In-vivo function of human plantar intrinsic foot muscles

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B.HlthSci (Pod)

A thesis submitted for the degree of Doctor of Philosophy at

The University of Queensland in 2014

School of Human Movement Studies

Abstract

This thesis investigates the in-vivo function of the plantar intrinsic foot muscles. Though much speculation has been made of the function of these muscles, scant detail exists pertaining to their function. This thesis provides a novel description of the function of these muscles in providing active support for the longitudinal arch (LA) during postural tasks and locomotion. Furthermore, the following chapters provide evidence of an active mechanism to stiffen the LA, primarily provided by the graded activation of these muscles in response to increasing load. This mechanism may have important implications for how energy is stored and released within the foot. Chapter one provides a general overview of the existing literature pertaining to the function of these muscles. Chapters two, three, four and five contain the individual manuscripts from each experiment performed as part of this thesis. Chapter six provides a summary of the findings from the thesis and some general suggestions for the direction of future research in this field.

Chapter two investigates the role of the plantar intrinsic foot muscles in providing postural support for the foot during quiet standing. Intra-muscular electromyographic (EMG) activity was recorded from abductor hallucis (AH), flexor digitorum brevis (FDB) and quadratus plantae (QP) while participants performed two balance tasks of graded difficulty. Each task was performed while standing on a force plate, allowing appraisal of any relationship between loading, postural sway and intrinsic foot muscle activity. Intrinsic foot muscle activation increased in response to postural demand, with these muscles displaying highly correlated inter-muscular activation patterns in response to medial postural sway. Contrary to previous thoughts, these muscles are clearly important in postural control and are recruited in a highly co-ordinated manner to stabilise the foot and maintain balance, particularly during single leg stance, in the medio-lateral direction.

The purpose of Chapter three was to investigate if the neurophysiological properties of the largest intrinsic foot muscle (abductor halluces) are matched to its suggested postural function. A highly selective, quadrifilar arrangement of fine wire EMG electrodes was employed to describe the discharge properties of AH motor units during ramp and hold isometric contractions, as well as during a submaximal, constant force, fatiguing contraction. Abductor hallucis motor units displayed small rate coding ranges, relatively low peak discharge rates and were largely resistant to fatigue. This muscle is comparatively fatigue resistant and appears to rely predominantly on recruitment to generate force, optimizing the use of slow twitch, fatigue resistant fibres to generate moderate to large amounts of force for sustained periods of time. These properties appear well matched to AH's postural function that involves providing stabilisation of the LA during weight-bearing tasks.

Chapter four examined the potential for the intrinsic foot muscles to actively control LA compression and recoil that occurs due to the application and release of external load. This study tested the hypotheses that activation of AH, FDB and QP is associated with muscle stretch that occurs in response to LA compression produced by external loading on the foot, and that activation of these muscles (via electrical stimulation) will generate sufficient force to counter LA compression. Muscle tendon units (MTU) of AH, FDB and QP stretched in response to LA compression occurring due to external load. Recruitment of these muscles increased with increasing load beyond specific force thresholds. LA deformation and muscle stretch plateaued towards the maximum load of 150% body weight, when muscle activity was greatest. Electrical stimulation of the plantar intrinsic muscles countered the deformation that occurred due to the application of external load by reducing the length and increasing the height of the LA. These findings demonstrate that these muscles have the capacity to control LA deformation and may buttress the LA during foot loading.

Chapter five tested the hypothesis that AH, FDB and QP will actively lengthen and shorten during the stance phase of gait in response to variable loading of the foot that occurs during walking and running at different speeds. For both walking and running the LA compressed during the initial loading phase (early stance) and recoiled as the load subsided (late stance), with the magnitude of compression increasing with gait velocity and the associated increase in vertical ground reaction force. All muscles underwent a process of slow active lengthening during LA compression, followed by a rapid shortening as the arch recoiled during the propulsive phase. MTU length change and peak muscle activity increased with gait velocity for all muscles. This thesis provides in-vivo evidence that the plantar intrinsic foot muscles actively lengthen and shorten during the stance phase of gait and are therefore capable of contributing to power dissipation and generation during gait. We suggest that the intrinsic foot muscles actively contribute to the foot spring mechanism and are regulated in response to the magnitude of load encountered.

In summary, this thesis has provided a detailed description of the function of the three largest plantar intrinsic foot muscles, AH, FDB and QP during postural and dynamic tasks. These muscles are activated in a highly co-ordinated manner in order to adjust the stiffness of the longitudinal arch in response to the loading demands encountered during postural activity and locomotion.
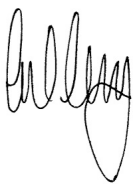
Declaration by author

This thesis is composed of my original work, and contains no material previously published or written by another person except where due reference has been made in the text. I have clearly stated the contribution by others to jointly-authored works that I have included in my thesis.

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Luke Anthony Kelly

Publications during candidature

Journal Publications

1. Kelly LA, Kuitunen S, Racinais S & Cresswell AG (2012). Recruitment of the plantar intrinsic foot muscles with increasing postural demand. *Clin Biomech* **27**, 46–51.

2. Kelly LA, Racinais S & Cresswell AG (2013). Discharge properties of abductor hallucis before, during, and after an isometric fatigue task. *Journal of Neurophysiology* **110,** 891–898.

3. Kelly LA, Cresswell AG, Whiteley R, Racinais S & Lichtwark GA (2014). The plantar intrinsic foot muscles have the capacity to counter deformation of the longitudinal arch. *J.R. Soc Interface*. **29**;11(93):20131188

4. Kelly LA, Cresswell AG & Lichtwark GA (2014). Active regulation of longitudinal arch compression and recoil during walking and running (2015). *J.R. Soc Interface*. 6;12(102):20141076

Conference Abstracts

1. Kelly LA, Kuitunen S, Racinais S & Cresswell AG. Recruitment of the plantar intrinsic foot muscles with increasing postural demand. Podium presentation − *International Society of Biomechanics Congress*, Brussels, Belgium. July 2011.

2. Kelly LA, Lichtwark GA & Cresswell AG. Dynamic function of the plantar intrinsic foot muscles. *Australasian Conference of Science and Medicine in Sport*. Phuket, Thailand October 2013.

3. Kelly LA, Lichtwark GA & Cresswell AG. Neuromechanical function of the plantar intrinsic foot muscles. *World Congress of Biomechanics 2014*. Boston, USA. July 2014.

Publications included in this thesis

The following manuscripts are included as chapters within this thesis and details of the contribution from my co-authors is provided below for each manuscript.

1. Kelly LA, Kuitunen S, Racinais S & Cresswell AG (2012). Recruitment of the plantar intrinsic foot muscles with increasing postural demand. *Clin Biomech* **27**, 46–51.

This manuscript is incorporated as Chapter two in the thesis.

Contributor	Statement of contribution
Luke Kelly (Candidate)	Designed experiments (80%) Collected and analysed data (80%) Drafted and revised the manuscript (80%)
Dr. Sami Kuitunen	Collected and analysed data (10%) Drafted and revised the manuscript (5%)
Dr. Sebastien Racinais	Designed Experiments (10%) Drafted and revised the manuscript (5%)
Professor Andrew Cresswell	Designed Experiments (10%) Collected and analysed data (10%) Drafted and revised the manuscript (10%)

2. Kelly LA, Racinais S & Cresswell AG (2013). Discharge properties of abductor hallucis before, during, and after an isometric fatigue task. *Journal of Neurophysiology* **110,** 891–898.

This manuscript is incorporated as Chapter three in this thesis

Contributor	Statement of contribution
Luke Kelly (Candidate)	Designed experiments (80%) Collected and analysed data (80%) Drafted and revised the manuscript (80%)
Dr. Sebastien Racinais	Drafted and revised the manuscript (5%)
Professor Andrew Cresswell	Designed Experiments (20%) Collected and analysed data (20%) Drafted and revised the manuscript (15%)

3. Kelly LA, Cresswell AG, Whiteley R, Racinais S & Lichtwark GA (2014). The plantar intrinsic foot muscles have the capacity to counter deformation of the longitudinal arch. *J.R. Soc Interface.* **29**;11(93):20131188

This manuscript is incorporated as Chapter four in this thesis

Contributor	Statement of contribution
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Professor Andrew Cresswell	Designed experiments (15%) Drafted and revised the manuscript (10%)
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Dr. Rodney Whiteley	Collected and analysed data (5%) Drafted and revised the manuscript (5%)
Dr. Glen Lichtwark	Designed Experiments (15%) Collected and analysed data (10%) Drafted and revised the manuscript (10%)

4. Kelly LA, Cresswell AG & Lichtwark GA (2014). Active regulation of longitudinal arch compression and recoil during walking and running (2015). *J.R. Soc Interface.* 6;12(102):20141076

This manuscript is included as Chapter five in this thesis.

Contributor	Statement of contribution
Luke Kelly (Candidate)	Designed experiments (70%) Collected and analysed data (100%) Drafted and revised the manuscript (80%)
Dr. Glen Lichtwark	Designed Experiments (15%) Drafted and revised the manuscript (10%)
Professor Andrew Cresswell	Designed Experiments (15%) Drafted and revised the manuscript (10%)

Contributions by others to the thesis

I would like to acknowledge the contributions of my supervisors Prof. Andrew Cresswell and Dr Glen Lichtwark to this thesis, who contributed to experimental design, as well as final editing of the document. I would also like to acknowledge my co-workers Dr Sebastien Racinais, Dr Sami Kuitunen and Dr Rodney Whiteley for the contribution to data collection and analysis of the individual experiments within this thesis. I hereby state that in jointly published work in which I was first author, the entire written manuscript (or associated thesis chapter) was my own work. The contribution of my colleagues- through data collection, data analysis, discussion of results and feedback on the manuscript itself- has been acknowledged through use of collective pronouns in the appropriate chapters, and co-authorship of the associated peer- reviewed manuscripts.

Statement of parts of the thesis submitted to qualify for the award of another degree

None

Acknowledgements

The process of undertaking this thesis has been an incredible learning experience, enabled by many people who have been willing share their knowledge, experience and skills. I would like to take this opportunity to thank a small, but very important number of people who, without their support, guidance and patience, this thesis would never have been undertaken, let alone achieved.

Firstly I would like to thank my principal advisor, Professor Andrew Cresswell. Thank you for being willing to take on the risk of a student who was based on the other side of the world and all the associated hassles that would come with that. Thank you for providing me with a very steep learning curve, encouraging me to push my knowledge boundaries, broaden my scientific horizons and for always having such great patience.

I would also like to thank Dr Glen Lichtwark for his contributions to this thesis and all the help and advice provided throughout my candidature. You have opened my eyes to the scope of biomechanics research and this has been incredibly inspiring.

To Dr Sebastien Racinais, I would like to say thank you for providing me with my first opportunities in research and for being such a great mentor over the past 6 years. Without your

patience and willingness to share your expertise, I would never have been in a position to undertake this thesis.

Finally, I would like to thank my amazing wife Candice and our beautiful children Ava, Flynn, Elliott and Charlysse. Thank you for you patience, support and for your willingness to sacrifice so much in order to allow me to undertake this experience. You inspire everything I do and words cannot express how grateful I am to have such an amazing family to come home to at the end of every day.

Keywords

foot muscles, longitudinal arch, electromyography, multi-segment foot model,

Australian and New Zealand Standard Research Classifications (ANZSRC)

ANZSRC code: 110601, Biomechanics, 60%

ANZSRC code: 110603, Motor Control, 40%

Fields of Research (FoR) Classification

FoR code: 1106, Human Movement and Sport Sciences, 100%

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List of Abbreviations

3D – Three-dimensional

AH – Abductor hallucis

ANOVA – Analysis of variance

AP – Antero-posterior

CNS – Central nervous system

COM – Centre of mass

COP – Centre of pressure

COP_{AP} - Centre of pressure antero-posterior

COP_{ML} - Centre of pressure medio-lateral

CV – Co-efficient of variation

DLS – Double leg stance

DR – Discharge rate

EMG – Electromyography

EMG_{IM} – Intramuscular electromyography

ES – Effect size

F-AB – Flexion – abduction

FC – Foot contact

FDB – Flexor digitorum brevis

Fz – Vertical ground reaction force

GRF – Ground reaction force

ISI – Inter-spike interval

LA – Longitudinal arch

ML – Medio-lateral

MTP – Metatarso-phalangeal

MTU – Muscle tendon unit

MVC – Maximal voluntary contraction

PCSA – Physiological cross sectional area

QP – Quadratus plantae

REL – Relaxed

RMS – Root mean square

SEM – Standard error of mean

SLS – Single leg stance

SMU – Single motor unit

TO – Toe off

CHAPTER ONE - INTRODUCTION

1.1 Background

The evolution to habitual bipedalism un-constrained our hands and allowed the development of skills such as throwing and carrying that were hallmarks of the hunter-gatherer lifestyle (Bramble & Lieberman, 2004; Rolian *et al.*, 2009; 2010). In order to enable habitual bipedalism, the anatomical structure of the human foot has undergone a number of key adaptations. These structural alterations have increased the structural integrity of the foot, allowing it to cope with the increased loading demands that are associated with terrestrial bipedalism, while also facilitating forward propulsion at reduced metabolic cost (Li *et al.*, 1996; Bramble & Lieberman, 2004; Wang & Crompton, 2004; Rolian *et al.*, 2009; 2010; Crompton *et al.*, 2012). Adaptations such as an adducted hallux, enlarged and re-aligned tarsal bones and shortened lateral digits reflect the transformation in functional requirement of the human foot from a grasping and balancing structure designed for arboreal life on compliant branches to that of a primary load bearing structure that is responsible for maintenance of upright balance, impact attenuation and forward propulsion on the stiff and uneven surfaces that are encountered in terrestrial environments (Bramble & Lieberman, 2004; Thorpe *et al.*, 2007; Rolian *et al.*, 2009; Crompton *et al.*, 2010).

Specifically, the adducted hallux and shortened lateral digits represent a change in the line of progression of the foot that occurred with the adoption of a bipedal gait, with the line of leverage of the foot shifting to between the first and second metatarsal, enabling forward progression (Morton, 1924). The enlarged calcaneus that is evident in the human foot is reflective of the relative increase in loading demand that was encountered with the advent of habitual bipedalism (Bramble & Lieberman, 2004; Morton *et al.*, 1930). The human foot also displays a re-arrangement of the tarsal bones with the calcaneo-cuboid and talo-navicular joints having substantially less range of motion, which has subsequently increased the structural stiffness of the hind-foot (Crompton *et al.*, 2012; Bates *et al.*, 2013).

