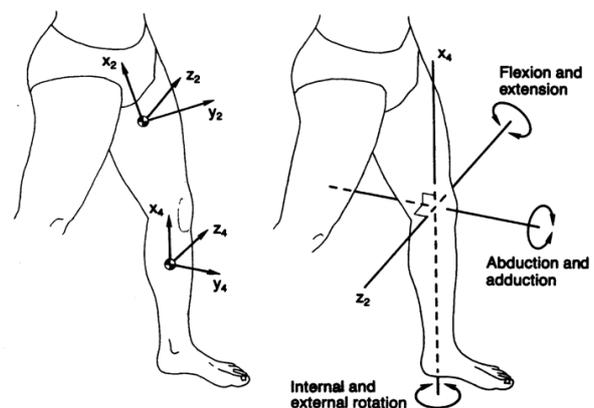


Figure 13
Anatomical axes of rotation.

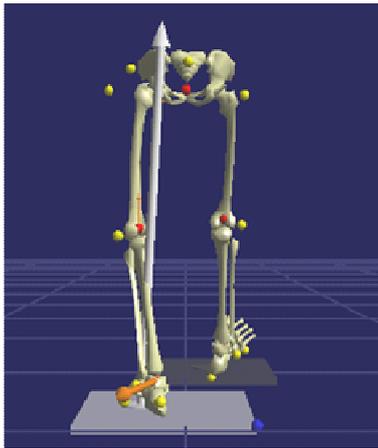


Figure 14
The Vaughan marker setup (yellow balls) and the calculated joint centers (red balls).

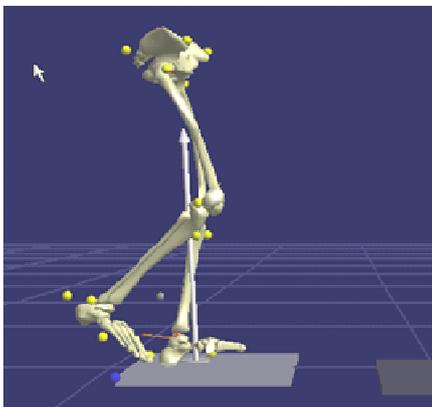


Figure 15
A fictive skeleton is animated on the markers (yellow balls) and COP is animated on the force platform.

“disturb” the normal pattern. An example of this is P7 in which study we asked the subjects to walk with the upper body in a reclined, an inclined and in normal position (Fig. 17). In P5 high-heeled shoes were used to impair the function of the ankle joint. Heel height was 9 cm and a kind of sandal was used, so the shoe was strapped to the foot allowing the reflective markers to be attached to the foot instead of the shoe (Fig. 18).

ELECTROMYOGRAPHY.

In most of the studies electromyography (EMG) was measured by surface electrodes and custom-built amplifiers as well as pre-amplifiers. In P5 a wireless system MQ16 (Marq Medical, Farum, Denmark) was used. This system also uses pre-amplifiers at the electrodes but also an analog to digital converter at the electrodes before the signal is lead through wires to a small transmitting unit using Bluetooth technology to transmit the signals to a PC (Fig. 19).

An earlier version of this system was used in P7 called MQ8, the only difference being the maximum number of channels. A small wireless trigger unit (Fig. 19) was used to synchronize the EMG signals sampled with Bluetooth to analog signals sampled by an ad-converter in a PC.



Figure 16
The Helen Hayes marker setup with markers on wands at the thigh and leg.

In P7 intramuscular fine wire EMG was used to record from the hip flexor m. iliacus (IL), a part of m. iliopsoas, the most important hip flexor, which is very difficult to record using surface electrodes. Stainless steel wires were uninsulated for a few millimeters at both ends, inserted in a hypodermic needle and sterilized. A safe location for insertion of the wires in the groin was found by palpating the femoral artery, the anterior superior iliac spine and the pubic tubercle (Fig. 20). This procedure was first developed on cadaver specimens and used in a study of kicking [25].

H-REFLEX RECORDINGS.

In P1, P2, P3 and P9 the soleus H-reflex [26] was measured during walking and running by stimulating the tibial nerve in the popliteal fossa (Fig. 21). The stimuli were delivered by a custom-built constant current stimulator.

During walking and running a computer program controlled the stimulator and was set to produce M-waves 25% of the maximal M-wave in twenty phases of the gait cycle. An electronic integrator was reset by a foot-switch under the heel and produced a ramp function increasing by 2 V per second. The stimuli were given every two seconds and therefore dispersed randomly over the gait cycle (Fig. 25). By reading the ramp value just before triggering the stimulator, the program would know the time position in the gait cycle. In a previous study we found that the maximal M-wave varied considerably during the gait cycle [27], therefore double stimuli were used in the studies of the present thesis. This meant that a supramaximal stimulus was given 60 ms after each stimulus for measuring the H-reflex (Fig. 22). In this way the actual H-reflex could be expressed relative to the maximal M-wave elicited in the same sweep [27].

In P9 the gastrocnemius H reflex was also measured during walking and running. It appeared that the tibial nerve had to be stimulated at a lower intensity regarding the gastrocnemius H-reflex. This was most likely because the axons from the α -motoneurons



Figure 17

Inclined walking

Normal walking

Reclined walking

in gastrocnemius are thicker than those to the soleus and therefore easier to activate electrically. Likewise the H-reflex in gastrocnemius was always lower than the H-reflex in the soleus, which is seen in Fig. 24. The data are from study P9 and as such unpublished because the reference excitability curves were not used to normalize the data in P9.

As it was necessary to stimulate separately for the H-reflexes in soleus and gastrocnemius, every other stimulus was aimed only at one of the two muscles, respectively (Fig. 25).

CROSS-TALK

As cross-talk from the more profound soleus to the superficial gastrocnemius is a well known phenomenon, a special procedure was conducted to reduce cross-talk during the stimulations. This may not be a problem during normal EMG recordings, but dealing with compound synchronized signals like the M-wave and the H-reflex this may become a severe problem. Three recording electrodes were mounted over the medial gastrocnemius with an interelectrode distance of 2 cm. The top and the middle electrode were connected to one EMG amplifier and the middle and the lowest positioned electrode to another EMG amplifier, making the middle electrode common to the two channels. Later the two signals were subtracted in the computer to reduce cross-talk from the soleus. This method has been described as a double-

differential electrode by Vugt and van Dijk [28] (Fig. 23).

To illustrate the effect on cross-talk of the double differential electrode, the common peroneal nerve was stimulated to produce a maximal M-wave in the anterior tibial muscle (TA) (Fig. 26).

In P3 fine wire intramuscular EMG was measured in the soleus muscle during H-reflex measurements. It was clear that wire electrodes, although 250 µm in diameter and inserted two cm apart, were much more variable when measuring H-reflexes and M-waves compared with surface electrodes (Fig. 27; Fig. 28). This was also reported for one subject by Simonsen et al. [29].

THE V-WAVE

Normally the H-reflex is extinguished completely at a supra maximal stimulus due to collision of orthodromic and antidromic action potentials on the efferent axons just outside the spinal cord. However, if the muscle is activated voluntarily, descending potentials originating from the motor cortex will collide with antidromic signals and clear the axon for an H-reflex (Fig. 29). The V-wave expresses a combination of motoneurone excitability, presynaptic inhibition and motor output from the brain. It has been used in studies of muscle strength training to indicate increased firing frequency after a training period [30,31].



Figure 18

Walking on high heels.

Note that the markers are fixed on the foot and not the shoe.



Figure 19
The Bluetooth transmitter

Pre-amplifiers with 16 bit ad-converter

Wireless synchronisation

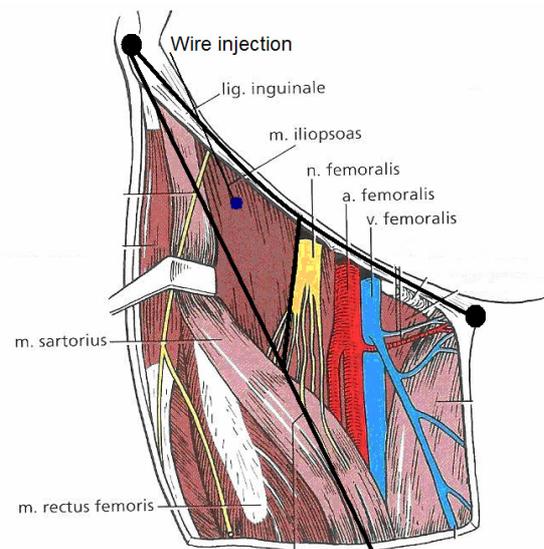


Figure 20
Top: Wires were entered at the blue spot.
Bottom: A needle is inserted to the iliopsoas muscle.