Arguably the most important structural adaptation of the human foot was the development of a pronounced longitudinal arch (LA) (Morton, 1924; Ker *et al.*, 1987; Crompton *et al.*, 2010; Lieberman, 2012; McKeon *et al.*, 2014). This structure functions as a mechanical truss which is supported by a strong, well developed plantar aponeurosis and plantar ligaments that provide resistive tension at its proximal and distal ends when it is encumbered with load (Hicks, 1954; 1955). This osseous arrangement optimises structural integrity under substantial load with minimal muscular contribution (Hicks, 1954; Basmajian & Stecko, 1963), allowing humans to stand for prolonged periods of time at very low metabolic cost (Wang & Crompton, 2004).

While the LA is considerably stiffer than our arboreal ancestors, it does retain some capacity for compliance (Wang & Crompton, 2004; Vereecke & Aerts, 2008; Crompton *et al.*, 2010) allowing it to compress and recoil in response variations in terrain and load. This compression-recoil process allows impact forces to be attenuated and stored as elastic strain in the stretched plantar soft tissues, with some of this being returned via elastic recoil prior to propulsion (Ker et al., 1987) providing forward and upward acceleration. This function, known as the "foot spring" mechanism is thought to contribute substantial metabolic energy savings (Ker et al., 1987). Another crucial function of the plantar aponeurosis and the LA during locomotion is the windlass mechanism that produces transient increases in LA stiffness to assist forward propulsion. During late stance as the toes extend, the plantar aponeurosis is wound around the metatarsal heads, increasing the tension in this structure, resulting in extension of the calcaneus and flexion of the metatarsals (Hicks, 1954; Caravaggi et al., 2009). The resulting series of rotations about a number of small joints serves to elevate the LA and increase its stiffness, allowing ankle plantar flexion forces to be transferred rapidly to the ground (Erdemir et al., 2004) propelling the body forward. This process is unique to humans and is thought to be metabolically advantageous as it reduces the muscular contributions required to propel the body forward during locomotion (Alexander, 1991).

While the LA is considered a key evolutionary adaptation enabling efficient bipedal locomotion, it is also a structure that is repeatedly encumbered with substantial loads for extended periods of time during daily activities such as standing, walking and running. As a result of this high loading demand, it is commonly the source of physiological ailment (Morton, 1930). Impaired function of the LA, either due to excessive compliance or stiffness may hinder the capacity of the leg to absorb and generate mechanical power during dynamic activity and has been implicated as a contributing factor in the development of musculoskeletal injury (Morton, 1930; Bojsen-Møller, 1979; Thordarson *et al.*, 1995; Mootanah *et al.*, 2012). For many years, army recruits displaying increased LA compression during stance, otherwise known as "flat feet" were banned from active military service due to the perception that this foot structure places excessive burden on the lower limb in order to maintain function, with these people being more likely to succumb to the rigorous demands of active service (Morton, 1930). Indeed the relative importance of a pronounced LA for human locomotion can be appreciated when we consider the plethora of clinical conditions that have been linked to dysfunction of this structure, including plantar fasciitis (Wearing et al., 2006), tibialis posterior dysfunction (Semple et al., 2009), hallux valgus (Fuller, 2000), osteoarthritis (Rao et al., 2009) Achilles tendonopathy (Chuter & de Jonge, 2012), knee pain syndromes (Barton et al., 2010) and tibial stress injuries (Bandholm et al., 2008). While direct causal relationships between

dysfunction of the LA and injury to the lower limb have been scarce (Chuter & de Jonge, 2012) it is apparent that rehabilitation techniques aimed at improving LA function, such as foot orthoses are known to be successful in the treatment of a number of the previously mentioned conditions (Collins et al., 2009; Barton et al., 2010). Furthermore, complex surgical techniques aimed at restoring function of the LA are commonly employed as treatment for diseases that lead to excessive LA compliance, such as plantar aponeurosis rupture and tibialis posterior tendon dysfunction (Watanabe et al., 2012).

Running is a common recreational past time with known health benefits. However, running also has an extremely high incidence of injury, with between 30-70% of participants reporting an injury in each calendar year (Kaufman et al., 1999; Taunton et al., 2002; Daoud et al., 2012; Lieberman, 2012). Interestingly, data from the Taunton study (Taunton et al., 2002) indicates that a large number of the reported injuries were to structures within or attaching into the LA (22%), while an even greater number of injuries (>50%) were to lower limb structures that may be affected by the function of the LA. As a result of the large number of recreational and competitive runners that become injured each year, a multi-billion dollar footwear industry has arisen aimed at developing, promoting and selling footwear designed to reduce the risk of lower limb injury to runners. Furthermore, substantial efforts have been made by researchers and clinicians in attempt to prevent and manage these injuries in the running population. Sport shoes have been designed with enhanced cushioning features, aimed at reducing the potentially harmful impact forces that are encountered during running (Yan et al., 2012). Structural features of running shoes have been designed to increase the stiffness of the LA, aiming to reduce excessive strain on the passive structures of the arch and the musculature of the legs and feet (Cheung & Ng, 2009; 2010). However despite the massive intellectual and financial investments into developing footwear, running injury rates remain relatively unchanged across the last 30 years (Lieberman, 2012). This mismatch between technology and outcomes has led many to question the long held belief that the foot and more specifically the LA, needs to be supported in order to prevent injury, resulting in the emergence of the barefoot running movement (Robbins, 2006; Jenkins & Cauthon, 2011; Lieberman, 2012).

The concept of barefoot running emerges from an evolutionary medical perspective that questions why modern humans need to wear highly supportive and cushioned footwear when we have actually evolved to run barefoot and have done so successfully for million of years (Lieberman, 2012). In fact proponents of the evolutionary medicine paradigm and the barefoot running movement suggest that modern footwear may actually hinder our ability to run (Jungers, 2010; Lieberman et al., 2010; Collier, 2011) by inhibiting sensory feedback and altering natural running

biomechanics (Robbins, 2006; Lieberman, 2012). Specifically, it is argued that running barefoot facilitates with enhanced sensory feedback and allows the body to cope more effectively with the large magnitudes of forces that are encountered repetitiously during running (Lieberman, 2012). For example, it has been suggested that when running barefoot, people tend to run with an increased cadence and shorter stride length, landing with greater knee flexion and ankle plantar flexion (Divert *et al.*, 2005; Robbins, 2006; Lieberman *et al.*, 2010; Braunstein *et al.*, 2010). This alteration in landing mechanics is thought to enhance running efficiency by improving leg and foot spring function, allowing for a softer landing with impact forces being absorbed (Perl *et al.*, 2012).

While debate continues regarding the potential benefits and pitfalls of barefoot running, or various running techniques in the prevention of injuries and enhancement of running performance (Jenkins & Cauthon, 2011; Lieberman, 2012; Hatala *et al.*, 2013), a common element of this argument has emerged that is of interest to coaches, clinicians and researches on both sides of the debate. This common theme relates to the relative importance of the spring-like qualities of the lower limb that assist absorption, transmission and generation of forces during running (Divert *et al.*, 2005; Lieberman *et al.*, 2010; Daoud *et al.*, 2012; Lieberman, 2012; Franz *et al.*, 2012). The human leg is known to act like a spring during running, compressing during the first half of stance in response to rising ground reaction force, and recoiling during late stance as ground reaction force subsides, providing forward and upward acceleration of the centre of mass (Cavagna & Kaneko, 1977). This spring like behaviour is believed to enhance the efficiency of locomotion by increasing utilisation of elastic energy storage in tendinous tissue and reducing the net mechanical work performed by the contractile element of muscles (Cavagna & Kaneko, 1977; Zelik & Kuo, 2010).

An important aspect of the spring-like behaviour of the leg is the capacity of the central nervous system to change the effective stiffness of the leg in response to variations in sensory stimuli allowing it to adapt to locomotion through changing environments and with different demands (Kerdok *et al.*, 2002; Müller *et al.*, 2010). For instance, it has been shown that there is an increase in human leg stiffness with increased running velocity, driven primarily through changes in knee stiffness (Arampatzis *et al.*, 1999). Likewise the stiffness of the leg spring is known to change in response to variations in surface compliance (Kerdok *et al.*, 2002; Müller *et al.*, 2010). The spring-like function of human legs has principally focussed on the major three joints in the leg – the hip, the knee and ankle. These joints contribute to the majority of the power absorption and generation during most movements like walking or running (Zelik & Kuo, 2010). The role of muscles in utilisation of elastic energy storage and return from tendons during spring-like gaits has been well established (Alexander, 1984; Ishikawa, 2005; Lichtwark, 2005; Lichtwark & Wilson, 2006). For

example, at the ankle the gastrocnemius and soleus muscles are known to utilise the long Achilles tendon to store elastic strain energy during the first half of stance phase, which is subsequently returned via elastic tendon recoil prior to propulsion (Roberts & Azizi, 2011) with the contractile component of the muscle regulating the magnitude of energy stored within the Achilles tendon in response to the requirements of the task (Lichtwark & Wilson, 2006). This mechanism provides substantial metabolic energy savings (Ker *et al.*, 1987; Alexander, 1991). The foot is also known to contribute to the leg spring function via compression and recoil of the LA (Ker *et al.*, 1987; Simkin & Leichter, 1990; Vereecke & Aerts, 2008). However, in contrast to the active contribution to energy storage and release and return provided by the plantar flexors at the ankle, regulation of LA compression and recoil has traditionally been considered passive in nature. Ker and colleagues (Ker et al., 1987) have shown that the plantar aponeurosis and plantar ligaments stretch and recoil in response to LA deformation produced by external load and that this process may allow storage and return of up to 17% of the metabolic energy requirements of each foot contact, which is equivalent to approximately half of that stored within the Achilles tendon. Ker and colleagues performed their experiments on cadaveric specimens using a protocol that sequentially resected each of the passive structures of the LA and measured changes in LA deformation at specific load magnitudes following the resection of each structure. As expected, they reported that the plantar aponeurosis, long plantar ligament and spring ligament provide significant structural integrity for the LA, with LA deformation increasing substantially with the magnitude of load encountered. Furthermore they found that as each of these structures was resected, the magnitude of LA deformation increased substantially.

Recent in-vivo experiments exploring the dynamic function of the LA and plantar aponeurosis (Pataky *et al.*, 2008; Caravaggi *et al.*, 2009; 2010; Bates *et al.*, 2013) have provided divergent findings from the earlier work of Ker and colleagues (Ker et al., 1987). Caravaggi and colleagues reported that while the LA does deform under load during gait, the magnitude of LA deformation and peak plantar aponeurosis strain does not increase with gait velocity despite significant increases in ground reaction forces (Caravaggi et al., 2010). The speculated that this finding may indicate the presence of an active arch stiffening mechanism, possibly produced by the muscles located in the arch of the foot. This hypothesis is further supported by the findings of Bates et al (Bates et al., 2013)and Pataky et al (Pataky et al., 2008)who also reported that deformation of the arch appears to plateau at higher gait velocities, despite substantially larger deformation forces being born by this structure. The suggestion that the musculature of the LA may contribute to maintenance of LA function, acting in parallel to the passive ligamentous structures in order to provide "on demand" support for the LA in response to the forces or deformation experienced provides a potentially

important mechanism that may enhance efficiency and versatility of the leg during locomotion, providing further explanation for the capacity for the central nervous system to adapt the mechanical characteristics of the lower limb in response to varying environmental or task requirements. However at present we have little direct evidence for this mechanism, nor do we have a clear understanding of the function of the plantar intrinsic foot muscles that are located within the LA.

Given the emergence of a potential link between the plantar intrinsic foot muscles and dynamic function of the LA, as well as the apparent dearth of direct information pertaining to their function, it is of great interest to gain a deeper understanding of the neuromechanical function of these muscles. This knowledge may provide novel insights for human functional anatomy, while also providing valuable information that may be applicable in the fields of human athletic performance and musculoskeletal rehabilitation. Therefore the aim of this thesis is to investigate the in-vivo function of the human plantar intrinsic foot muscles.

1.2 Literature Overview

1.2.1 Anatomy of the longitudinal arch

Anatomy of the longitudinal arch

The LA is an elaborate structure that is unique to the human foot. It provides substantial stiffness to enable forward propulsion, whilst also maintaining sufficient compliance to enable adaptability to variations in environmental and loading demands (Donatelli, 1985; Erdemir *et al.*, 2004; Vereecke & Aerts, 2008; Crompton *et al.*, 2010). This diversity of function is achieved by a complex interaction of displacements between numerous small bones of the foot (Leardini *et al.*, 2007; Arndt *et al.*, 2012; Nester *et al.*, 2014). In order to simplify this complexity and allow descriptive clarity, larger functional joints have been described, with each functional joint including a number of articulations with similar movement patterns. These joints are outlined below;

Sub-talar joint

The sub-talar joint has been defined as the articulation between the superiorly located talus and the inferiorly located calcaneus (Sarrafian, 1993; Rockar, 1995; Stagni *et al.*, 2003). The sub-talar joint consists of three separate concavo-convex articulations, otherwise known as the posterior, middle and anterior articulations between the talus and calcaneus (Figure 1.1) (Sarrafian, 1993; Rockar, 1995). Traditionally the sub-talar joint has been considered a modified hinge joint with one axis passing obliquely from the posterior, lateral and plantar aspect of the calcaneus to the anterior,

medial and superior margin of the talus. Rotation about this obliquely oriented axis provides simultaneous tri-planar motion of flexion, eversion and abduction or extension, inversion and adduction (Hicks, 1953), commonly referred to as pronation and supination, respectively (Manter, 1941; Hicks, 1953; Perry, 1983; Rockar, 1995; Kirby, 2001; Stagni *et al.*, 2003; Arndt *et al.*, 2004; Sheehan *et al.*, 2007; Sheehan, 2010; Arndt *et al.*, 2012). While a small amount of flexion and extension occurs between the calcaneus and talus, the predominant motions are thought to be inversion / eversion and adduction / abduction (Arndt *et al.*, 2004; Sheehan, 2010).
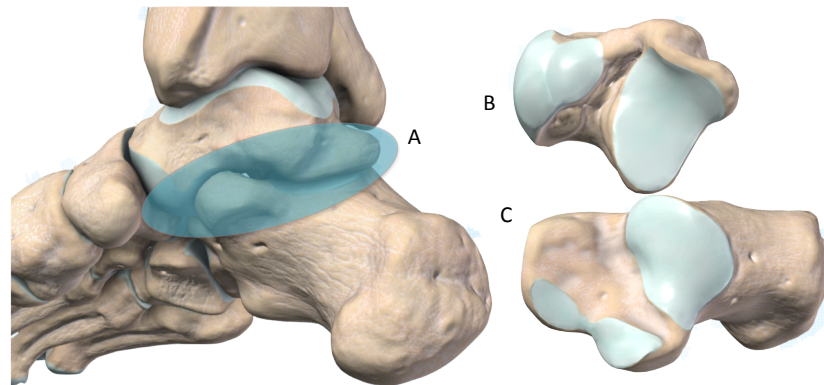
Figure 1.1. The sub-talar joint (green shaded area, A) is formed by the articulation between the talus (B) superiorly and the calcaneus (C) inferiorly. The joint is comprised of three facets known as the anterior, middle and posterior facets. Image adapted from Bone Box (2014) (Iso-Form LLC, 2014)

Transverse tarsal joint

The transverse tarsal joint consists of articulations between the calcaneus and talus with the cuboid and navicular. The two primary articulations is this functional joint are the calcaneo-cuboid and talo-navicular joints, these articulations are concavo-convex joints that move as a functional unit allowing rotation about all three planes (Manter, 1941; Huson, 2000; Arndt *et al.*, 2012; Nester *et al.*, 2014).

Tarso-metatarsal joint

This functional joint consists of a number of small joints made up of the articulations between the cuneiforms with the navicular and cuboid, as well as the articulations between the cuneiforms and the metatarsals and the cuboid and metatarsals (Figure 1.2) (Bojsen-Møller, 1979). These joints are all generally considered gliding type joints, that rotate as a functional unit to provide relatively equal amounts of motion about the three anatomical planes (Kido *et al.*, 2013; Nester *et al.*, 2014).
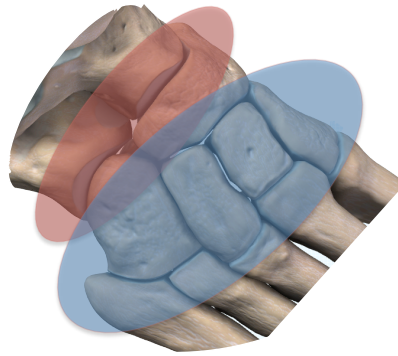
Figure 1.2. The transverse tarsal joint (red shaded area) is formed by the articulations between the calcaneus, cuboid, talus and navicular bones, with the two key joints being the calcaneo-cuboid joint which is located laterally, and the talo-navicular joint, which is located medially. The tarso-metatarsal joint (blue shaded area) is located anterior to the transverse tarsal joints and comprises many small articulations between the tarsals and metatarsals. Image adapted from BoneBox (Iso-Form LLC, 2014)

1.2.2 Biomechanics of the longitudinal arch

The LA is a key anatomical feature of the human foot (Hicks, 1955; Crompton *et al.*, 2010)allowing a structurally sound base of support that requires minimal muscular contributions during quiet stance and walking (Basmajian & Stecko, 1963; Mann & Inman, 1964), while also possessing a spring like function, whereby the LA compresses and recoils in response to cyclical loading and unloading of the foot during locomotion (Ker et al., 1987; Erdemir et al., 2004; Caravaggi et al., 2009) allowing storage and return of elastic energy (Ker et al., 1987; Alexander, 1991).

Early experiments by Hicks (Hicks, 1955) delivered valuable insight to the function of the LA providing evidence that the LA functions as both an arch and a beam during weight bearing, in the absence of any requirement for muscular control. The beam function of the LA is provided by the dorsal compression of the articulations within the tarso-metatarsal joint, while the plantar aponeurosis provides passive tension at either end of the LA resisting longitudinal lengthening and arch collapse (Hicks, 1954; 1955). Extension of the toes in mid- to late-stance, creates increased tension in the plantar aponeurosis, resulting in shortening of the LA via flexion and adduction of the metatarsals in combination with supination of the rear-foot (Hicks, 1954; Caravaggi *et al.*, 2009). This function, known as the windlass mechanism (Hicks, 1954) acts to stiffen the foot and transform it from a compliant attenuator to a rigid lever, allowing ankle plantar flexor torque to be efficiently transmitted to the ground (Donatelli, 1985).

Due to the substantial complexity and technical difficulties involved when investigating and describing rotation of all the small joints that contribute to overall LA motion (Arndt *et al.*, 2007; Lundgren *et al.*, 2008; Nester *et al.*, 2014) the vast majority of research describing LA biomechanics in-vivo has involved simplified kinematic models that describe the rotation of the metatarsals, relative to the calcaneus using two and three dimensional modelling techniques (Scott & Winter, 1993; Leardini *et al.*, 2007; Caravaggi *et al.*, 2009; 2010; Levinger *et al.*, 2010; Caravaggi *et al.*, 2011; Dixon *et al.*, 2012). While not providing the detailed information that is obtainable from in-vitro studies (Morton, 1924; Hicks, 1953; 1954; 1955; Ker *et al.*, 1987) or the accuracy and detail of invasive bone pin studies (Arndt *et al.*, 2004; 2007; Lundgren *et al.*, 2008; Arndt *et al.*, 2012) the use of a multi segment foot modelling approach allows for time efficient analysis that can be applied to normal (Leardini *et al.*, 2007; Caravaggi *et al.*, 2009; Levinger *et al.*, 2010; Caravaggi *et al.*, 2011; Bishop *et al.*, 2012; Arnold *et al.*, 2012) and clinical populations (Rao *et al.*, 2007; 2009; Levinger *et al.*, 2010). Recent advances in three-dimensional motion analysis and kinematic modelling techniques have increased the utility of multi segment foot modelling, providing advances in our knowledge of LA biomechanics (Bishop *et al.*, 2012). Leardini and colleagues (Leardini et al., 2007) employed a multi-segment foot model to show that LA compression during stance phase is primarily due to extension, inversion and abduction of the metatarsals relative to the calcaneus, with these rotations reversing in late stance, presumably due to the combined effects of elastic recoil of the plantar aponeurosis (Ker et al., 1987; Erdemir et al., 2004) with the windlass mechanism. Caravaggi and colleagues (Caravaggi et al., 2010) investigated how LA biomechanics alters with gait velocity. Their results confirmed the previous findings of previous research that the LA compresses and recoils during early stance (Hicks, 1954; Ker et al., 1987; Erdemir et al., 2004). However their findings also highlighted that this compression appears to plateau at higher walking velocities, despite substantial increases in ground reaction force (Caravaggi et al., 2010). This finding is in contrast to the cadaveric experiments performed by Ker (Ker et al., 1987), Erdemir (Erdemir et al., 2004) and Hicks (Hicks, 1954) who found that LA compression increased with increasing ground reaction forces. Caravaggi hypothesised that the divergence in findings may be due to the presence of active muscular support that may be delivered when the body encounters high loads. Dynamic support for the LA has generally been considered primarily passive in nature, however this idea has been primarily based on data from cadaveric studies, where no active muscular contributions are possible. The findings of Caravaggi and colleagues (Caravaggi et al., 2010) as well as those by Bates (Bates et al., 2013) and Pataky (Pataky et al., 2008) findings have highlighted that active muscular control may also be an important factor in LA biomechanics.

Structural support for the longitudinal arch

As mentioned previously, structural support for the LA has traditionally been considered passive in nature. The plantar aponeurosis is known to provide the majority of structural support for the LA (Hicks, 1954; Ker *et al.*, 1987; Erdemir *et al.*, 2004), applying tension at proximal and distal ends of the LA, via its origin at the calcaneus and insertion into the toes (Hicks, 1955). This structural arrangement acts as a truss, resisting LA lengthening under load (Hicks, 1955; Ker *et al.*, 1987; Erdemir *et al.*, 2004) and also provides transient increases in LA stiffness during late stance, via the windlass mechanism (Hicks, 1954). Additionally the long plantar and short plantar ligaments also provide considerable structural support to the plantar aspect of the LA (Ker et al., 1987)while osseous compression in the dorsal margins of the tarso-metatarsal joints also provide considerable structural integrity for the LA during stance (Hicks, 1955).

While it has been observed that minimal muscular control is required to maintain LA integrity during quiet standing (Basmajian & Stecko, 1963; Wang & Crompton, 2004), muscles of the leg and foot are also known to provide transient influences on LA biomechanics (Basmajian & Stecko, 1963). The extrinsic muscles such as tibialis posterior, tibialis anterior and the peroneal muscle group are known to be active during the stance phase of locomotion (Mann *et al.*, 1986) providing frontal plane control of sub-talar and transverse tarsal joint motion (Kirby, 2001; Watanabe *et al.*, 2012).

The plantar intrinsic foot muscles are known to be active during the stance phase of gait (Mann & Inman, 1964) and it has been suggested that these muscles may also provide active support for the LA when it is encumbered with excessive loads (Basmajian & Stecko, 1963). The largest intrinsic foot muscles span similar anatomical pathways to that of the plantar aponeurosis (Kura *et al.*, 1997; Ledoux *et al.*, 2001; Tosovic *et al.*, 2012), thus when considered in the context of their known activation patterns (Basmajian & Stecko, 1963; Mann & Inman, 1964) it is possible that these muscles may also contribute to LA support.

Figure 1.3. The plantar aponeurosis viewed from the medial (A) and plantar (B) aspect of the left foot. The plantar aponeurosis courses from the medial and lateral tuberosity of the calcaneus to the insert in the intermediate phalanx of the toes, providing primary structural support for the longitudinal arch. Images adapted from Ankle and Foot Pro III (C3D4 Medical, 2014)

1.2.2 Plantar intrinsic foot muscle anatomy

The plantar intrinsic foot muscles have both origin and insertion contained within the foot. According to a study by Kura et al. (1997) the abductor hallucis (AH), flexor digitorum brevis (FDB) and quadratus plantae (QP) muscles have the greatest length, physiological cross sectional area (PCSA) and muscle volume of all the intrinsic foot muscles. Table 1.1 gives a summary of the architectural properties of these muscles, while Figure 1.4 provides a representation of their anatomical locations within plantar aspect of the foot.

Abductor hallucis (Fig 1.4) is located in the first (superficial) fascial compartment of plantar aspect of the foot and is the most medially located of all the intrinsic foot muscles (Hing *et al.*, 2009; Tosovic *et al.*, 2012). It arises from the medial posterior aspect of the calcaneus and inserts into both the plantar aspect or the proximal phalanx and medial sesamoid of the first metatarsophalangeal (MTP) joint and is known to consist of relatively low motor unit numbers (Johns & Fuglevand, 2011). Its function is to both abduct and plantar flex the great toe at the first MTP joint. It has also been reported that this muscle provides active support for the LA during weight bearing (Fiolkowski *et al.*, 2003; Headlee *et al.*, 2008).

Flexor digitorum brevis (Fig 1.4) is also located in the first (superficial) fascial layer of the foot. It is fusiform in shape and arises from the medial plantar calcaneal process, as well as the plantar aponeurosis (Locke *et al.*, 2010). The FDB contains three or four discreet muscle compartments,

with each giving rise to a tendon, inserting into the plantar aspect of the proximal phalanx in toes 2-5 (Locke *et al.*, 2010). Interestingly, the fourth muscle belly and tendinous slip (inserting into the fifth toe) is often described as being absent in cadaveric specimens(Kura *et al.*, 1997; Ledoux *et al.*, 2001). The proposed function of this muscle is to flex the second, third, fourth and fifth toes at the MTP joints, as well as stabilizing the toes during the push-off phase of gait (Thibodeau & Patton, 2007).

Quadratus plantae (Fig 1.4) arises from two heads. The smaller lateral head arises from the plantar surface of the lateral plantar calcaneal tubercle. This lateral head has been reported to be absent in some humans (Kura *et al.*, 1997). The large medial head arises prom the medial plantar calcaneal tubercle. Both heads unite to form a flattened band, which inserts in to the posterior surface of the flexor digitorum longus tendon (Sooriakumaran *et al.*, 2005). The role of QP is to aid in the flexion of the lesser toes, while aligning the longitudinal pull of the FDL tendon (Sooriakumaran *et al.*, 2005). To the author's knowledge, the precise function of this muscle in gait and posture is unknown.

	abductor hallucis	flexor digitorum brevis	quadratus plantae
Muscle Length (mm)	115.8 (4.9)	103.0 (9.2)	81.3 (20.1)
PCSA (cm^2)	6.7 (2.7)	4.6 (2.0)	2.9 (1.3)
Muscle Volume (cm^3)	15.2 (5.2)	10.3 (5.0)	8 (4.6)
Fibre Length (mm)	23 (5.5)	23 (4.3)	25.4 (7.0)
Pennation Angle (deg)	16.5 (7.5)	11.4 (7.1)	8.1 (4.9)

Table 1.1 Muscle architectural properties (mean (SD)) of three plantar intrinsic foot muscles - abductor hallucis, flexor digitorum brevis and quadratus plantae. Figures summarized from Kura et al. (1997) and Ledoux et al (2001). PCSA, physiological cross sectional area.
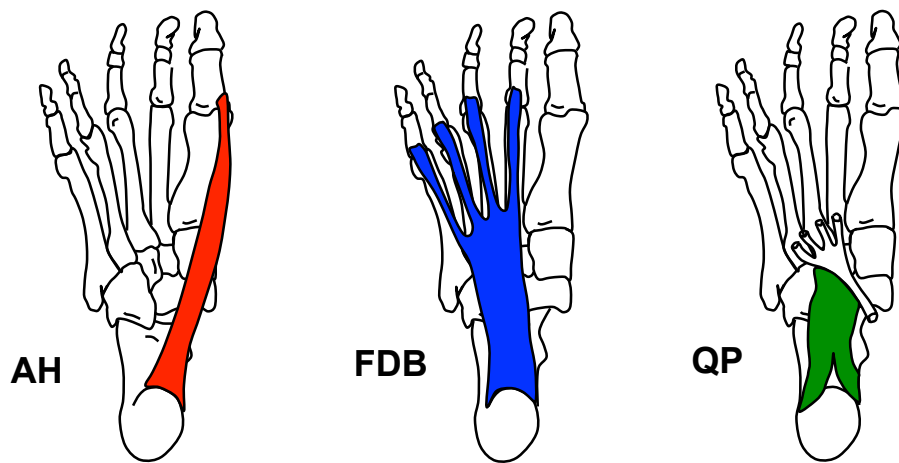
Figure 1.4 Intrinsic foot muscle anatomy. Depiction the anatomical location of abductor hallucis (AH), flexor digitorum brevis (FDB) and quadratus plantae (QP) in the plantar aspect of a right foot.