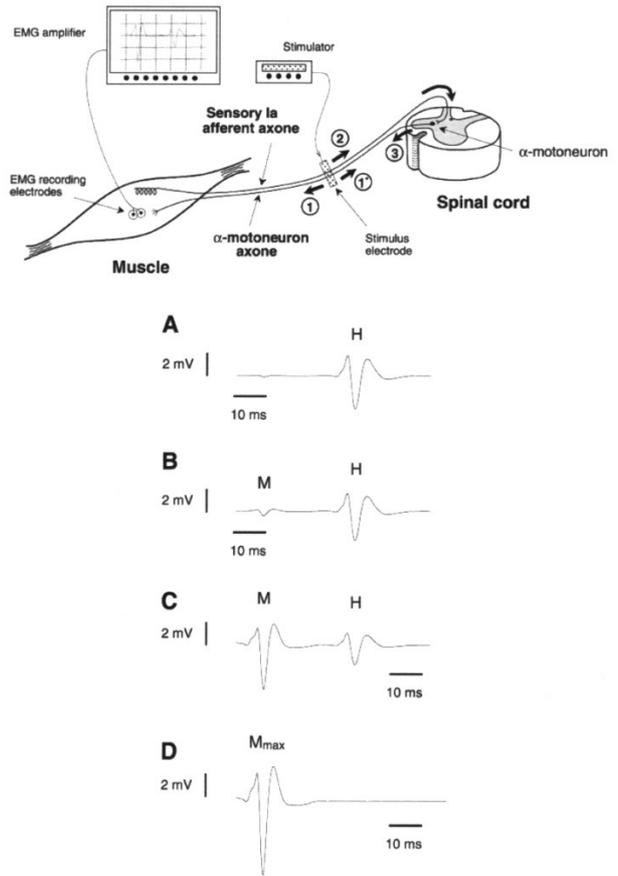


Figure 21
Schematic drawing of the procedure used to measure the Hoffmann reflex in the soleus muscle.

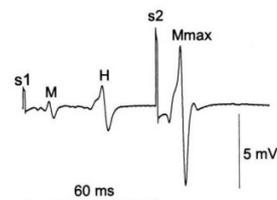


Figure 22
The first stimulus (s1), the M-wave (M), the H-reflex (H), the second and supramaximal stimulus (s2) and the maximal M-wave (Mmax).

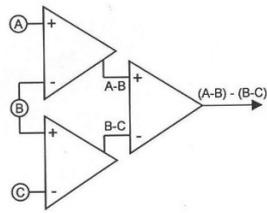


Figure 23
Schematic of a double-differential electrode used to reduce cross-talk.

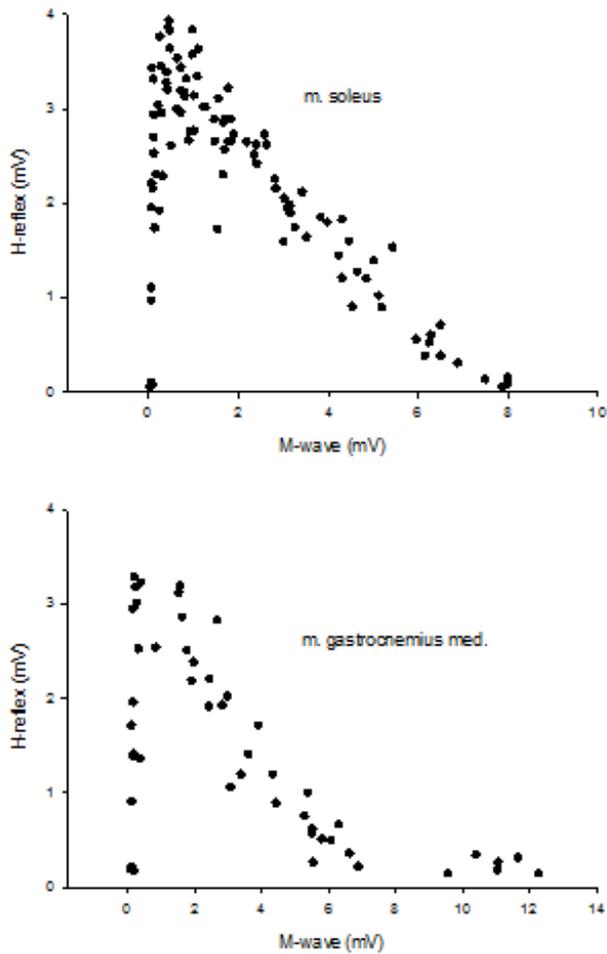


Figure 24
Reference excitability curves in *m. soleus* and *m. gastrocnemius medialis* in the same subject in standing position. The data are from study P9.

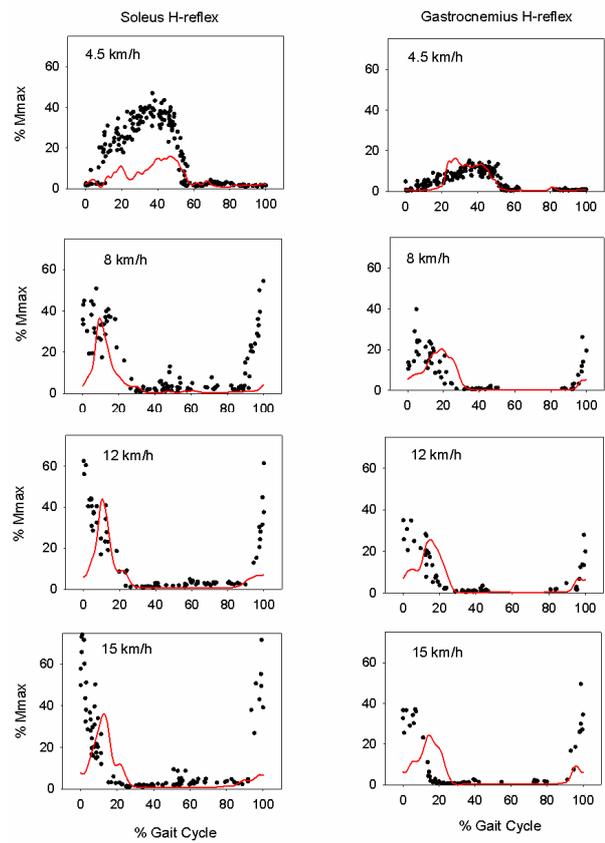


Figure 25
The soleus and the medial gastrocnemius H-reflex during walking and running in one subject. Each dot represents one stimulus in a gait cycle. Red curves show the averaged EMG in arbitrary units. The figure is from P9.

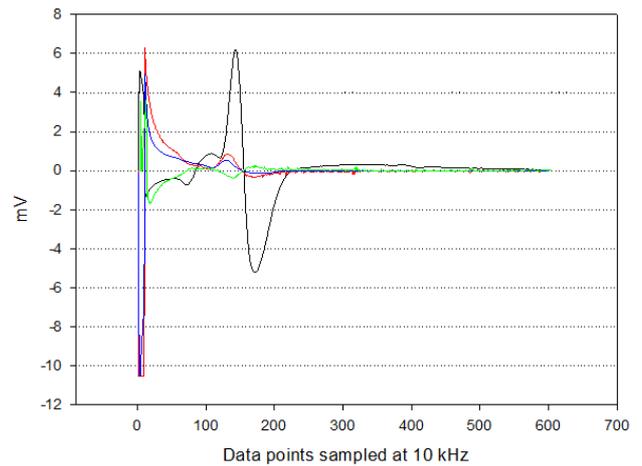


Figure 26
The black curve shows the maximal M-wave in TA, the red and the green curve are EMG in the passive gastrocnemius muscle measured by two sets of electrodes with a common electrode. The blue curve is the result of subtracting the green from the red curve.

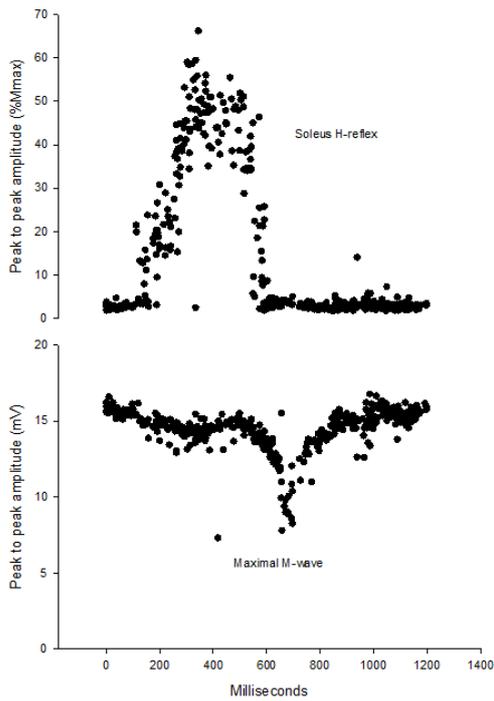


Figure 27
 Surface electrodes. On top: soleus H-reflex modulation during the gait cycle of walking 4.5 km/h. Each dot represents one stimulus in one step. All data are from one subject. Below: variations in the maximal M-wave during the gait cycle. Heel strike is at 0 ms and toef off at 600 ms.

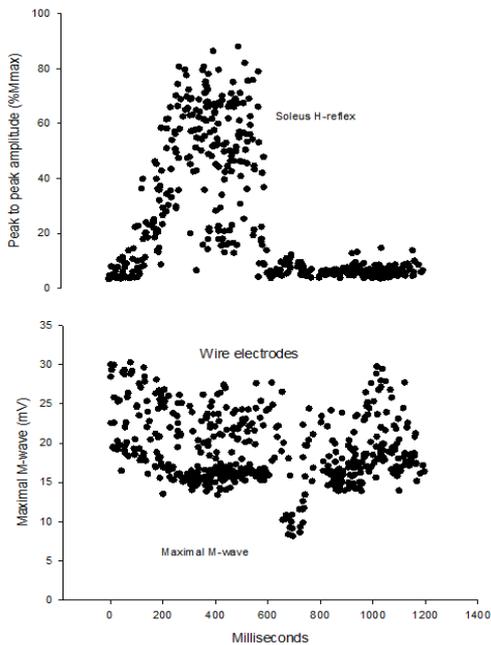


Figure 28
 Wire electrodes. On top: soleus H-reflex modulation during the gait cycle of walking 4.5 km/h. Each dot represents one stimulus in one step. All data are from one subject. Below: variations in the maximal M-wave during the gait cycle. Heel strike is at 0 ms and toef off at 600 ms.