1.2.3 Motor unit discharge characteristics of the plantar intrinsic foot muscles

Neurophysiological properties of muscles are closely linked to their biological function (Enoka, 1995; Duchateau & Enoka, 2011), allowing each muscle to perform its given task with optimal efficiency. The human foot is primarily a load bearing structure and is commonly encumbered with forces far exceeding body weight (Nilsson & Thorstensson, 1989). Given the magnitude of forces encountered within the foot, it could be speculated that the muscles contained within this structure would be well adapted to produce and sustain substantial levels of force for prolonged periods, in order to provide dynamic and postural support during stance and locomotion.

Active muscle force is regulated by the nervous system via two mechanisms; recruitment (and de-recruitment) and rate coding, with the utilisation of recruitment and rate coding strategies varying greatly between muscles. Postural muscles, such as soleus, that are active for sustained periods maintaining upright posture (Sherrington, 1915) generally display relatively low peak discharge rates (10-25 Hz) (Bellemare *et al.*, 1983; Kuchinad *et al.*, 2004; Oya *et al.*, 2009; Dalton *et al.*, 2009) and are reliant on recruitment to generate and maintain force across their full range of force production (Oya *et al.*, 2009). Whereas muscles requiring precise control of movement, such as hand muscles, tend to have complete recruitment achieved at relatively low force levels ($\approx 30 - 50\%$ of maximal voluntary contraction (MVC), thereafter relying on rate coding to generate and maintain force (De Luca *et al.*, 1982; Thomas *et al.*, 1986; Zijdewind, 2002; Moritz *et al.*, 2005).

In addition to recruitment and rate coding strategies, the number of motor units within a particular muscle will also have a significant impact on the ability to generate and grade active force

(Campbell *et al.*, 1973). Muscles with a lower number of motor units, relative to their PCSA, tend have a reduced ability to precisely control gradation of force (Enoka, 1995). Abductor hallucis, the largest intrinsic foot muscle with a PCSA of 6.7 cm^2 (Kura et al., 1997) is known to be comprised of approximately 43 motor units (Johns & Fuglevand, 2011). The ratio of motor units to PCSA for AH appears quite low when considered in context of similar muscles from the hand, such as the abductor pollicis brevis which has a PCSA of 1.6 cm^2 and possesses approximately 136 motor units (Sica *et al.*, 1974). A relatively low number of motor units innervating a larger number of muscle fibres may allow relatively large amounts of force to be summated from each motor unit in order to provide postural stability for the LA, however this may occur at the expense of force precision.

Despite the apparent importance of the plantar intrinsic foot muscles in providing postural support for the LA during stance and locomotion, the neurophysiological characteristics of these muscles remain largely unknown.

1.2.3 Role of the plantar intrinsic foot muscles in support for the LA during stance and locomotion
The AH, FDB and QP muscle-tendon units span the length of the LA (Kura et al., 1997; Ledoux et al., 2001; Tosovic et al., 2012) coursing a similar anatomical pathway to the plantar aponeurosis. The function of these muscles during stance and gait has been the subject of speculation for many years and remains an area of intense interest. Anatomy texts describe these muscles as accessory toe flexors, which may also aid in forefoot stabilization during the push-off phase of gait (Thibodeau & Patton, 2007). However there is very little data describing the specific role of the plantar intrinsic foot muscles during stance and locomotion, thus any interpretation of their functional roles has been drawn from a small number of electromyography studies (Basmajian & Stecko, 1963; Mann & Inman, 1964; Gray & Basmajian, 1968). A Seminal study by Basmajian and Stecko (Basmajian & Stecko, 1963) shed some light on the function of these muscles as providing secondary support for the LA in addition to the plantar aponeurosis, reporting that AH and FDB were recruited at forces exceeding bodyweight, and that once recruited, the activation of these muscles increased in response to load. Further supporting this hypothesis, individuals with a lower LA height in stance (i.e., greater LA deformation) were shown to display greater levels of intrinsic muscle activity during waking (Gray & Basmajian, 1968). Additionally, Mann and Inman reported that these muscles act as a functional unit during the stance phase of gait to stabilise the forefoot during propulsion (Mann & Inman, 1964).

While providing valuable insight to the possible function of these muscles, the early studies by Basmajian and colleagues (Basmajian & Stecko, 1963; Gray & Basmajian, 1968) and Mann and

Inman (Mann & Inman, 1964) are subject to a number of limitations. For example, as these studies were performed in the 1960's, the researchers were unable to use real time ultrasound to ensure the correct location of each electrode within the arch of the foot. The intrinsic foot muscles are quite small (Kura et al., 1997) and given that the morphology of the LA varies considerably between individuals (Morton, 1930) it is difficult to assume that recordings made during these experiments (Basmajian & Stecko, 1963; Mann & Inman, 1964; Gray & Basmajian, 1968) were from the correct muscles. Furthermore, as these recordings were made from a seated position with weights being loaded on the leg (Basmajian & Stecko, 1963)and during walking (Mann & Inman, 1964), it is difficult to determine if these muscles respond in a similar fashion to the extrinsic foot muscles in response to postural sway (Winter, 1995).

From a clinical perspective, weakness or dysfunction of the plantar intrinsic foot muscles has been linked to numerous lower limb pathologies, including plantar fasciitis (Wearing et al., 2006), hallux valgus (Arinci İncel et al., 2003) and medial tibial stress syndrome(Senda et al., 1999). Additionally, weakness of the plantar intrinsic foot muscles has been implicated as a contributing factor to balance impairment and an increased falls risk in the elderly (Menz *et al.*, 2005; Mickle *et al.*, 2009) and intervention programs including strengthening of these muscles have been shown to reduce the risk of falls in this population (Spink et al., 2011).

Recent studies have highlighted the potential for the plantar intrinsic foot muscles to contribute to regulation of LA stiffness. For example Caravaggi and colleagues (Caravaggi *et al.*, 2009; 2010) used a multi-segment foot model to describe the behaviour of the plantar aponeurosis in relation to gait velocity. Their findings confirmed the earlier work of Hicks (Hicks, 1954) that peak tension in the plantar aponeurosis occurs in mid- to late-stance (80% of contact time). However, they reported no effect of gait velocity on peak aponeurosis tension, despite the increased vertical ground reaction forces that occurred at higher velocity. They speculated that their findings indicated the presence of an active LA stiffening mechanism, possibly produced by muscles such as the plantar intrinsics (Vereecke & Aerts, 2008; Caravaggi *et al.*, 2010). Adding further credence to this suggestion, Pataky (Pataky et al., 2008) and Bates (Bates et al., 2013) have used plantar pressure measurement techniques to show that LA deformation does not increase with walking speed, despite increased ground reaction forces.

Despite the indirect evidence suggesting that the plantar intrinsic foot muscles may have the capacity to actively contribute to regulation of foot stiffness and postural stability during stance and gait (Pataky *et al.*, 2008; Caravaggi *et al.*, 2010), the specific mechanical functions of these muscles

are yet to be described. It is also unknown whether these small muscles are able to generate sufficient force to produce a significant alteration in foot biomechanics under loaded conditions, in order to influence LA biomechanics.

1.3 Research Aims

The above literature overview has outlined areas in the literature that need further exploration, in order to gain a deeper understanding of the in-vivo function of the plantar intrinsic foot muscles. Below are the general aims of the four studies that will contribute towards this thesis.

1.3.1 Study 1

It has been speculated that the plantar intrinsic foot muscles provide support for the LA during stance and postural activities. While weakness and dysfunction of these muscles has been linked to poor balance and an increased risk of falls in the elderly. Despite the apparent link between these muscles and postural support for the foot, the precise role of these muscles in balance control remains unknown. Therefore, the aim of this study was to determine the difference in activation patterns of three plantar intrinsic foot muscles, during two standing tasks with increasing postural difficulty.

1.3.2 Study 2

It has been suggested that the plantar intrinsic foot muscles are important in balance and postural control. As such it could be hypothesised that motor units in AH would have relatively slow discharge rates, while displaying relatively high levels of fatigue resistance. Therefore, the aims of this study were to describe the single motor unit (SMU) discharge properties AH, the largest plantar intrinsic foot muscle, during controlled ramp and hold contractions as well as during an isometric submaximal constant load fatigue task.

1.3.3 Study 3

Despite some evidence suggesting that the plantar intrinsic foot muscles may actively control LA deformation during stance and gait (Basmajian & Stecko, 1963; Pataky *et al.*, 2008; Caravaggi *et al.*, 2010), the specific mechanical functions of these muscles are yet to be described. It is also unknown whether these small muscles are able to generate sufficient force to produce a significant alteration in foot biomechanics under loaded conditions, in order to influence LA biomechanics. This study will aim to address two hypotheses, firstly, that the LA deforms under increasing load, producing stretch of the plantar intrinsic foot muscles (AH, FDB and QP) and an increase in

involuntary muscle activation. Secondly, when activated these same muscles are capable of generating sufficient forces to attenuate LA deformation produced by the load, effectively increasing LA stiffness. Activation of these muscles with load and their ability to generate sufficient force to counter LA deformation may have important implications for how the foot can absorb and generate energy during gait.

1.3.4 Study 4

It is well established that plantar aponeurosis stretches and recoils in response to LA deformation occurring during the stance phase of gait, allowing storage and return of mechanical energy. Given that the MTU's of AH, FDB and QP span the length of the LA, following a similar anatomical pathway to the plantar aponeurosis and that they are active during stance, it is possible that these muscles actively lengthen and shorten during this phase of gait and thus have the potential to contribute to force dissipation and generation. Therefore this study aims to determine if the MTU's of AH, FDB and QP undergo an active stretch and recoil process in response to LA deformation during stance phase, and therefore are capable of contributing to energy dissipation and generation. Additionally this study aims to determine if the magnitude of MTU stretch and also muscle activation increases with increased loading forces that are encountered when gait velocity is increased during walking and running.

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CHAPTER TWO – RECRUITMENT OF THE PLANTAR INTRINSIC FOOT MUSCLES WITH INCREASING POSTURAL DEMAND

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2.1 Abstract

Background; The aim of this study was to determine the difference in activation patterns of the plantar intrinsic foot muscles during two quiet standing tasks with increasing postural difficulty. We hypothesised that activation of these muscles would increase with increasing postural demand and be correlated with postural sway.

Methods: Intra-muscular electromyographic (EMG) activity was recorded from abductor hallucis, flexor digitorum brevis and quadratus plantae in 10 healthy participants while performing two balance tasks of graded difficulty (double leg stance and single leg stance). These two standing postures were used to appraise any relationship between postural sway and intrinsic foot muscle activity.

Findings: Single leg stance compared to double leg stance resulted in greater mean centre of pressure speed (0.24ms^{-1} versus 0.06 ms^{-1}, respectively, $P \leq 0.05$) and greater mean EMG amplitude for abductor hallucis (P≥0.001, ES=0.83), flexor digitorum brevis (P ≤ 0.001, ES=0.79) and quadratus plantae (P ≤ 0.05, ES=0.4). EMG amplitude waveforms for all muscles were moderate to strongly correlated to COP medio-lateral waveforms (all r ≥ 0.4), with muscle activity amplitude increasing with medial deviations of the centre of pressure. Intra-muscular EMG waveforms were all strongly correlated with each other (all r ≥ 0.85).

Interpretations: Activation of the plantar intrinsic foot muscles increases with increasing postural demand. These muscles are clearly important in postural control and are recruited in a highly co-

ordinated manner to stabilise the foot and maintain balance in the medio-lateral direction, particularly during single leg stance.

Key words: Electromyography, Intrinsic foot muscles, Postural control, Balance.

2.2 Introduction

Upright stance has been described as an unstable inverted pendulum, where continuous small fluctuations in body position (postural sways) are accompanied by bursts of lower limb muscle activity (Tokuno *et al.*, 2007). The majority of muscular activity during quiet stance appears to occur in the ankle plantar flexors and is associated with anterior-posterior body sway (Winter, 1995). However, given that weakness in the plantar intrinsic foot muscles has previously been implicated as a contributing factor to balance impairment (Menz *et al.*, 2005; Mickle *et al.*, 2009), it is likely that these muscles are also involved in maintaining balance and as such, they may be significant in postural control.

The plantar intrinsic foot muscles are a unique group of muscles, with both origins and insertions contained within the foot. It has been proposed that these muscles provide structural support for the medial arch of the foot (Basmajian & Stecko, 1963) however their precise function remains unclear (Kura *et al.*, 1997). It has been proposed that weakness and dysfunction of these muscles can contribute to clinical pathologies such as plantar fasciitis (Wearing *et al.*, 2006), hallux valgus (Arinci İncel *et al.*, 2003), and medial tibial stress syndrome (Senda *et al.*, 1999), through a reduced ability to control foot pronation (Headlee *et al.*, 2008).

Early intramuscular electromyographic (EMG) studies (Mann & Inman, 1964; Gray & Basmajian, 1968) suggested that the plantar intrinsic foot muscles act as a functional unit to stabilise the toes during the push off phase of gait, as well as providing resistance to sub-talar joint pronation. These early reports provided valuable insight into the function of these muscles. However, evidence of electrode location and sufficient detail of the procedures used to acquire and process the EMG signals were not provided. More recently, surface EMG evaluation of the plantar intrinsic foot muscles has provided some evidence for their role in maintaining the height of the medial longitudinal arch (Fiolkowski *et al.*, 2003) and reducing foot pronation (Headlee *et al.*, 2008) during static stance. These studies are, however, limited by the inability of surface EMG electrodes to capture the individual drawn from the larger and more superficial abductor hallucis (AH). Given the methodological limitations of existing literature, combined with the lack of data pertaining to the role of the plantar intrinsic foot muscles in postural support, it is judicious to use ultrasound

guided EMG to provide reliable and accurate recordings of these muscles during basic postural tasks.

Therefore, the aim of this study was to determine the difference in activation patterns of three plantar intrinsic foot muscles, during two standing tasks with increasing postural difficulty. Recording of specific patterns of activation from these muscles was achieved using ultrasound guided intramuscular EMG. We hypothesised that these muscles would be active during stance and that their level of activation would be regulated in response to postural demand.

2.3 Methods

2.3.1 Participants

Ten healthy male participants (mean (SD) for age 33 (4) yr; mass: 76 (4) kg; height: 181 (4) cm) with no history of diagnosed neuromuscular disorder or lower limb injury in the previous six months volunteered to participate in the study. All subjects were informed of the study requirements, benefits and risks before giving written informed consent. All procedures conformed to the standards set by the Declaration of Helsinki and the protocol was approved by the scientific research ethics committee of Aspetar, Qatar Orthopedic and Sports Medicine Hospital.