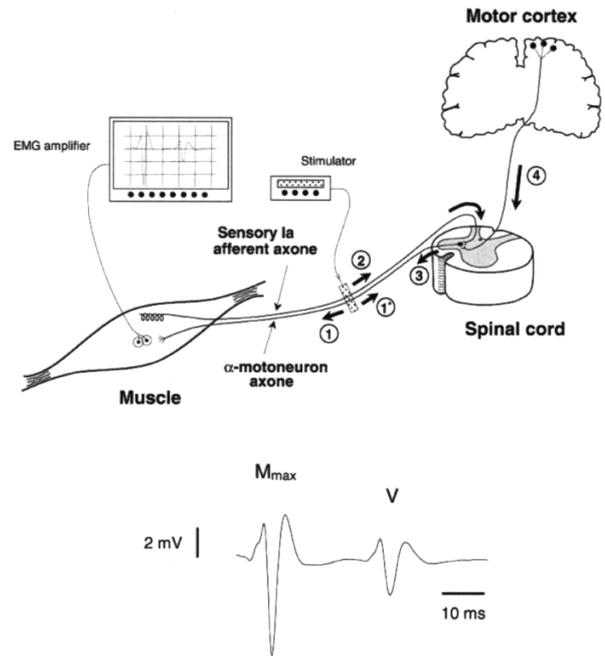


Figure 29
 The V-wave in *m. soleus* was elicited by a supramaximal stimulus during voluntary activity.

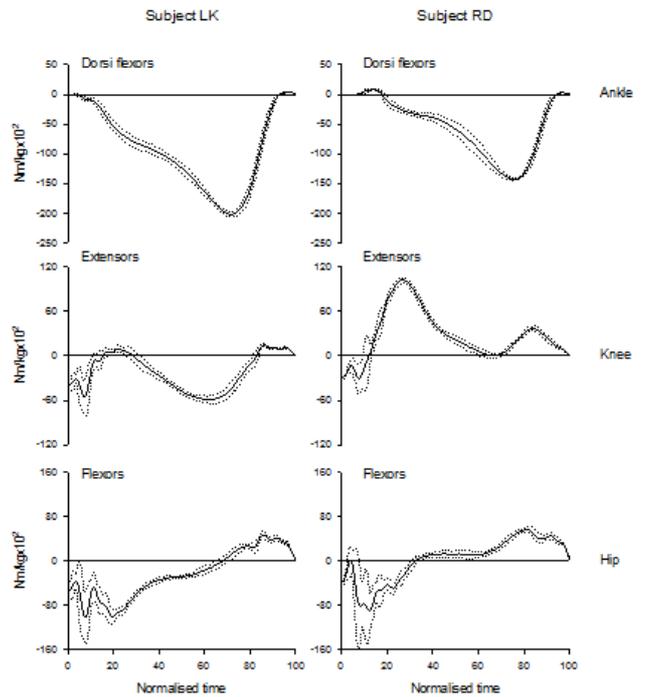


Figure 30
 Two subjects with very different joint moments. Average of six trials with SD.

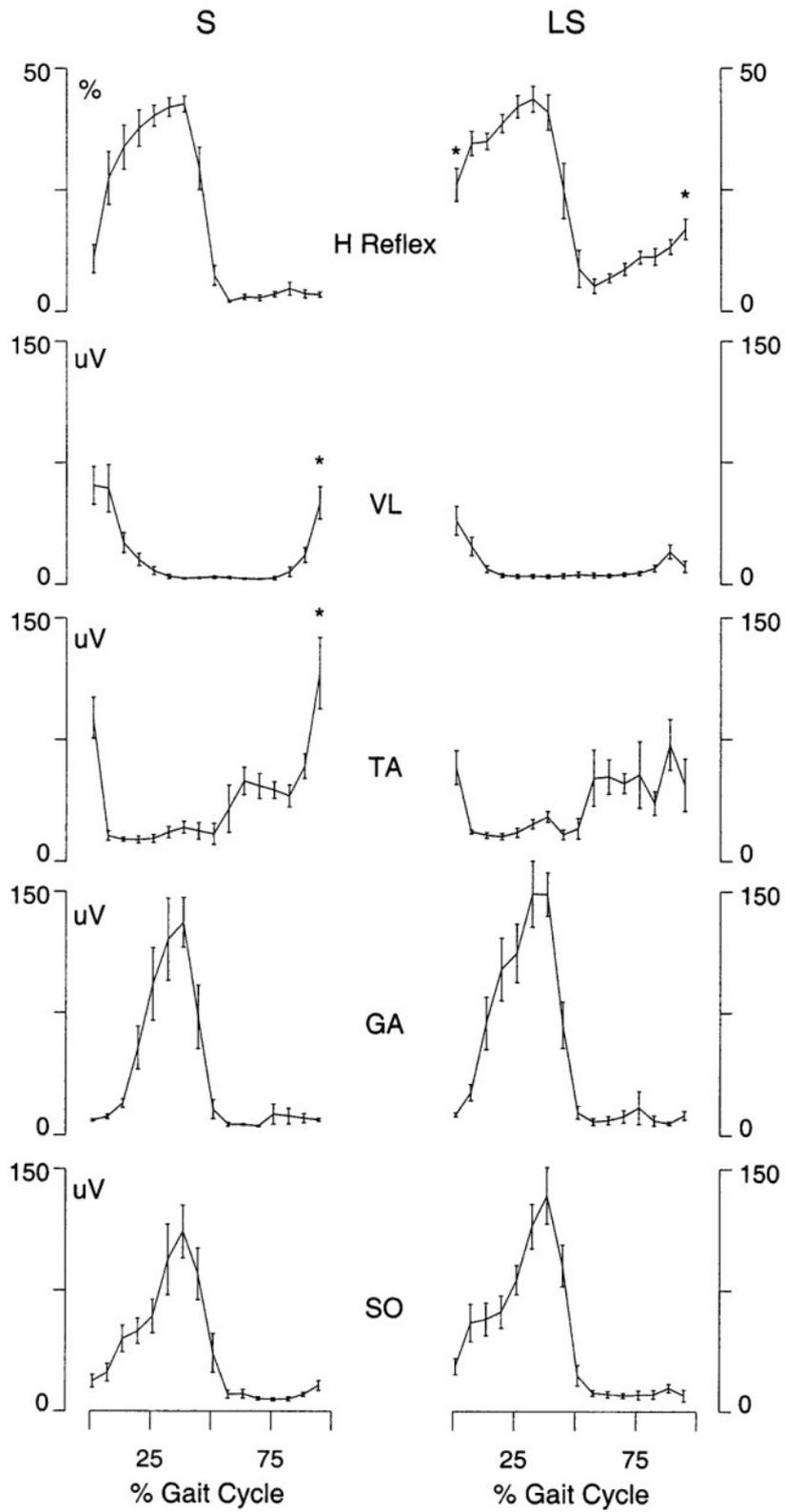


Figure 31
 Group S with the suppressed H-reflex during the swing phase and group LS with the less suppressed H-reflex during swing. On top: the soleus H-reflex.
 Below: EMG from vastus lateralis, tibialis anterior, gastrocnemius medialis and soleus.

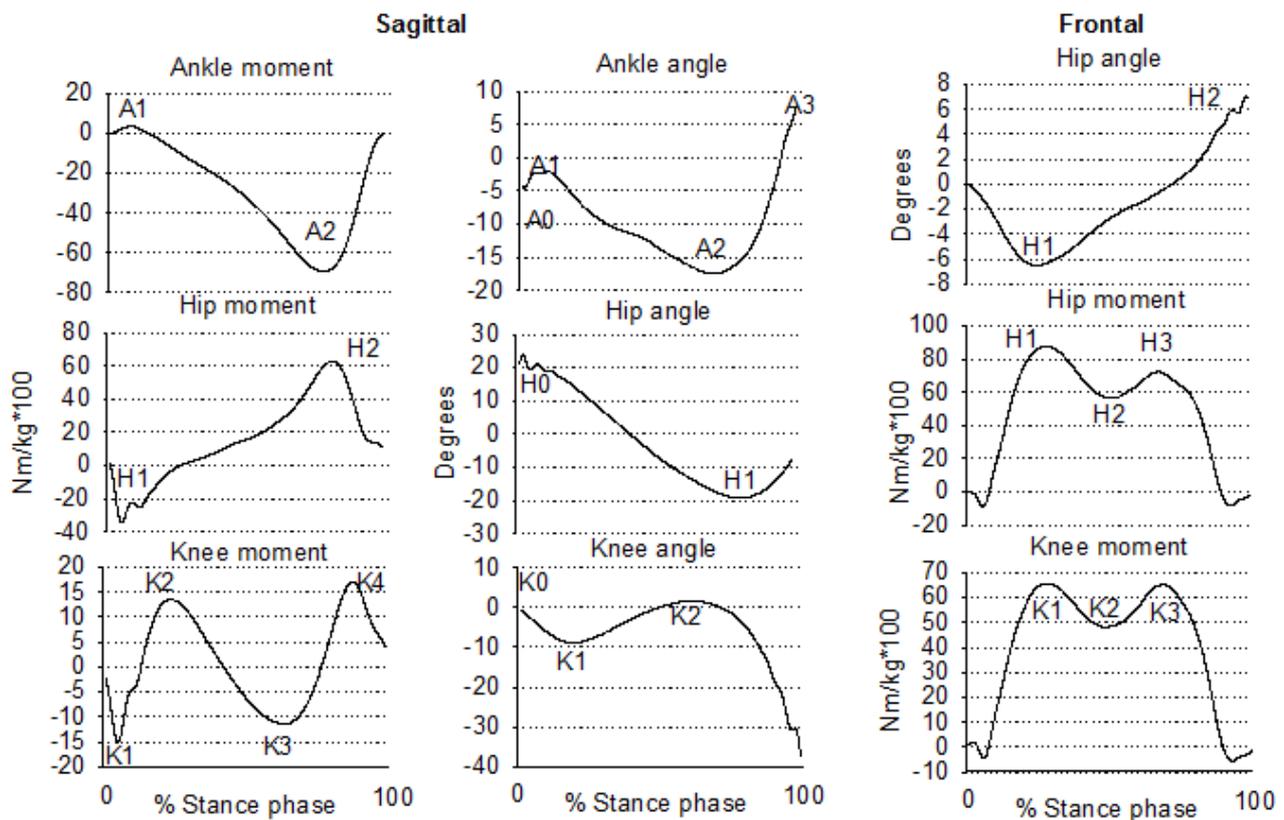


Figure 32
Definition of the peaks used to extract parameters for statistical tests.

RESULTS AND DISCUSSION

MECHANICAL INTER-INDIVIDUAL DIFFERENCES

Dynamics of human walking were reported as early as 1939 [32]. Pedotti conducted the first computer-based study, in which net joint moments were calculated by inverse dynamics using movement data and ground reaction forces [13]. The results of this study showed very large differences between individual subjects. It was especially noted that some subjects walked with flexor dominance about the knee joint during the entire stance phase while other subjects showed extensor dominance during the entire stance phase. The results of the present thesis confirmed that large differences exist regarding the knee joint moment (P6, P2) and several studies by Winter have shown the same [14] as well as Pedotti and Crenna [33]. However, most people seem to walk with two extensor peaks in the knee joint moment separated by flexor dominance in the middle of the stance phase or at least a moment close to zero (Fig. 30). Despite the same overall pattern, the size of the knee joint moment may vary tremendously in size, as displayed in Fig. 30 for two different subjects. It is also noteworthy that subject RD, with the high extensor moment about the knee joint, used a lower plantar flexor moment about the ankle joint compared with subject LK (P6) (Fig. 30). This illustrates the principle of the so-called support moment suggested by Winter [34]. He considered the hip, knee and ankle joint moment positive for extensor domi-

nance and added them to a support moment of the whole leg. The size of this moment should then be large enough to work against gravity and to bring the body forward at the desired speed. With this concept, e.g. the knee joint moment may be flexor dominated in certain intervals as long as the hip and ankle joint moments can compensate. This is, however, only possible during dynamic conditions.

The moment pattern seems to be unique for each single subject [35], but it was shown by Henriksen et al. [36] that induced muscle pain in m. quadriceps femoris changed the knee joint moment from extensor to flexor dominance in one subject. This effect was still present 30 minutes after cessation of pain.

Walking at different speed and with different shoes or barefooted may have caused differences in joint moments between several studies during the last decades. Therefore, the subjects walked at controlled speed and with identical shoes (or barefooted) in all the studies of the present thesis.

In order to identify the main kinetic and kinematic differences among healthy individuals during walking, ten selected kinematic and kinetic parameters from 15 subjects were input to a cluster analysis, which identified two groups of five and ten subjects, respectively. It was found that the knee joint extensor moment in the first half of the stance phase was significantly higher in one of the groups. Furthermore, the subjects in this group walked with more flexed knee joints during the stance phase and higher EMG activity in the quadriceps muscle (P6). It has previously been

shown in ACL-patients that walking with a more flexed knee joint coincided with increased extensor moments [37].

INTER-INDIVIDUAL DIFFERENCES IN H-REFLEX MODULATION.

In P2 it was shown that at least two different soleus H-reflex modulations exist during normal human walking. Each individual appears to have a unique pattern of H-reflex modulation, which is highly reproducible between days (P3). Fifteen subjects could be divided into two groups. In group S (suppressed) (6 subjects) the H-reflex was almost completely suppressed during the swing phase while in group LS (less suppressed) with 9 subjects the H-reflex increased towards the end of the swing phase and started the stance phase at a more excitable level (Fig. 31). In a few subjects, the reflex was only increased just prior to heel strike. It was further revealed that group LS had significantly lower TA EMG activity during the swing phase (P2) (Fig. 31). However, even if the TA activity had been unchanged, it would still be possible to reduce reciprocal antagonist inhibition by descending pathways from the brain [38]. This suggests that group LS is more careful about heel strike and relies on a stretch reflex to save them from a sudden perturbation. In support of this, the soleus H-reflex has been shown to increase in subjects walking on high-heeled shoes [39]. Group S, on the other hand, demonstrated significantly higher knee joint extensor moments and lower ankle joint plantar flexor moments during the stance phase, which may indicate that this movement strategy puts more emphasis on the knee joint during walking.

IMPLICATIONS OF INDIVIDUAL DIFFERENCES

In P6 it was calculated that the group of subjects with the highest knee joint extensor moments also showed significantly higher bone-on-bone forces in the knee joint (64 N/kg body mass versus 55 N/kg). As a normal human being takes between 10.000 and 20.000 walking steps per day, this could explain, why some people seem pre-disposed regarding development of knee joint arthritis.

The fact that normal healthy subjects walk very differently makes it more difficult to identify significant differences between groups of subjects, even when the subjects walk at the same velocity and barefooted and when the joint moments are normalized to body mass and/or body height.

WALKING SPEED

It is often argued that self-selected walking speed is preferable because a controlled speed may disturb the natural movement pattern of individuals, but this has never been demonstrated experimentally. It is in fact more likely that subjects are unaware of their preferred speed under the circumstances of an experiment in a laboratory. In P4 both controlled and self-selected velocity were used. However, the drop-foot patients chose to walk at a speed significantly slower than the healthy controls, which made it impossible to use the self-selected speed. Walking speed has been shown to have a significant influence on the joint moments in the sagittal plane [40] though not in the frontal plane [41]. Holden et al. [42] demonstrated a substantial influence on joint moments in the sagittal plane as increasing the speed from 3.5 to 4.7 km/h (25% increase) almost doubled the knee joint extensor moment.

KINEMATIC AND KINETIC PATTERNS AND PEAK VALUES

It is easy for the human eye to recognize that each individual walks with a moment and angle pattern unique for the person in question. Larsen et al. [43] were able to identify 21 subjects walking on different days by use of only three angular velocities in the frontal plane. However, mostly walking is quantified by certain peak values, which are easy to obtain from all subjects (Fig. 32).

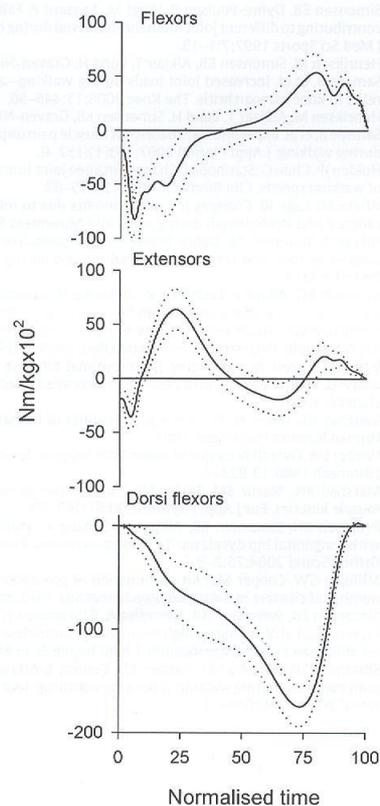


Figure 33

A net joint moment with a positive sign indicates flexor dominance about the hip joint, extensor dominance about the knee joint and dorsiflexor dominance about the ankle joint. The figure shows moments averaged for a group of subjects \pm SD.

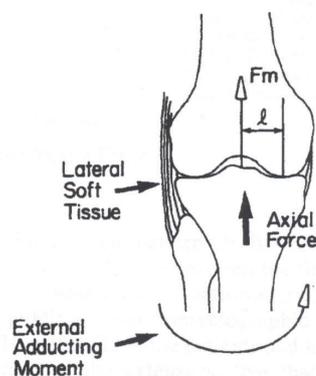


Figure 34

The external adductor moment corresponds to an internal abductor moment. It is illustrated that *m. quadriceps femoris* has a moment arm for abduction when the joint center is located under the medial femoral condyle.

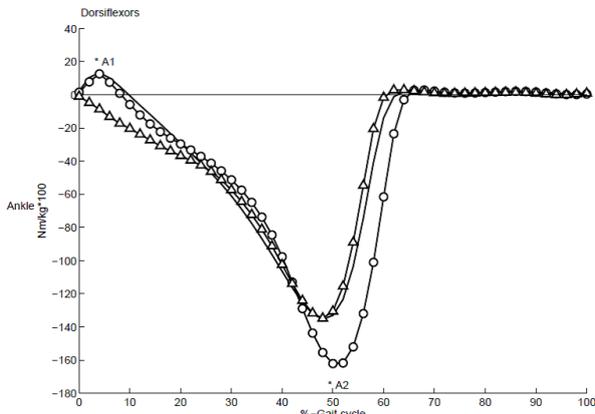


Figure 35
At A1 the affected leg (triangles) could not generate a dorsiflexor moment right after touch-down and the unaffected leg showed a compensatory and higher plantar flexor moment at A2.