2.3.2 Experimental design

Postural Tasks

Two quiet standing postures with varying degrees of difficulty (double leg stance, DLS; and single leg stance, SLS) were used to appraise any relationship between postural sway and intrinsic foot muscle activity, measured using fine wire intramuscular electromyography (EMG). The DLS trial was performed once only, for a 120-s period, while the more difficult SLS trial was performed three times, each for a 60-s period.

2.3.3 Data Collection

Balance measurements

The DLS and SLS postural trials were performed with the subject standing on a force platform (Type 9286AA Kistler, Zurich, Switzerland) facing forward with their eyes open and arms folded across their chest. Two strips of adhesive tape were placed on the force plate, measuring 15 cm apart and extending from the posterior to anterior edge. During the DLS trial, subjects were asked to align the medial aspect of their heel and forefoot (left and right foot) along the corresponding pieces of tape. For the SLS trial, subjects placed their foot in the middle of the force plate parallel

with the previously mentioned strips of tape. This procedure was employed to maintain consistency of foot placement between subjects and trials.

Electromyography (EMG)

Identification of the abductor hallucis, flexor digitorum brevis (FDB) and quadratus plantae (QP) muscles was conducted using real-time ultrasound imaging (12Hz, linear array, Siemens Acuson Antares, USA) in the right foot of each subject. An acupuncture needle (0.3 x 50mm, Seirin, Shizuoka, Japan) was inserted into the muscle of interest through the medial aspect of the foot, while continuously imaging the muscle. The acupuncture needle was used as a guide to determine the correct angle and depth for when the fine wire electrode was to be inserted later. Unlike fine wire delivery needles, the acupuncture needle could be retracted and repositioned with minimal discomfort to the participant, until the tester was satisfied that it was located within the appropriate muscle. Subsequently, bi-polar fine wire electrodes (0.051mm stainless steel, Teflon coated, Chalgren, USA) with a detection length of 2mm and inter-electrode distance of approximately 2mm were inserted using delivery needles (0.5mm x 50mm) into the bellies of AH, FDB and QP under ultra sound guidance, using the angle and depth of the acupuncture needle as a guide for correct placement. The size of the active area and separation between sites was chosen to give the best chance of recording representative activity from each muscle, while reducing the possibility of cross-talk from nearby muscles. Once the wires were positioned appropriately in each muscle, both the acupuncture and delivery needles were removed. The muscle was imaged once more to determine that the ends of the wires remained within the muscle after needle removal.. This method has been shown previously to be an accurate and reliable method of fine wire placement (Carpenter *et al.*, 2008). Sterile techniques were used for the insertion of all wires.

In two subjects, additional confirmation of electrode placement was made immediately after the experiment with the use of Computed Tomography (Siemens Somatom Sensation 40 Slice). Spiral blocks of 1-2mm slice thickness were recorded through the region from the metatarsal heads to the calcaneus. These images were reconstructed in axial, coronal and sagittal planes to verify wire position. Risk of radiation exposure was reduced with the use of lead gowns.

EMG signal quality was assessed by asking the participant to flex their toes against manual resistance. In some cases when the signal appeared to be contaminated by artefact or crosstalk, the position of the fine wire electrodes was adjusted by gently pulling on the exposed wires, withdrawing them approximately 1mm. The quality of the signal was then reassessed and the procedure repeated until an artefact free EMG signal was obtained.

EMG was continuously recorded from the right foot during all of the DLS and SLS trials. Ten seconds of EMG data was also recorded in a seated position, with the right foot unloaded and relaxed (REL). This procedure was undertaken in order to determine the level of resting base-line activity for each muscle.

2.3.4 Data Acquisition and Processing

All EMG signals were sampled at 5kHz, amplified 1000 times and band pass filtered between 30-1000Hz and (MP35, Biopac Systems Inc., Santa Barbara, CA). Data was subsequently exported to Spike2 (Cambridge Electronic Design, Cambridge, UK) for analysis. Each EMG signal had any DC offset removed prior to rectification and low-pass filtering at 5Hz using a fourth order Butterworth filter. Mean EMG root mean square (RMS) signal amplitude was calculated for the entire duration of each postural trial, as well as for the 10s REL condition.

Centre of pressure (COP) position in both the medio-lateral (ML) and antero-posterior (AP) directions was calculated for each sample from the vertical and horizontal forces recorded from the force plate. COP path excursion in both AP and ML directions was calculated over the entire standing period for each DLS and SLS trial. Different task durations were employed in this protocol, as single leg stance is difficult to maintain for periods of longer than 60 seconds, while longer durations of quiet stance are typically employed to provide an accurate reflection of postural demand during double leg stance (Tokuno *et al.*, 2007; 2009). Mean COP speed in both AP and ML directions was also determined, in order to normalize the time periods for each task. The calculated COP signal was additionally low pass filtered using a 5Hz fourth order Butterworth filter. For the purpose of this study COP was calculated to provide an indicator of postural sway. This assumption was made in accordance with previous literature (Gatev *et al.*, 1999; Tokuno *et al.*, 2008; 2009).

To enable changes in the EMG signal to be cross-correlated with changes in the force plate signals, the rectified and smoothed EMG data was down sampled to 50Hz, the same frequency at which the force data was sampled. Synchronisation between both force plate and EMG signals was achieved with the use of an external trigger.

2.3.5 Statistical Analysis

A repeated measures analysis of variance (ANOVA) was used to compare differences in mean EMG RMS amplitude between DLS, SLS and REL trials. Sphericity (homogeneity of covariance) was verified by the Mauchly's test. When the assumption of sphericity was not met, the significance of F-ratios was adjusted according to the Greenhouse-Geisser procedure. Pair-wise comparisons, including Bonferroni corrections, were applied as post-hoc analyses. Effect size (ES) was calculated

using *partial-eta squared*, to determine the magnitude and the practical relevance of the significant findings. Differences in mean COP speed between DLS and SLS trials were assessed using a paired T-test. For all analysis, the level of significance was set at $P \leq 0.05$.

A cross (waveform) correlation function was applied to compare correlations between rectified EMG and COP path excursion (in AP and ML directions), as well as inter-muscular correlations. This analysis was conducted using SPIKE 2 software. Correlation (r) values were classified as follows; small ± 0.1-0.3, moderate ± 0.3-0.5, and strong ± 0.5-1.0 (Nelson-Wong, 2009).

2.4 Results

The single leg balance task induced a higher level of postural demand, as evidenced by a significantly greater mean COP speed in both AP ($T_9 = 5.84$, $P < 0.001$) and ML ($T_9 = 7.84$, $P < 0.001$) directions (Fig 2.1). Mean EMG RMS amplitudes were significantly higher in the SLS task (Fig 2.2) in AH ($F_{2,18} = 44.3$, $P < 0.001$, ES = 0.83), FDB ($F_{2,18} = 32.2$, $P < 0.001$, ES = 0.79) and QP ($F_{2,18} = 5.45$, $P < 0.02$, ES = 0.40), compared to both DLS and REL. No significant differences in EMG RMS were found between DLS and REL tasks ($P > 0.05$). However, most subjects displayed intermittent recruitment of a small number of motor units, in one or more muscles, during DLS (Fig. 2.3). AH was the most commonly active muscle during DLS, displaying consistent recruitment in 7 of the 10 subjects.
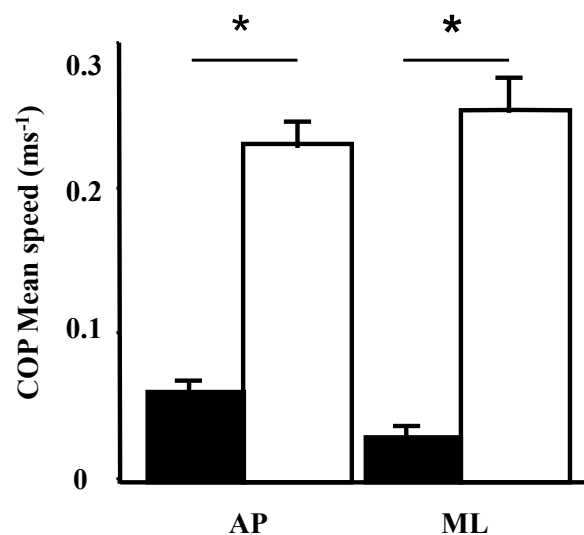
Figure 2.1. Mean (SEM) speed of the centre of pressure (COP) in antero-posterior (AP) and medio-lateral (ML) directions during double leg stance (DLS, solid) and single leg stance (SLS, open) trials. * significantly different between conditions.
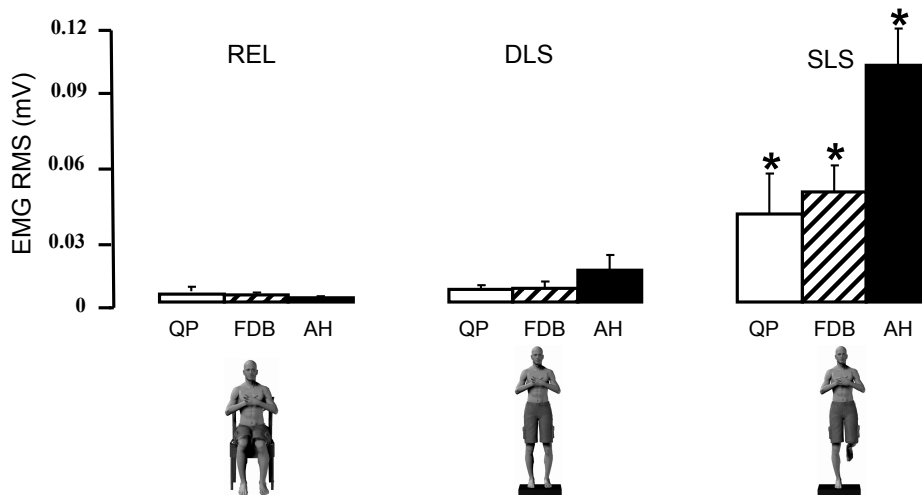
Figure 2.2. Mean (SEM) EMG Root mean square signal amplitude during relaxed sitting (REL), double leg stance (DLS) and single leg stance (SLS), for quadratus plantae (QP, white), flexor digitorum brevis (FDB, diagonal black stripes) and abductor hallucis (AH, black). * significantly different from REL and DLS conditions.

Activation of AH ($r = 0.62$), FDB ($r = 0.40$) and QP ($r = 0.40$) was correlated to ML sway during the SLS task (Fig 4), with increased recruitment during medial shifts of the COP. No correlation was evident for AP sway and muscle activation (all $r < 0.2$), nor were there any significant COP-muscle correlations during the DLS task (all $r < 0.2$). Strong correlations were observed between all muscles during the SLS task (all $r > 0.85$, Fig 4).
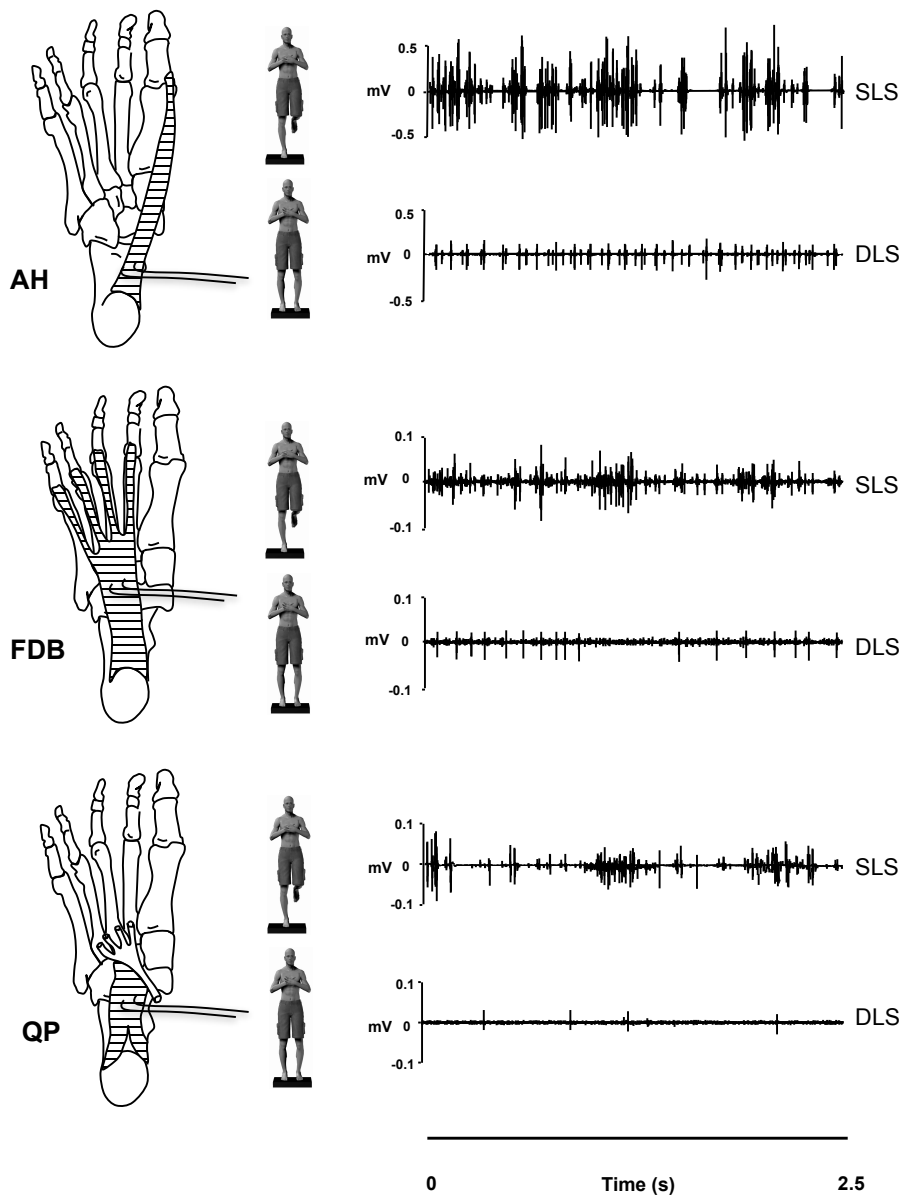
Figure 2.3. Anatomical location of abductor hallucis (AH), flexor digitorun brevis (FDB) and quadratus plantae (QP) in a right foot, as well as a sample of EMG signal recorded during the single (SLS) and double (DLS) leg stance trials. Bi-polar fine wire electrodes have been drawn in the approximate recording region within each muscle. All recordings are taken from the same representative individual, with all SLS (upper trace) and DLS (lower trace) recordings taken from the same time period in each respective trial.
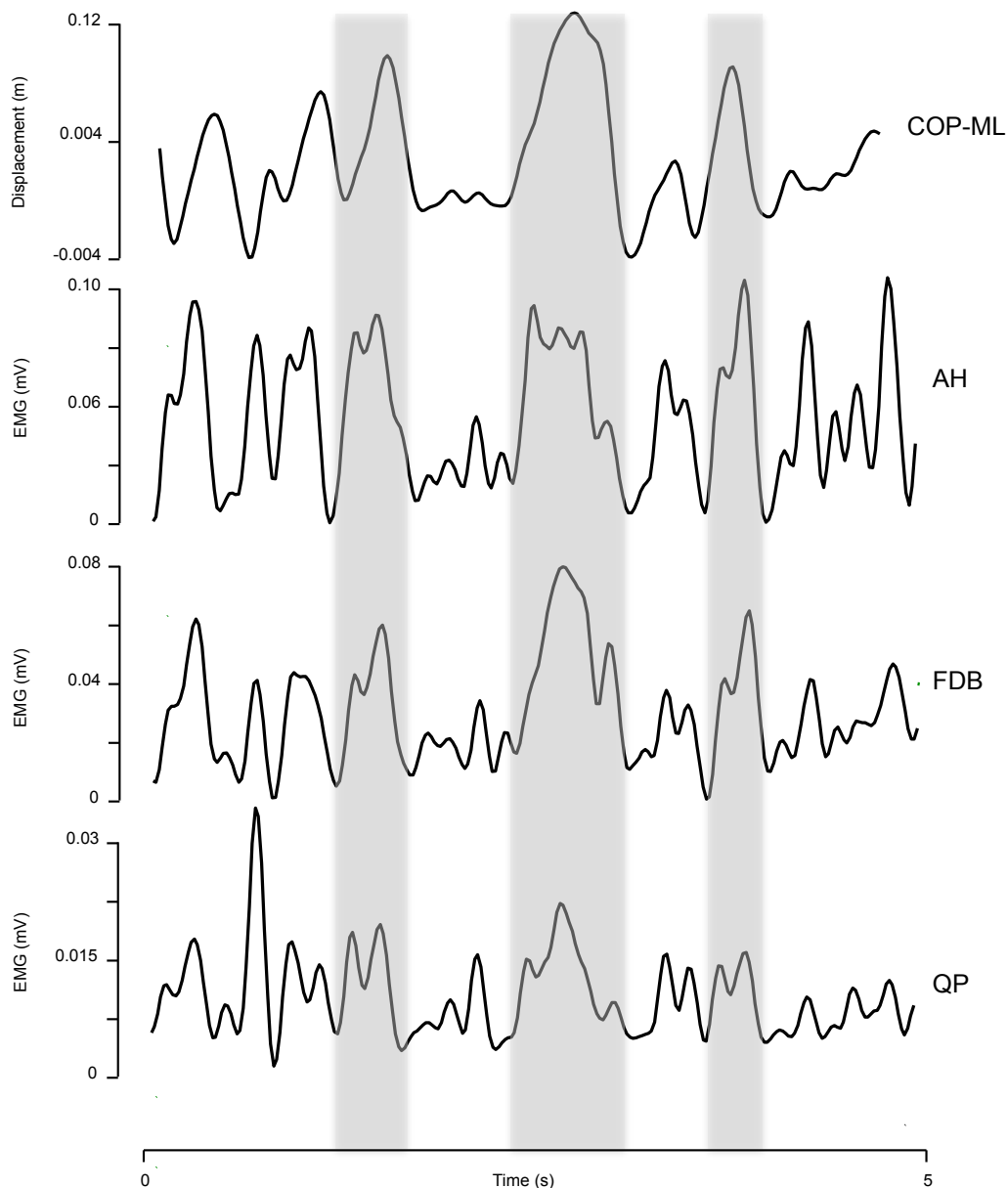
Figure 2.4. Waveforms for medio-lateral centre of pressure (COP-ML) and for EMG of abductor hallucis (AH), flexor digitorum brevis (FDB) and quadratus plantae (QP) during single leg stance (SLS) for a representative subject. Moderate to high correlations between COP-ML and muscle activation in AH, FDB and QP (all $r \geq 0.4$). High inter-muscular correlations were observed between all muscles (all $r \geq 0.85$). Shaded areas show the synchronous EMG bursts that correspond to the COP-ML excursion.

Computed Tomography images in two subjects confirmed the location of the fine wire electrodes within each respective muscle belly after the completion of the balance tasks. Thus, providing further evidence of correct electrode placement whilst also indicating that the electrodes remained in their correct location for the duration of testing period.

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2.5 Discussion

The aim of this study was to describe the activation patterns of the plantar intrinsic foot muscles during standing, where task demand and loading varied. We hypothesised that activation of these muscles would increase with increasing postural demand, and that recruitment and activity of these muscles would be correlated with postural sway. Our results indicate that recruitment of the plantar intrinsic foot muscles is regulated in response to postural demands. These muscles are moderate to strongly correlated with ML postural sway, thus suggesting a function in balance control.

This is the first study to use ultrasound guided intramuscular EMG to describe the activation patterns of the plantar intrinsic foot muscles during quiet stance. Previous studies examining the EMG activity of the plantar intrinsic foot muscles have either been limited by the inability to confirm the exact location of fine wire electrodes (Basmajian & Stecko, 1963; Mann & Inman, 1964; Gray & Basmajian, 1968), or by the inability of surface EMG electrodes to record the individual activity of small, deep and underlying musculature (Fiolkowski *et al.*, 2003; Headlee *et al.*, 2008). Given that the physiological cross-sectional area of these muscles are quite small (Kura *et al.*, 1997; Ledoux *et al.*, 2001) and that the use of real-time ultrasound is now quite readily available for use in EMG studies, it is prudent to use these techniques to provide reliable and effective intra-muscular electrode recordings (Carpenter *et al.*, 2008). In addition to real-time ultrasound guidance, we have used Computed Tomography (in 2 individuals) to confirm the location of our fine wire electrodes after the completion of the balance tasks.

Our results indicate that the plantar intrinsic foot muscles are active during quiet stance, increasing activation in accordance with postural demand. An early study by Basmajian and Stecko (1963) involved incrementally adding weights to the legs of seated subjects. They reported that activation of these muscles increased with loading of the foot, providing secondary structural support to the medial longitudinal arch. The work of Fiolkowski et al. (2003) and Headlee et al. (2008), using surface electromyography reported reduced muscle activation in AH in association with increased medial arch deformation. Our study delivers evidence that the plantar intrinsic foot muscles provide postural support for the feet during quiet stance.

A major finding of this study was that plantar intrinsic foot muscle activation was strongly correlated with medio-lateral postural sway in single leg stance, with increasing activity observed during sway to the medial border of the foot. Additionally, these muscles display highly correlated inter-muscular activation patterns during standing. Cross (waveform) correlation functions have been used widely in research related to balance and posture (Nelson-Wong, 2009), establishing

relationships between postural sway and muscle activation in the lower limb. Using these techniques, it has been established that the posterior lower limb muscles are recruited in response to AP body sway, with muscle waveform peaks occurring prior to the peak of anterior sway(Winter, 1995; Gatev *et al.*, 1999). Suggestions have been made that a central balance control mechanism is responsible for the activation of posterior leg muscles, in response to anterior body sway (Gatev *et al.*, 1999; Loram *et al.*, 2011) and that recruitment of the posterior leg muscles may be dictated by common neural drive (Mochizuki *et al.*, 2006). In the current study, plantar intrinsic foot muscle activity was positively correlated with medial shifts in COP during single leg stance, with EMG waveform peaks occurring in synchrony with medial COP excursion. Thus, we suggest that a similar central mechanism may also be responsible for the highly synchronised recruitment of AH, FDB and QP, in response to medial sways in COP. Although these muscles are relatively small in size compared to the extrinsic foot muscles (Kura *et al.*, 1997; Ledoux *et al.*, 2001), the synchronised manner in which they respond to ML sway may be an essential response to maintain balance. According to Mann and Inman (1964), the plantar intrinsic foot muscles function as a unit to resist sub-talar joint pronation, observed as calcaneal eversion (frontal plane), combined with medial deviation (transverse plane) and reduced vertical height (sagittal plane) of the navicular (Razeghi & Batt, 2002). As foot posture and function are known to impact on single leg balance (Menz *et al.*, 2005; Tsai, 2006), activation of the plantar intrinsic foot muscles may be utilised to help stabilise the foot, thereby improving balance. Our results also support the conclusions of Menz et al. (2005) and Mickle et al. (2009) who hypothesised that weakness in the intrinsic foot muscles is associated with poor balance and increased risk of falls in the elderly.

Limitations

The plantar intrinsic foot muscles are relatively small in size, thus there is always a risk of crosstalk from adjacent muscles when attempting EMG recordings (Solomonow *et al.*, 1994). Within the current study we took care to use a recording area on the intramuscular electrode that was large enough to record representative muscle activity, while small enough to minimise the risk of crosstalk. Additionally, visual inspection of our data revealed periods when only one muscle was active at a given time (Fig 2.5), providing evidence that our electrodes were in fact recording electrical activity from different muscles.
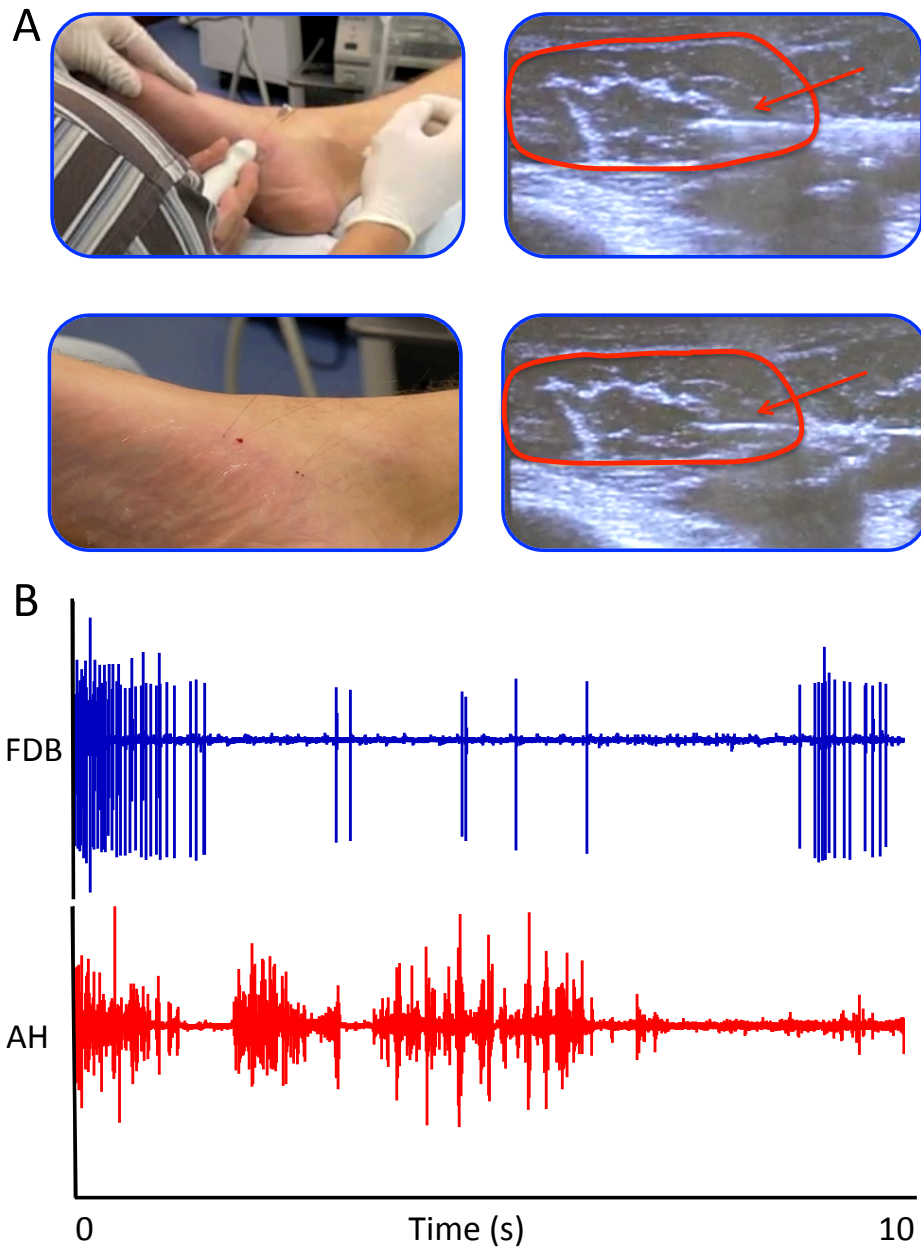
Figure 2.5. A - Ultrasound view of fine wire electrodes being inserted into the flexor digitorum brevis (FDB) muscle using delivery needles (top) and the fine wire electrodes remaining within the muscle tissue after the delivery needle is removed (bottom). B – Raw intramuscular electromyography recordings from abductor hallucis (AH, red) and FDB (blue) during voluntary isometric contractions showing periods of synchronous activation in both muscles and also periods of independent activation in each muscle.

2.6 Conclusion

This study investigated the function of the plantar intrinsic foot muscles during quiet upright stance. Our results indicate that recruitment of these muscles increases with increasing postural demand and that high levels of inter-muscular co-ordination occur in response to ML sway during single leg stance.

2.7 Acknowledgements

2.8 References

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CHAPTER THREE – DISCHARGE PROPERTIES OF ABDUCTOR HALLUCIS BEFORE, DURING AND ATER AN ISOMTERIC FATIGUE TASK.

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3.1 Abstract

Abductor hallucis is the largest muscle in the arch of the human foot, and is comprised of relatively few motor units, relative to its physiological cross sectional area. It has been described as a postural muscle, aiding in the stabilization of the longitudinal arch during stance and gait. The purpose of this study was to describe the discharge properties of abductor hallucis motor units during ramp and hold isometric contractions, as well as its discharge characteristics during fatigue. Intramuscular electromyographic recordings from abductor hallucis were made in five subjects, from those recordings 42 single motor units were decomposed. Data were recorded during isometric ramp contractions at 60% maximum voluntary contraction (MVC), performed before and after a submaximal, isometric contraction to failure (mean force $41.3\pm15.3\%$MVC, mean duration 233 ± 116s). Motor unit recruitment thresholds ranged from $10.3 - 54.2\%$ MVC. No significant difference was observed between recruitment and derecruitment thresholds or their respective discharge rates for both the initial and post fatigue ramp contractions (all $P>0.25$). Recruitment threshold was positively correlated with recruitment discharge rate ($r=0.47$, $P<0.003$). All motor units attained similar peak discharge rates (14.0 ± 0.25Hz) and were not correlated with recruitment threshold. Thirteen motor units could be followed during the isometric fatigue task, with a decline

in discharge rate and increase in discharge rate variability occurring in the final 25% of the task (both $P<0.005$). We have shown that abductor hallucis motor units discharge relatively slowly and are considerably resistant to fatigue. These characteristics may be effective for generating and sustaining the substantial level of force that is required to stabilize the longitudinal arch during weight bearing.