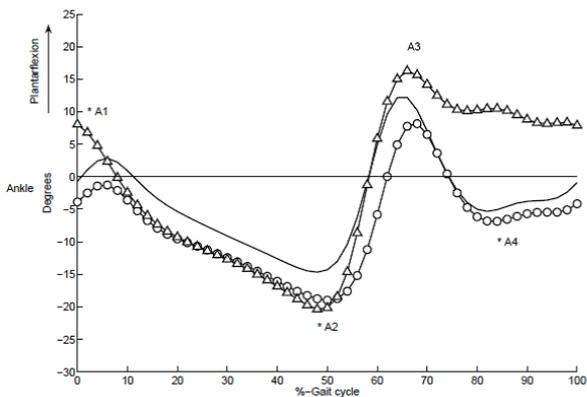


Figure 36
The drop-foot (triangles) was plantar flexed at touchdown and during the entire swing phase. The swing phase started at approximately 60% gait cycle. The graphs are the average of five trials and across all subjects and patients, respectively.

These characteristic peaks were used in several of the studies in the present thesis and have been used extensively for the sagittal plane by e.g. Winter [14]. In the sagittal plane a moment with a counter-clockwise pulling direction was considered positive in the present thesis.

This implies that a positive moment about the ankle joint corresponds to dorsiflexor dominance, a positive knee joint moment extensor dominance and a positive hip joint moment flexor dominance (Fig. 33). These moments are so-called internal muscle moments. A few research groups express the same moments as external moments, e.g. Kerrigan et al. [44].

Concerning joint moments in the frontal plane, it appears that several research groups display the knee joint moment for abduction/adduction as an external moment e.g. Foroughi et al. [45]. This is probably because human anatomy does not define any abductor muscles for the knee joint. It is a hinge joint with the possibility for rotation when flexed close to 90 deg. Therefore,

what should be termed an internal abductor moment is very often called an external adductor moment or adduction moment.

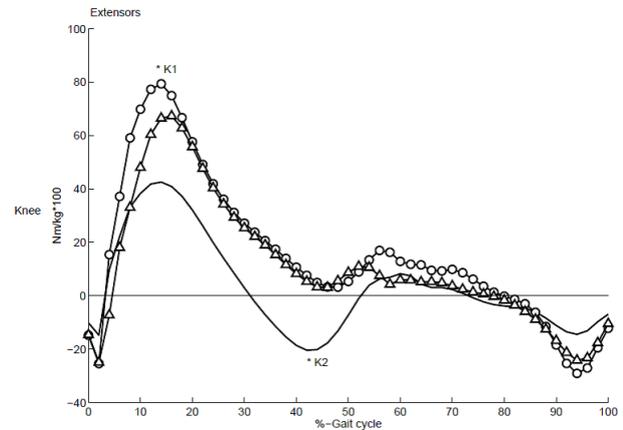


Figure 37
The knee joint extensor moment (K1) in the first half of the stance phase was significantly higher in both the affected and unaffected leg compared with the healthy group.

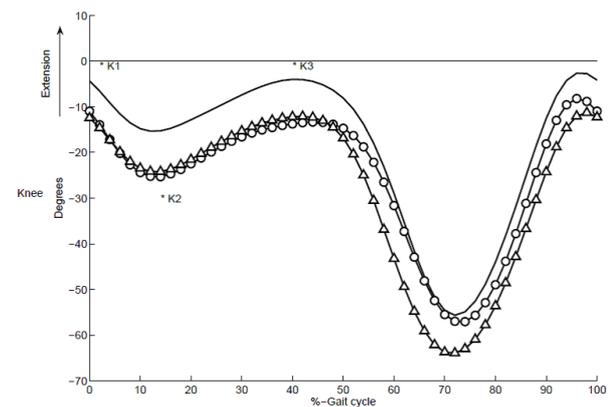


Figure 38
The explanation for the increased knee joint extensor moment was obviously that the drop-foot patients flexed the knee joint significantly more, which will increase the external moment arms as shown for ACL-patients (Alkjaer et al. [38]). The reason why both legs were affected by the drop-foot is most likely that the patients adapt to a new gait pattern to avoid asymmetry between the legs.

Ironically, the same authors mostly report all the other joint moments as internal moments. Because the movement of a joint is not indicated by the sign of the moment, it seems important to term the moments in relation to the dominant muscle group, for example flexors instead of flexion etc.

INTERPRETATION OF THE FRONTAL KNEE JOINT MOMENT.

It has been suggested that the quadriceps muscle is capable of applying an abductor moment about the knee joint [46]. This theory assumes that the instantaneous joint center in the knee joint is located in the medial compartment during for example the stance phase of walking and the lateral compartment is opened by a slight varus position. The quadriceps tendon (lig. patellae) passes laterally to the instantaneous joint center and has a moment arm of 1-2 cm for abduction (Fig. 34).

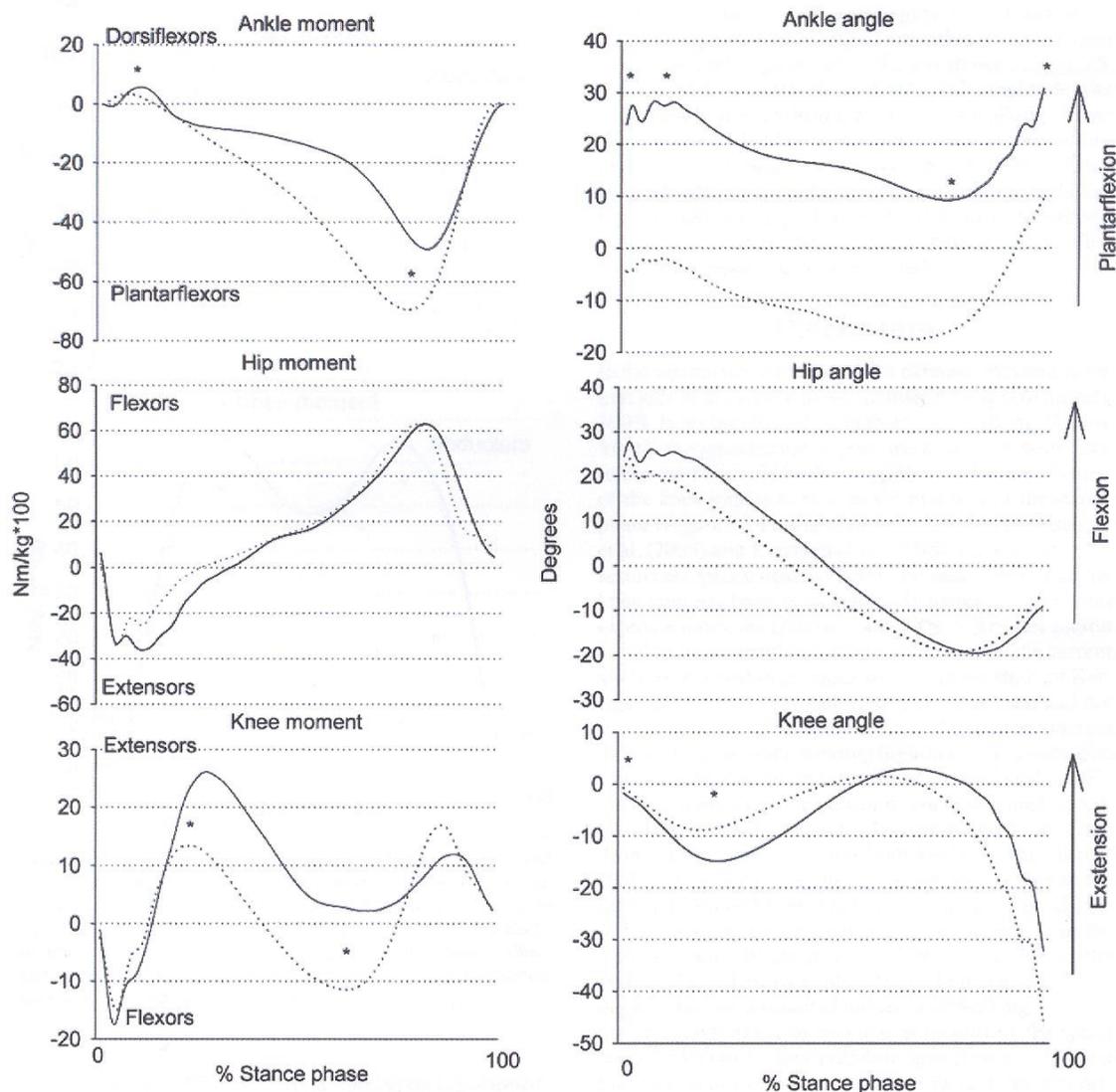


Figure 39
Net joint moments and joint angles during high-heeled (solid) and barefooted (dotted) walking.

SEGMENT INTERACTION

In a closed kinematic chain, e.g. during the stance phase of walking, movement of one segment of the leg will result in movement of connected segments. This is due to joint reaction forces as well as moments pulling on adjacent segments. In fact, a muscle can move a joint even when it is not spanning the joint because of joint reaction forces. Furthermore, the existence of biarticular muscles also complicates the understanding of muscle function during human walking.

One way to study this complexity is to disturb the system. In P4 it was studied how a drop-foot and thereby a changed ankle joint moment would affect the knee and the hip joint.

It is considered a serious problem that a drop-foot leads to almost 100% higher knee joint extensor moments as this will also lead to much higher bone-on-bone forces [36].