3.2 Introduction

Abductor hallucis (AH) is the largest and most medially located of the plantar intrinsic foot muscles (Kura *et al.*, 1997; Ledoux *et al.*, 2001) and is comprised of a relatively low number of motor units (Johns & Fuglevand, 2011). Its function is to both abduct and flex the great toe at the first metatarso-phalangeal (MTP) joint. Abductor hallucis has recently been shown to be involved in postural stabilization during upright stance, with activation patterns being highly correlated with medial postural sway (Kelly *et al.*, 2012). It has also been suggested that AH is involved in maintaining longitudinal arch (LA) height during gait (Basmajian & Stecko, 1963; Mann & Inman, 1964). However little is known about the neurophysiological properties of this muscle, as well as how these properties may influence force production.

Active muscle force is regulated by the nervous system via two mechanisms; recruitment (and derecruitment) and rate coding. The utilisation of recruitment and rate coding strategies varies greatly between muscles. Postural muscles, such as soleus, are active for sustained periods maintaining upright posture (Sherrington, 1915) generally display relatively low peak discharge rates (10-25 Hz) (Bellemare *et al.*, 1983; Kuchinad *et al.*, 2004; Oya *et al.*, 2009; Dalton *et al.*, 2009) and are reliant on recruitment to generate and maintain force across their full range of force production (Oya *et al.*, 2009). Whereas muscles requiring precise control of movement, such as hand muscles, tend to have complete recruitment achieved at relatively low force levels ($\approx 30 - 50\%$ of maximal voluntary contraction (MVC), thereafter relying on rate coding to generate and maintain force (De Luca *et al.*, 1982; Zijdewind, 2002; Moritz *et al.*, 2005; Thomas, 2006).

In addition to recruitment and rate coding strategies, the number of motor units within a particular muscle will also have a significant impact on the ability to generate and grade active force (Campbell *et al.*, 1973). Muscles with a lower number of motor units, relative to their physiological cross sectional area (PCSA), tend have a reduced ability to precisely control gradation of force (Enoka, 1995). Interestingly, AH has been shown to possess few motor units (Johns & Fuglevand, 2011) relative to its PCSA and thus these motor units may be inherently large, compared to other

muscles of the foot (Campbell *et al.*, 1973) and hand (Sica *et al.*, 1974) which contain greater motor unit numbers, relative to their PCSA (Linscheid *et al.*, 1991; Kura *et al.*, 1997).

During sustained submaximal (fatiguing) contractions, a decline in force producing capacity is generally accompanied by an increase in excitatory drive to the alpha motoneurone pool (Löscher *et al.*, 1996; Hoffman *et al.*, 2009). If the contraction force is below the upper limit of motor unit recruitment, an increase in excitatory drive will generally incite recruitment of new motor units in order to help maintain the required force. Despite an increase in central drive to the motoneurone pool, motor unit discharge behaviour can vary considerably during sustained submaximal contractions, with studies reporting a decrease (Garland *et al.*, 1997; Mottram, 2004; Riley *et al.*, 2008*b*; Dalton *et al.*, 2010), an increase (Griffin *et al.*, 2001; Kuchinad *et al.*, 2004) and also no change in discharge rate (Christie & Kamen, 2009; Pascoe *et al.*, 2011). It has been suggested that the reported inconsistencies between studies in discharge behaviour that occur during sustained submaximal contractions are due to varying interactions between cortical input and spinal motoneurone responsiveness (Kernell & Monster, 1982; McNeil *et al.*, 2011*a*), as well as the nature of the task (ie. high versus low intensity) (Kuchinad *et al.*, 2004) and the recruitment threshold of the motor units being investigated (Riley *et al.*, 2008*b*).

Another factor determining the discharge behaviour of a particular muscle during a fatiguing contraction is the composition of muscle fibres within that muscle, that is the percentage of fatigue resistant slow twitch fibres to the more fatigue sensitive fast twitch fibres (Kernell & Monster, 1982; 2004). Postural muscles, which have a higher percentage of fatigue resistant, slow twitch fibres tend to be relatively resistant to fatigue induced alterations in motor unit discharge behaviour (Macefield *et al.*, 2000; Kuchinad *et al.*, 2004).

Fluctuations in resting membrane potential (due to synaptic noise) are known to lead to increased discharge variability, which also influences the ability of a muscle to maintain target force (Calvin & Stevens, 1968). The co-efficient of variation (CV) of inter-spike interval (ISI) is a relative measure of motor unit discharge variability and provides an insight to the interplay between increased central drive and spinal motoneurone inhibition that occurs during sustained contractions (Calvin & Stevens, 1968). Motor unit discharge variability significantly hinders force output and steadiness (Enoka *et al.*, 2002; Tracy *et al.*, 2005; Moritz *et al.*, 2005) and has been shown to increase under conditions of muscle fatigue (Christie & Kamen, 2009).

The manner in which a postural muscle with a low number of motor units relative to its PCSA, such as AH, utilises recruitment and rate coding strategies to generate and sustain force remains unclear. Given the suggestion that AH is responsible for postural support of the LA during stance we hypothesised that motor units in AH would have relatively slow discharge rates, while displaying relatively high levels of fatigue resistance. Therefore, the aims of this study were to describe the single motor unit (SMU) discharge properties of AH during controlled ramp and hold contractions as well as during an isometric submaximal constant load fatigue task.

3.3 Methods

3.3.1 Participants

Five healthy males who had no history of neuromuscular disorder volunteered to participate in this study (mean ± standard deviation (SD) for age, height and weight were 30 ± 5yrs, 180 ± 3cm and 79 ± 7 kg, respectively). The procedures were approved by the local scientific ethics committee and performed according to the Declaration of Helsinki. All subjects gave their written informed consent.

3.3.2 Familiarization Procedure

Precise control of isometric force development and relaxation is imperative when studying the recruitment and derecruitment characteristics of a SMU. However an isolated contraction of AH (abduction and flexion of the hallux) is a novel task that can be particularly difficult to perform with accuracy. As such, all subjects attended the laboratory between two and six times to familiarize themselves with the required experimental tasks to reduce task variability. This included performing controlled isometric ramp and hold flexion/abduction (F-AB) contractions of the hallux, sustained isometric F-AB contractions at a constant submaximal force, as well as maximal voluntary effort isometric F-AB contractions. Participants were trained to flex and abduct their hallux at the first MTP joint, in the absence of inter-phalangeal joint flexion. The hallux F-AB task was designed based on pilot experimental data that indicated this was an effective method to isolate contraction of the AH and reduce the risk of co-contraction of agonist hallux flexors. Force feedback was given visually via a computer monitor located at eye level directly in front of the subject. The acceptable error for force tracking was set at ±3%MVC (De Luca *et al.*, 1996). All participants conducted several practice trials, until the investigator was satisfied that the participant could adequately follow the target force templates.

3.3.3 Experimental set-up

Participants sat comfortably with the right shank and foot secured with Velcro straps in a rigid, custom-built brace, which stabilized the leg, ankle and mid-foot, preventing changes in ankle and mid-foot joint angles (Figure 3.1A). The shank was positioned perpendicular to the plantar surface of the brace and the foot was positioned in approximately 10° of eversion and parallel to the plantar surface of the brace. The inner lining of the boot contained an air bladder that was inflated to improve comfort and further reduce any possible change in joint angle. A compression load cell (model MB miniature beam, Interface, Scottsdale Arizona, USA) able to detect a minimal mass of 0.0056kg, was aligned to the plantar surface of the big toe and secured with an additional Velcro strap.
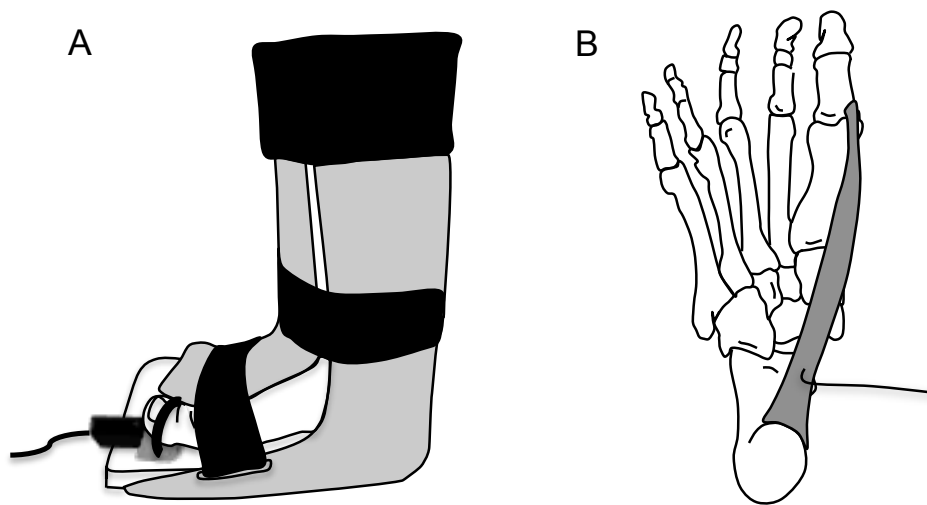
Figure 3.1. Experimental set up for recording of intramuscular EMG during isometric contractions of abductor hallucis. (A) The foot and shank were stabilised in a rigid, custom-built brace with a force transducer aligned to the plantar aspect of the big toe, allowing measurement of flexion-abduction force. (B) A medial approach was used to insert the quadrifilar fine wire electrodes, under ultrasound guidance, into the abductor hallucis muscle, which is located along the medial longitudinal arch of the foot.

3.3.4 Intramuscular electromyography and force measurement

Intramuscular EMG (EMG_{IM}) recordings were collected in the right foot of each subject, using a quadrifilar fine wire electrode (Micro-probes, Gaithersberg, MA, USA), which was inserted in the largest and most proximal segment of the AH muscle (Tosovic *et al.*, 2012) with the aid of a delivery needle (0.5mm diameter x 50mm, Figure 3.1B). Quadrifilar electrodes consist of four insulated fine wires glued together at the tip, with reduced area cut ends acting as the recording surfaces, making them highly selective (Adam, 2003). Ultrasound guidance was used to ensure accuracy of electrode placements for all needle insertions. Two channels of EMG_{IM} were recorded

from these electrodes in order to improve both the precision and yield of SMU's from the recordings. A reference surface electrode was placed on the medial malleolus of the right ankle.

All EMG_{IM} signals were amplified 1000 times, recorded with an open bandwidth (Delsys Bagnoli, Boston, USA), analogue to digitally converted at a sampling rate of 20KHz and collected using Spike2 software (Cambridge Electronic Design, Cambridge, UK). Electromyography signal quality was assessed by asking the participant to conduct a brief, low intensity, isometric contraction. In the case of apparent signal contamination due to movement artefact, the position of the fine wire electrodes were adjusted by gently pulling on the exposed wires, withdrawing them approximately 1mm. The quality of the signal was subsequently reassessed and the procedure repeated until at least one SMU could be easily distinguished by visual inspection.

Force was amplified 1000 times, recorded with an open bandwidth (Delsys Bagnoli, Boston, USA) and digitized at the same rate as the EMG_{IM} using the same collection equipment and software as for the EMG_{IM}.

Isometric ramp-up, hold, ramp-down protocol

Each subject performed three isometric MVC F-AB contractions of the hallux. A minimum of 120-s was allowed for full recovery between each effort. The maximal force recorded during this task was used to normalize force levels during the subsequent isometric ramp-up, hold, ramp-down contractions.

Subjects were asked to conduct between three and five controlled isometric ramp-up (5s), hold (3s), ramp-down (5s), F-AB contractions to 60% of MVC. This task was conducted while following visual feedback of the real-time force signal super-imposed on a ramp template, on a computer monitor. In order to record activity from a wider range of the AH motor unit pool, the position of the fine wire electrodes was adjusted slightly after the completion of each trial by gently withdrawing the electrodes by approximately 1mm. Ramp contractions were then repeated, thereby analysing the activity of a separate motor unit. This was conducted 3-5 times for each participant until at least 5 motor units had been collected. Immediately after the completion of the subsequent fatigue task (described below), subjects were asked to complete the same ramp-up, hold, ramp-down contractions that were performed at 60% of the pre-fatigue MVC, following identical procedures.

3.3.5 Fatigue Protocol

Subjects were asked to sustain a constant submaximal force, isometric F-AB contraction of the hallux. A SMU that could be clearly distinguished during the preceding ramp and hold contractions was selected as a target unit for the following fatigue trial. The target force was set at 1.5 times the recruitment threshold for the target unit. Participants were strongly encouraged to maintain the target force until failure, which was defined as when the force recording dropped by more than 5% of the target force trace for a period of more than 5 seconds and could not subsequently return to the target force level (Christie & Kamen, 2009; Vila-Cha *et al.*, 2010). In a number of the fatigue trials additional motor units could be identified and discriminated from the beginning of the fatigue task. For these motor units, the target force did not correspond to 150% of their recruitment thresholds, however given that they could be discriminated for the entire duration of the fatigue task, they were also included the analysis.

3.3.6 Data analysis and statistics

Rate of force production was defined as the slope of the force time data from the onset of force production to the hold phase. Rate of force relaxation was defined as the slope from the end of the hold phase to when the force returned to baseline. The accuracy of the force-tracking task was calculated by subtracting the force signal from the target force trace. The tracking accuracy was defined as the mean RMS value of the residual force signal. This value was calculated for both the force production and relaxation phases of the ramp contractions.

EMG_{IM} signals were decomposed semi-automatically, offline, into trains of individual SMU's, using an interactive software program (EMGLAB, McGill et al., 2005), based in a MATLAB environment (The Mathworks, Nattick, MA, USA) which has been described in detail elsewhere (McGill *et al.*, 2005; Oya *et al.*, 2009). The signal was processed in 0.5 s segments, which were digitally high-pass filtered at 1kHz. When decomposition of a segment was complete, the time window was advanced to the following 0.5s segment. If SMU super-impositions could not be clearly resolved, the adjacent EMG_{IM} channel from the quadrifilar electrodes was decomposed and used to aid in verifying the units involved.