In P5, fourteen female subjects were studied during barefooted and high-heeled walking (9 cm heel). The plantar flexor moment about the ankle joint during push off was significantly decreased

in the high-heeled condition and the knee joint extensor moment was almost doubled in the first half of the stance phase (Fig. 39). The latter was accompanied by a more flexed knee joint in the high-heeled condition and a significantly higher EMG activity in the knee joint extensors. The ankle joint angle was naturally much more plantar flexed during the whole gait cycle in the high-heeled condition and this may have caused the reduced plantar flexor moment due to a shorter moment arm at the Achilles tendon and a shorter muscle fiber length. However, walking is a submaximal activity with the peak soleus and gastrocnemius EMG activity between 30 and 50% maxEMG. Therefore, it was possible for the subjects to increase the muscle activity and maintain the ankle joint moment. They did in fact increase the soleus peak activity, but at the same time also the tibialis activity was increased resulting in a significantly higher level of co-contraction during push off. This could also have led to the lower ankle joint moment as net joint moments are strongly affected by co-contraction.

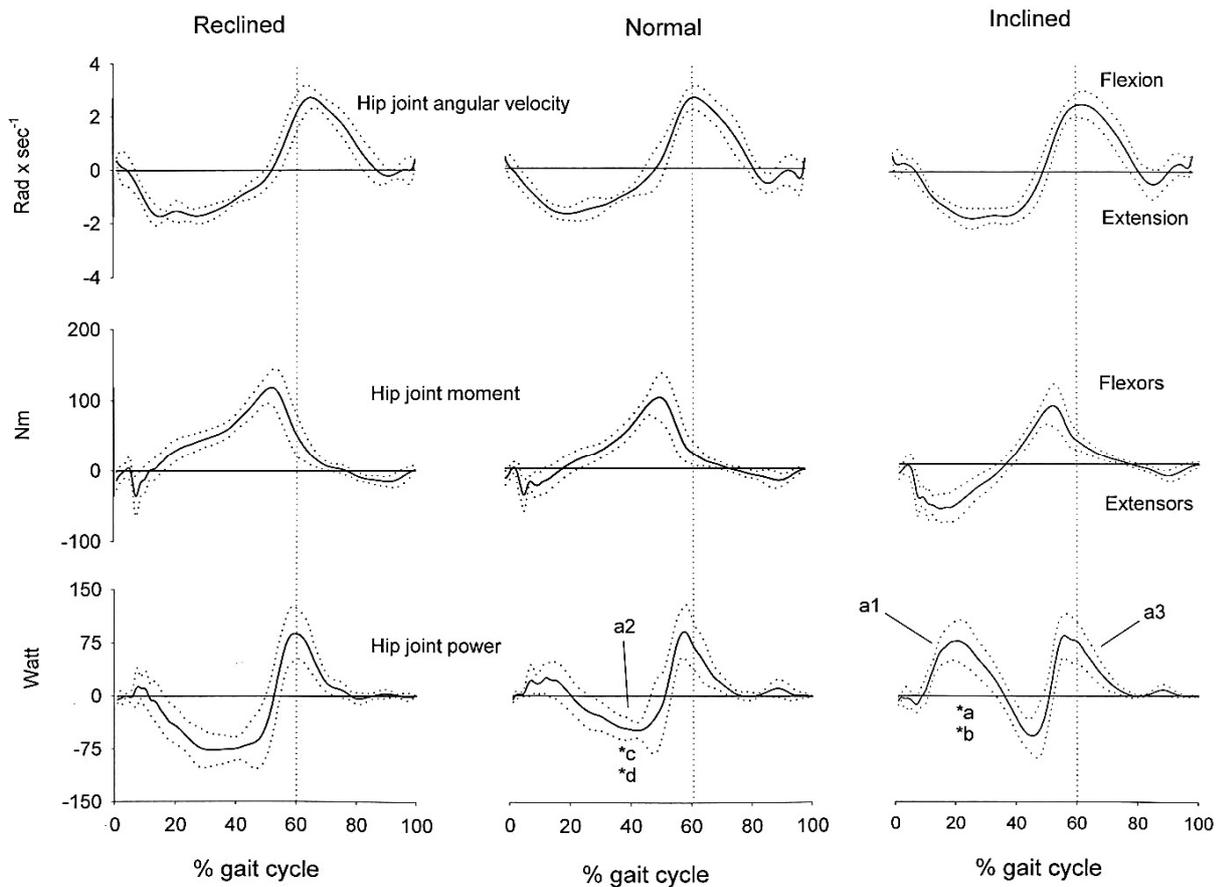


Figure 40
 Angular velocity, net joint moments and joint power for the hip joint during reclined, normal and inclined walking. Negative hip joint work was significantly increased when the upper body was reclined (area a2). In contrast, positive hip joint work was higher during inclined walking (area a1).

No differences were observed for the hip joint in the sagittal plane (P5). In the frontal plane both the hip and knee abduction moment were significantly higher during high-heeled walking. The knee abductor moment was approximately 10% higher, which may seem moderate compared with the approximately 100% increase in the knee extensor moment. However, it has been reported that in patients with osteoarthritis an increase of only 1% in this moment increases the risk of progression of osteoarthritis by 6.46 times [47]. Equivalent differences were observed in patients with generalized joint hyper mobility (P8), which indicated that these patients had started to develop osteoarthritis, which again could explain that they experienced pain regularly.

MANIPULATING THE HIP JOINT MOMENT

In P7 nine healthy male subjects were asked to walk at a velocity of 4.5 km/h with the upper body in three different positions: normal, reclined and inclined (Fig. 17). The purpose of the study was to seek explanations pertaining to the always existing hip joint flexor moment during the last half of the stance phase of human walking (and running) (Fig. 34; Fig. 39; Fig. 40). Fig. 40 illustrates that most of the hip joint flexor moment during normal walking is generated by eccentric muscle work (a2). It was revealed that the balance of the upper body was not controlled by

the hip joint flexor moment as suggested by Mann and Sprague [48] and by Hunter et al. [49] because the moment did not increase when walking with the upper body in a reclined position. Furthermore, it was found that this flexor moment was not generated by muscles but instead by ligaments about the hip joint resisting hip extension. This means that the leg is brought forward only by use of stored elastic energy, which must be considered extremely energy conserving and contribute to the low energy cost of human walking. Apparently evolution has preferred low energy cost more than range of motion regarding hip joint extension.

Intramuscular EMG from indwelling fine-wires showed that the iliacus muscle was active at a very low level (app. 5 %maxEMG) in the first part of the stance phase and the rectus femoris likewise (app. 12 %maxEMG), so these muscles could not have generated the hip joint flexor moment in the last half of the stance phase. In the swing phase the iliacus also showed very low activity during normal and reclined walking, but surprisingly it was highly active during inclined walking. The explanation for this was apparently that the hip joint ligaments were stretched less during hip extension in the inclined condition and therefore the leg had to be

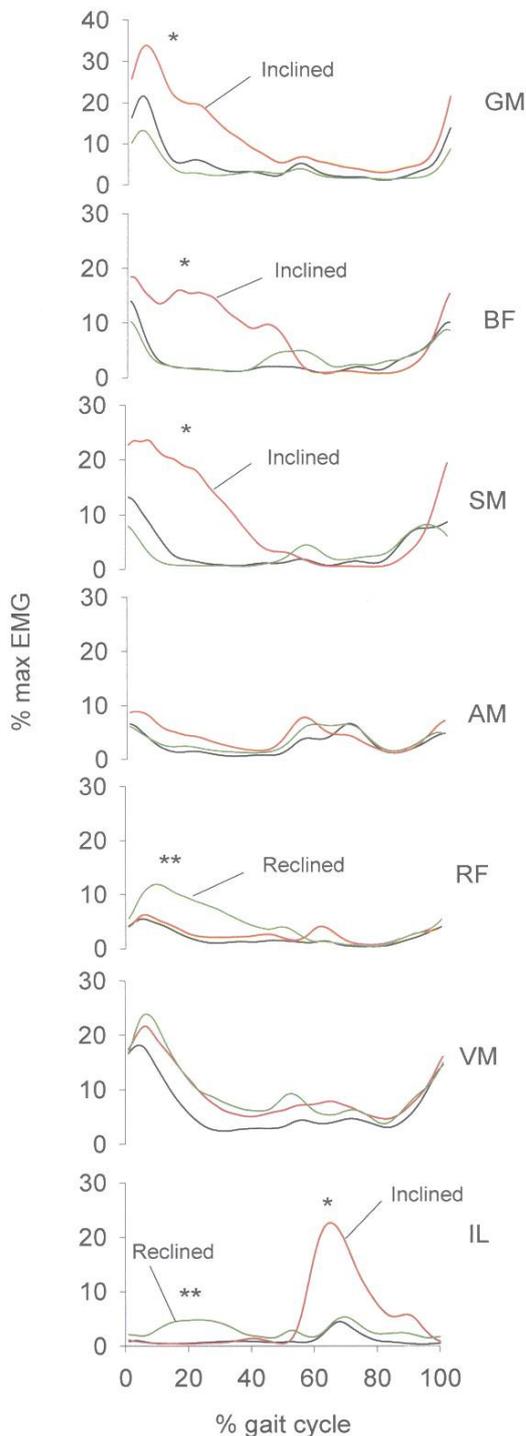


Figure 41
 EMG from walking with the upperbody reclined, normal and inclined. From top: gluteus maximus (GM), biceps femoris (BF), semimembranosus (SM), adductor magnus (AM), rectus femoris (RF), vastus medialis (VM) and iliacus (IL).

brought forward by muscle force. Judging from the EMG activity of the rectus femoris muscle in the beginning of the stance phase, this muscle may contribute to balance the upper body in the reclined condition while the opposite phenomenon was seen for the gluteus maximus and the hamstring muscles in the inclined condition (Fig. 41). Apart from this the upper body may be balanced by accelerations of the pelvis but not by the hip joint flexor moment during takeoff as earlier suggested.

During running the leg swings forward at much higher angular velocity in the hip joint. Therefore, in addition to elastic energy from the ligaments, it seems necessary to add muscle force from the iliacus muscle, which can be seen in the studies of Andersson et al. [50] and Cappellini et al. [51]. Regarding the psoas major muscle it normally appears to be active at the same time as the iliacus [52].

THE SIGNIFICANCE OF AFFERENT INPUT DURING WALKING AND RUNNING

The stretch reflex is normally associated with a brief and powerful muscle contraction as a response to a sudden stretch of the muscle. This can also be detected in the EMG as a short lasting peak due to synchronous firing of a large number of motor units [53]. However, during walking the soleus muscle is stretched during most of the stance phase and at a rather slow rate and with no EMG peaks indicating that a stretch reflex is elicited.

The soleus H-reflex reflects the central (spinal) part of the stretch reflex and it is seen to be facilitated and gradually increasing during the stance phase of walking (P1, P2, P3, P9, P10) (Fig. 42). It is therefore likely that the afferent input contributes to the motor output together with descending activity from the brain as the soleus is being gradually elongated during the stance phase. The latency of a stretch reflex is about 40 ms electrically and about 90 ms mechanically. Because the stance phase of human walking lasts about 600 ms, a short lasting powerful reflex contraction could disturb the motor pattern severely. During running the stance phase is about 300 ms (P1) and a fast stretch of the soleus muscle is initiated approximately 50 ms after heel strike (Fig. 42). If this stretch would elicit a powerful reflex contraction of the soleus muscle it could theoretically assist the muscle during the plantar flexion at takeoff (P1). Moreover, distinct EMG peaks were observed in the soleus muscle occurring app. 50 ms after a stretch of the muscle was initiated as indicated by a goniometer placed at the ankle joint (P1). Similar peaks were never observed in the gastrocnemius muscle corroborating the results of Voigt et al. (1998) from human hopping.

At toeoff the soleus H-reflex is always suppressed both during walking and running (P1,P2,P3,P9,P10). This is obviously because a stretch reflex elicited by the fast dorsiflexion of the ankle joint just after toeoff would disturb the movement pattern severely. During running the soleus H-reflex was strongly facilitated about 200 ms prior to heel strike. This was seen consistently in all subjects of the present thesis (P1, P9, P10). Moreover, the H-reflex excitability increased without concomitant EMG activity in the soleus and with relatively high EMG activity in the anterior tibial muscle (P1, P9) (Fig. 42). This type of reflex modulation was not seen in the studies of Capaday and Stein [54] and Edamura et al. [55]. Furthermore, the two latter studies reported the amplitude of the soleus H-reflex to be lower during running than during walking. In study P1 of the present thesis contradictory results were found. The peak soleus H-reflex amplitude was unchanged from walking at 4.5 km/h to running at 8 km/h, but

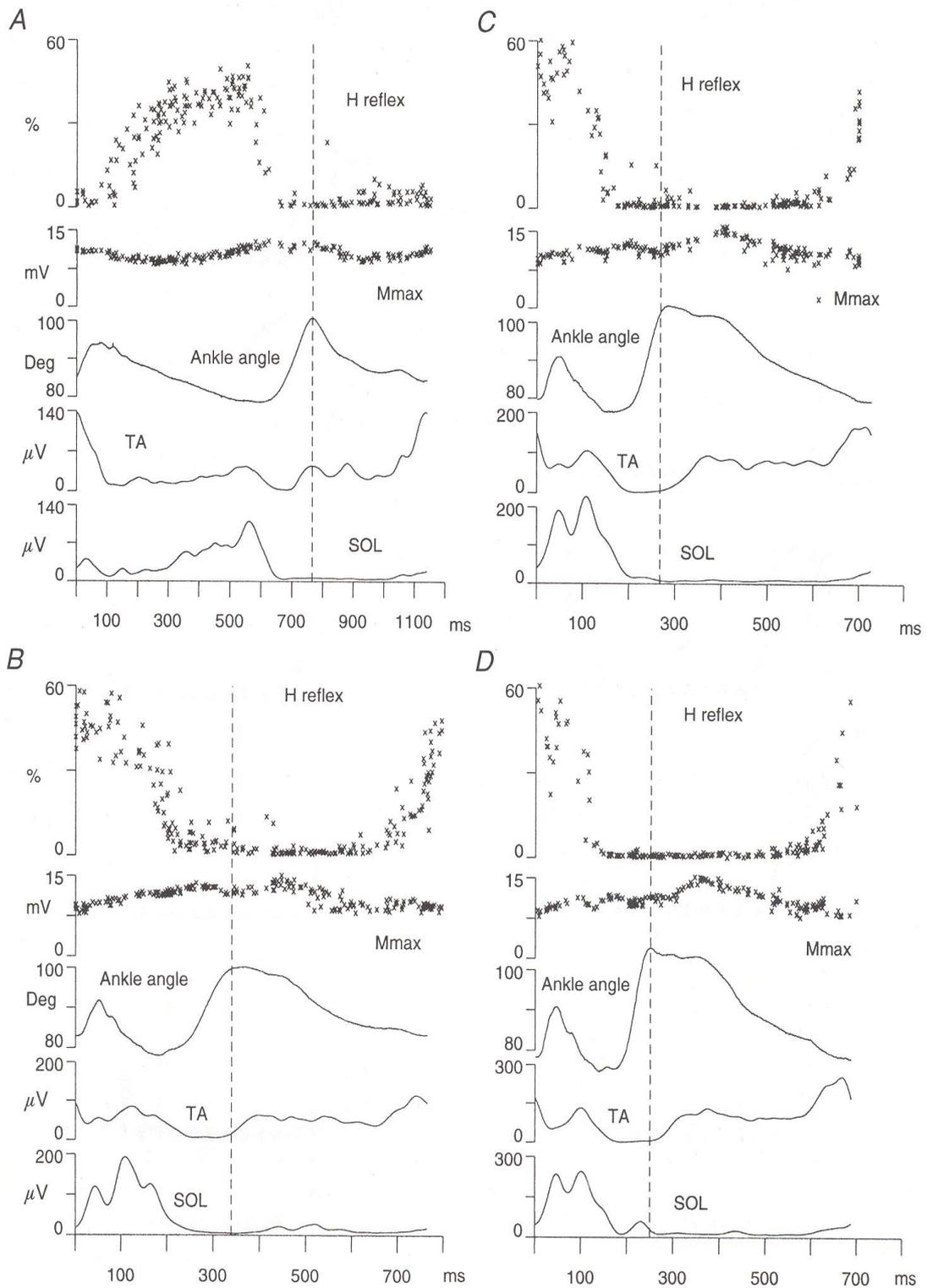


Figure 42

A typical subject during walking (A), running at 8 km/h (B), 12 km/h (C) and 15 km/h (D). On top of each graph is the soleus H-reflex, each dot represents one stimulus in one gait cycle. The variations in the maximal M-wave. The ankle joint angle. The tibialis anterior EMG and at the bottom the soleus EMG.

increased slightly but significantly during running at 12 and 15 km/h. It was tried to normalize and average the data in different ways, but with no conclusive result (P1) and in P10 it was tested whether too high stimulus intensity could have caused the diverging results. It was surprisingly found that the amplitude of the soleus H-reflex during running was more or less insensible to stimulus intensities eliciting M-waves up to 45 %Mmax (P10).

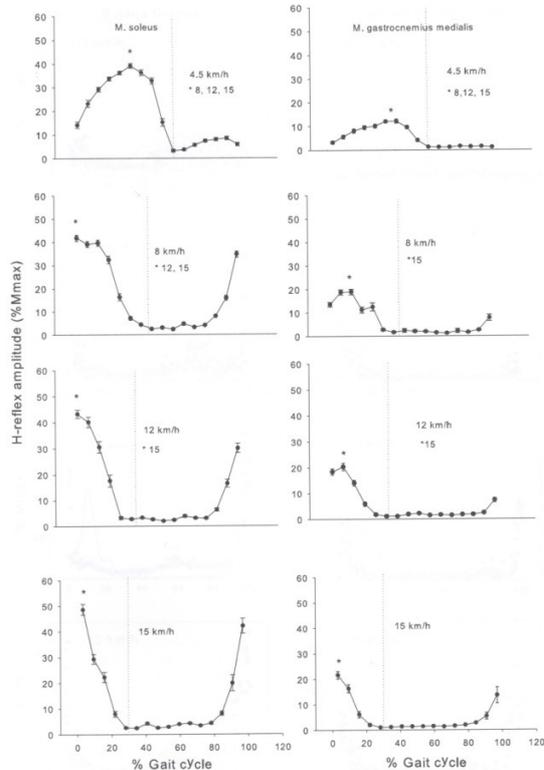


Figure 43
The soleus and the gastrocnemius H-reflex modulation during walking at 4.5 km/h and running at 8, 12 and 15 km/h. The gastrocnemius H-reflex was always lower than the soleus H-reflex but the peak of both reflexes increased significantly from walking to running and further with increasing running speed.

THE GASTROCNEMIUS H-REFLEX

As the gastrocnemius muscle is known to be a much faster muscle than the soleus, it was hypothesized in study P9 that the gastrocnemius H-reflex would increase even more than the soleus from walking to running and with increasing running speed. Data on one subject seemed to indicate such mechanisms [56,57]. Moreover, Duysens et al. [58] have shown that the soleus and the gastrocnemius were activated selectively regarding cutaneous reflexes during walking and running.

Regarding physiological cross sectional area, the medial gastrocnemius is twice as large as the lateral gastrocnemius, but the soleus is about three times larger than the lumped gastrocnemii [59]. The proportion of type I (slow twitch) muscle fibers has been reported to be 75%, 59% and 52% in the soleus, the medial gastroc and the lateral gastroc, respectively. This also implies that the soleus is innervated by a majority of small motoneurons with axons of low diameter [60].

The gastrocnemius H-reflex was in all walking and running conditions lower than the soleus H-reflex (P9) (Fig. 43). This may seem surprising, but as the soleus H-reflex was almost as high as it can be, it is evident that the gastrocnemius could not be facilitated to

a level even higher. This is due to the different fiber type distribution in the two muscles. In the soleus muscle the axons of the α -motoneurons have a much smaller diameter than those of the Ia afferents [61] and accordingly a maximal H-reflex can most often be measured by selectively stimulating Ia afferents without stimulating any α -motoneurons. This is in contrast to the gastrocnemius in which the average axon from α -motoneurons is thicker due to the larger proportion of fast twitch muscle fibers and larger motor units. Accordingly, a larger number of efferent and afferent axons will overlap in diameter, and the efferents participating in formation of the M-wave cannot contribute to the H-reflex due to a collision phenomenon between antidromic and orthodromic action potentials. For these reasons it is obvious that the absolute maximal H-reflex in gastrocnemius will have to be lower than that of the soleus and that the peak soleus H-reflex is very close to the absolute maximum during walking and running (P1,P9). Likewise Voigt et al. [62] found that the gastrocnemius H-reflex was lower than the soleus H-reflex during hopping. With this in mind it is difficult to understand the results of Moritani et al. [56,57], who reported a much higher H-reflex in gastrocnemius than in soleus during both hopping and running. In addition to using only one subject, these two studies must have been subject to methodological problems such as controlling the stimulus intensity during movement. In P9 the H-reflex increased from walking to running in both the soleus and the gastrocnemius and further with increased running speed. It was hypothesized that the contribution from the slow twitch soleus muscle would decrease at increased running speed (P9), but this never happened. One explanation could be that the physiological cross sectional area of the soleus is much larger than that of the gastrocnemius and that running cannot be performed without the soleus muscle. Furthermore, time to peak tension in slow twitch muscle fibers can be decreased significantly by the use of doublets, which includes the firing of two or three action potentials with a very short interval at the beginning of a contraction [63,64,65]. The very high V-waves observed in the soleus muscle during running (P9) could indicate the use of a very high firing frequency when the soleus is activated just prior to touchdown.

CONCLUSIONS

1. Normal human walking is performed by different dynamic strategies.
2. The size of the joint moments in the legs can be distributed in different ways as well as redistributed due to e.g. disabilities, footwear or pain.
3. The dynamics of the knee joint display the largest variations among individuals causing differences in bone-on-bone forces.
4. During walking the trailing leg is brought forward without the use of muscle force. During hip extension, elastic energy is stored in the strong ligaments about the hip joint and the succeeding release of this energy is used to flex the hip joint.
5. During walking, the upper body is balanced by acceleration and deceleration of the pelvis together with contractions of abdominal and back muscles.
6. The soleus H-reflex is strongly modulated during walking and running.
7. The pattern of modulation of the soleus H-reflex differs among individuals and is highly reproducible from day to day in the same subject.

8. The maximal soleus H-reflex is higher than that of the gastrocnemius. This is due to the difference in muscle fiber type composition.
9. About 50% of all people appear to walk with a suppressed soleus H-reflex during the swing phase while the other 50% show a gradually increasing H-reflex during the swing phase. This is accompanied by biomechanical differences and differences in antagonist EMG activity.
10. During running all subjects showed a pronounced increase in soleus H-reflex excitability before heel strike and before EMG onset. The same was only seen to a weak extent in the gastrocnemius.
11. Both the soleus and the gastrocnemius H-reflex increase from walking to running and with increased running speed.

SUMMARY

This thesis is based on ten published articles. The experimental work was carried out at the Faculty of Health Sciences, University of Copenhagen.

The aim was to investigate and describe a number of basic mechanical and physiological mechanisms behind human walking. The methodologies used were biomechanical movement analysis and electrophysiology. The walking experiments were carried out in a gait lab, where the subjects were video recorded while they walked across two force platforms, which measured the ground reaction forces. Net joint moments about the hip-, knee- and ankle joint were calculated by combining the movement data and the external reaction forces (inverse dynamics). Muscle activity and sensory input to the spinal cord were measured by electromyography (EMG) and electrical stimulation of peripheral nerves. The results showed that the gait pattern varies to a great degree between individuals. Some people choose to exert the highest forces about the ankle joint while others prefer to use the knee joint. By use of a cluster analysis, fifteen healthy subjects could be divided into two groups. The extensor moment about the knee joint was the main factor for separating the two gait patterns, but the group with the highest extensor moments about the knee joint also walked with more flexed knee joints, higher EMG activity in the quadriceps muscle and higher bone-on-bone forces. This may lead to development of osteoarthritis over the years. Walking on high-heeled shoes reduced the ankle joint moment significantly either because of reduced muscle fiber length and/or increased co-contraction about the joint. On the contrary, the extensor moment about the knee joint was almost doubled in the high-heeled condition compared to bare footed walking at the same velocity. Also the EMG activity increased in the leg muscles. This could be an explanation pertaining to the higher incidence of osteoarthritis in women than in men.

Patients with a drop-foot cannot put the foot to the ground with the heel first. Moreover, they have to increase flexion of the hip joint during the swing phase because the foot hangs in a plantar flexed position. It was shown that the ankle joint plantar flexor moment increased in the healthy leg and that the knee joint extensor moment increased significantly in both the affected and the healthy leg. The latter is most likely due to the patients trying to avoid an asymmetrical gait pattern. It is recommended to use an orthosis with drop-foot patients in order to keep the ankle joint dorsiflexed prior to touchdown, otherwise bone-on-bone

forces in both knee joints will increase and probably lead to osteoarthritis.

The hip joint moment varies less between individuals. However, both during walking and running an unexplained hip joint flexor moment is present during the last half of the stance phase. The moment appears to oppose the speed of progression and it has been suggested that it serves to balance the upper body. This was investigated in a group of healthy subjects who were asked to walk with their upper body in a reclined, inclined and normal position, respectively. It was shown that the hip joint flexor moment was similar in the reclined and the normal position but lower when walking in the inclined position and it can be concluded that the upper body is not balanced by hip joint flexor muscles but rather by accelerations of the pelvis and activity in abdominal and back muscles. These experiments also showed that the trailing leg is brought forward during the swing phase without activity in the flexor muscles about the hip joint. This was verified by the absence of EMG activity in the iliacus muscle measured by intramuscular wire electrodes. Instead the strong ligaments restricting hip joint extension are stretched during the first half of the swing phase thereby storing elastic energy, which is released during the last half of the stance phase and accelerating the leg into the swing phase. This is considered an important energy conserving feature of human walking.

The gating of sensory input to the spinal cord during walking and running was investigated by use of the Hoffmann (H) reflex in m. soleus and m. gastrocnemius medialis. This reflex expresses the central component of the stretch reflex, i.e. the transmission from Ia afferents to α -motoneurons in the spinal cord. The soleus H-reflex was shown to be strongly modulated during the gait cycle. In general, it was facilitated in the stance phase and suppressed in the swing phase. However, as it was the case with the biomechanical parameters, inter-individual H-reflex modulations were found and they were highly reproducible between days. One group of subjects had an almost completely suppressed H-reflex during the entire swing phase, while another group showed a gradually increasing reflex excitability during the swing phase. This group also walked with a lower extensor moment about the knee joint and higher plantar flexor moment about the ankle joint and it is speculated that this gait pattern highly relies on reflexes to deal with unexpected perturbations. The subjects with the suppressed reflex during the swing phase also showed a higher EMG activity in the anterior tibial muscle, so it is likely that the suppression of the H-reflex was at least partly due to reciprocal antagonist inhibition.

All subjects showed complete suppression of the H-reflex at toeoff. This seems necessary to avoid a stretch reflex being elicited in the soleus muscle as the ankle joint undergoes a fast dorsiflexion just after toeoff. The reflex modulation is clearly an integrated part of the human gait pattern and is absolutely necessary for normal gait function with smooth movements. Furthermore, it is anticipated that the afferent input from the muscle spindles is used to drive the motor output from the α -motoneurons together with descending activity from the motor cortex. During running the H-reflex increased in both the soleus and the gastrocnemius already before heel strike and before the onset of EMG activity in the same two muscles and with a relatively high activity in the anterior tibial muscle, but this was most pronounced in the soleus. The H-reflex was always higher in the soleus also when expressed as percentage of the maximal M-wave. This is due to the difference in muscle fiber type distribution between the two muscles. The H-reflex increased from walking to running in both muscles and further with increasing run-

ning speed. Unexpectedly, there were no signs of the faster gastrocnemius becoming more important at higher running speed. During walking it is not possible to observe a stretch reflex in the form of a synchronized activation of a large number of muscle fibers as this would disturb the movement pattern. It is rather likely that the input from Ia afferents directly contributes to activate the α -motoneurons. However, during running the stance phase is much shorter, which enables the possibility of a stretch reflex to contribute to a strong contraction during push off. EMG peaks in the soleus with an appropriate latency were observed in the soleus during running. This was not the case with the gastrocnemius and the explanation is most likely that the gastrocnemius is biarticular and not stretched to any great extent during running.

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