Recruitment of SMUs were determined by moving a 0.5s window of EMG_{IM} signal forward in steps of 1ms until the mean co-efficient of variation (CV) of ISIs within the 0.5s window was less than 50%. Derecruitment was determined in the same manner, but by moving the window backwards from the last segment of the signal (Moritz *et al.*, 2005). Forces corresponding to the calculated first

and last discharge within each 0.5s window were considered as recruitment and derecruitment thresholds, respectively. Recruitment and derecruitment thresholds, discharge rate at recruitment and derecruitment, as well as peak discharge rate were calculated during the ramp-up, hold, ramp-down contractions. The slope of the discharge rate as a function of the F-AB force was also calculated by dividing the amount of increase in the discharge rate by the amount of increase in the force from the recruitment threshold to peak discharge rate (Oya *et al.*, 2009). This process was completed for both pre- and post-fatigue ramp and hold isometric contractions.

During the constant force submaximal isometric fatigue task, mean discharge rate and the CV of ISIs were calculated from 5s epochs at times corresponding to 0, 25, 50, 75 and 100% of contraction duration. The initial time epoch was considered to commence when the force attained the target level and remained stable for 5s.

The ability of the participant to match the rate of force increase and decrease during the ramp up and ramp down phases of the contraction was assessed using a one-way, repeated measures ANOVA. The same test was also applied to compare any differences in accuracy of the force production and relaxation phases. A two-way repeated measures analysis of variance (ANOVA) was performed (discharge behaviour vs. fatigue) to determine within factors effects for discharge behaviour (recruitment / peak / derecruitment discharge rates and recruitment / derecruitment force thresholds) and between factors effects (pre- vs. post-fatigue). Between factors analysis was applied for pre- and post-fatigue comparisons as we could not be certain that the same motor units were being decomposed following the fatigue task. Linear correlations were performed on both pre- and post-fatigue data for the following variables: recruitment threshold, the discharge rate at recruitment, the peak discharge rate and the slope of increase in discharge rate as a function of the force. Correlations were classified as weak, r = 0.1 - 0.3; moderate, r = 0.3 - 0.5; and strong, r > 0.5 (Cohen, 1988). Alterations in mean discharge rate and the CV of ISIs occurring during the fatigue task was evaluated separately using a repeated measures one-way ANOVA.

Sphericity (homogeneity of covariance) was verified by the Mauchly's test. If the assumption of sphericity was not met, the significance of F-ratios were adjusted according to the Greenhouse-Geisser procedure. Pair-wise comparisons, including Bonferroni corrections, were applied as post-hoc analyses. For all analysis, the level of significance was set at $P \leq 0.05$. Effect size (ES) was calculated using partial-eta squared, to determine the magnitude and the practical relevance of the significant findings. Effect sizes were as follows; small ± 0.1-0.3, moderate ± 0.3-0.5, and strong ±

0.5-1.0 (Cohen, 1988). All data is presented as mean ± standard deviation (SD) unless otherwise stated.

3.4 Results

A total of 42 motor units were recorded from the isometric ramp contractions before and immediately after the fatigue task. Additionally, 13 motor units (recorded from five subjects) could be followed for the duration of the fatigue task. Typically between six and eight motor units were collected from each participant during the ramp and hold contractions prior to and following the fatigue task, while one or two motor units were tracked during each fatigue task. Two individuals returned for a second data collection session 7 days after the initial session (see Table 3.1).

3.4.1 Isometric ramp-up, hold, ramp-down contractions

All subjects were able to satisfactorily follow the ramp templates, with force increasing (contraction) at a rate of $7.6 \pm 1.2\%$ MVCs^{-1} and decreasing (relaxation) at a rate of at 8.2 ± 1.0 MVCs^{-1} (P = 0.12, Figure 3.2). However, the ability to accurately track the contraction and relaxation ramps was significantly different, with force relaxation being more difficult. This was shown by mean root mean square (RMS) force residuals over the force relaxation ramp being significantly greater than those during the force development ramp ($3.3 \pm 1.1\%$ MVC versus $2.3 \pm 0.5\%$ MVC, respectively, $P \leq 0.05$, ES = 0.57).

There was no significant difference between the mean recruitment and derecruitment thresholds of the identified motor units ($28.8 \pm 13.1\%$ MVC and $30.4 \pm 11.5\%$ MVC, respectively). Thresholds spanned a range of 10.3% MVC - 54.2% MVC for recruitment and 9.7% MVC - 52.0% MVC for derecruitment, P = 0.25).

Mean motor unit discharge rate at recruitment (6.6 ± 1.8Hz) and derecruitment (6.4 ± 1.1Hz) was not significantly different from each other and ranged from 3.4Hz to 10.5Hz at recruitment and 4.0Hz to 8.6 Hz at derecruitment (P = 0.4). Motor unit discharge rate increased with increasing force and mean peak discharge rate (14.0 ± 2.3Hz) was significantly higher than both recruitment and derecruitment discharge rates ($P \leq 0.05$, ES = 0.86). Peak discharge rates ranged from 10.7Hz - 21.3Hz for the ramp and hold contractions. A moderate positive correlation was evident between recruitment threshold and recruitment discharge rate, with higher threshold motor units discharging at a higher initial rates (r = 0.47, $P \leq 0.05$, Figure 3.3A). There was no correlation between recruitment threshold and peak discharge rate (r = 0.03, P = 0.89 Figure 3.3B). However, a

moderate positive correlation was evident between recruitment discharge rate and the slope of increase in discharge rate as a function of the force (r = 0.35, P ≤ 0.05), indicating that higher threshold motor units attained peak discharge frequency at a faster rate.

Subject	Session #	Motor Unit #	Fatigue target force (%MVC)	Fatigue task duration (s)	Pre-fatigue Recruit threshold (%MVC)	Pre-fatigue Recruit DR (Hz)	Pre-fatigue Peak DR (Hz)
1	1	1	36.5	432.0	24.7	6.9	13.3
1	1	2	36.5	432.0	37.7	8.7	15.6
1	2	3	70.9	97.0	44.3	5.1	11.4
2	1	4	53.1	152.0	35.6	5.5	15.3
2	1	5	53.1	152.0	43.5	5.6	15.6
3	1	6	37.7	212.0	25.5	8.6	12.3
3	1	7	37.7	212.0	29.6	10.5	12.6
3	2	8	27.7	178.0	18.3	5.8	13.2
3	2	9	27.7	178.0	12.8	5.3	11.8
4	1	10	31.5	215.0	18.6	3.4	16.0
4	1	11	31.5	215.0	24.2	4.6	16.3
5	1	12	32.1	345.0	40.0	8.3	18.4
5	1	13	32.1	345.0	19.4	5.8	16.1

Table 3.1. Data for individual motor units decomposed during the fatigue task, including the subject and session from which each motor unit was recorded, as well as the duration and intensity of the task. Motor units correspond to those presented in figure 4. MVC - maximal voluntary contraction, DR - discharge rates.
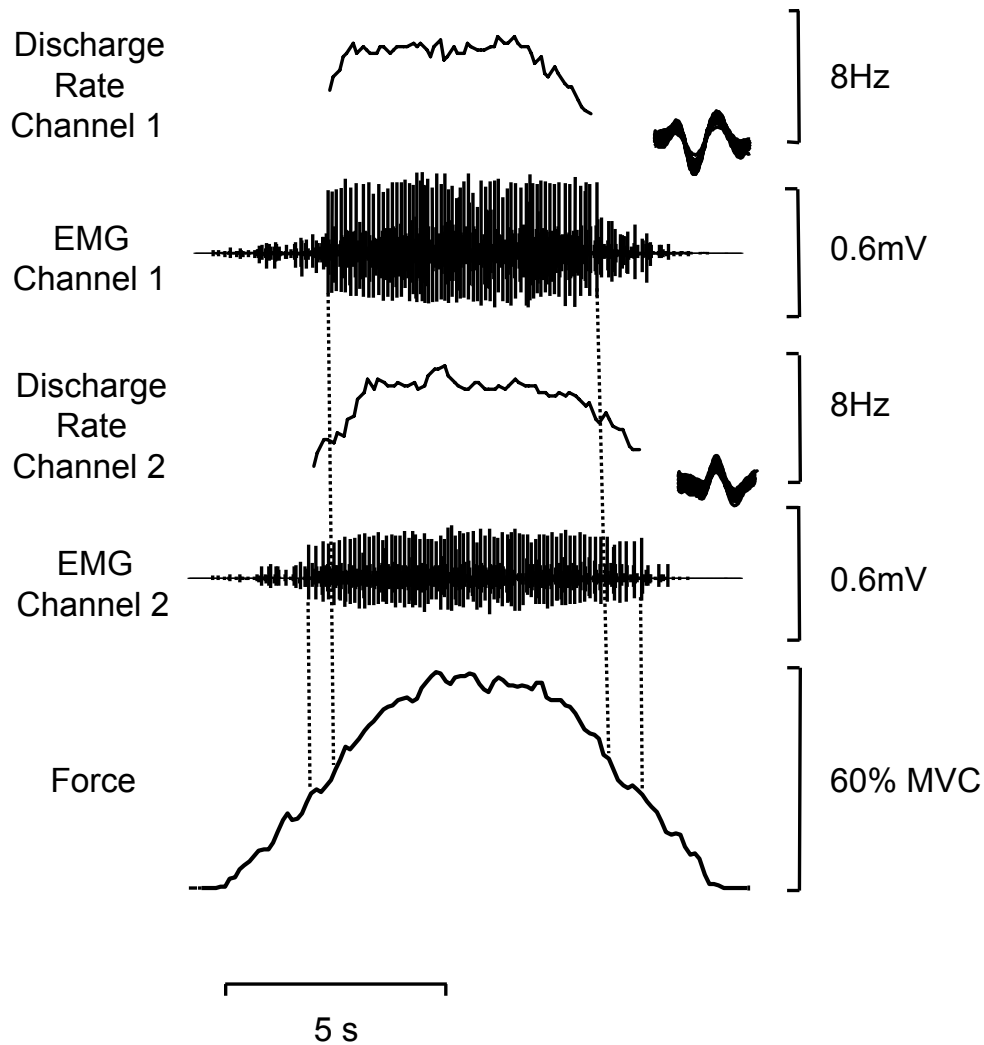
Figure 3.2. A representative recording of a ramp up, hold, ramp down contraction showing force (bottom trace) and two channels of intramuscular electromyography (EMG) from a quadrifilar fine wire electrode inserted into abductor hallucis (second and forth trace from the top). Single motor units were discriminated from the EMG signals and their instantaneous discharge rate is shown above each respective EMG trace. The motor unit recorded from intramuscular EMG Channel 1 is recruited at 27.2% MVC at a discharge rate of 8.8Hz, while the motor unit recorded from intramuscular EMG Channel 2 is recruited at 18.6% MVC at a discharge rate of 6.0Hz. Both motor units increase to similar peak discharge rates (13.1Hz and 13.9 Hz, respectively). Derecruitment occurs at 27.0% MVC for both motor units, with discharge rates of 6.9Hz and 7.6Hz, respectively. MVC, maximal voluntary contraction.
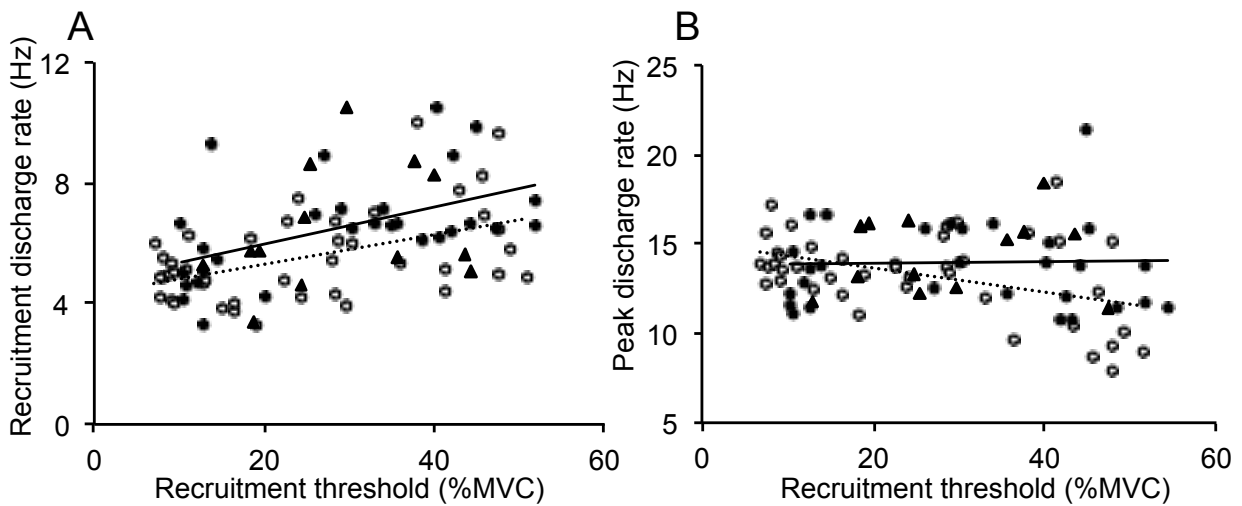
Figure 3.3. (A) Moderate positive linear correlation between recruitment threshold and discharge rate at recruitment for ramp and hold contractions prior to (filled circles, n=42 units, r = 0.45, P ≤ 0.05) and following (open circles, n=42, r =0.47, P ≤ 0.05) the fatigue task. (B) No significant correlation was observed between recruitment threshold and peak discharge rate prior to the fatigue task (filled circles, r = 0.03, P = 0.89). Following the fatigue task a negative correlation was evident between recruitment threshold and peak discharge rate (open circles, r = -0.43, P ≤ 0.05). MVC, maximal voluntary contraction.

3.4.2 Fatigue task

The submaximal fatigue task was performed at a mean force level of 41.3 ± 15.3% MVC (range 27.7% MVC – 70.9% MVC, Table 3.1), which resulted in mean task duration of 233 ± 116.2s (range 97s – 432s). An increase in neural drive was indicated by the recruitment of new motor units in all of the fatigue trials, with eight additional motor units being detected by our electrodes. Recruitment of new motor units was not limited to the end of the fatigue task with additional recruitment observed from 20% of task duration. However most additional motor units discharged in periodic bursts, thus only motor units that could be identified and followed for the entire duration of the task were analysed. Mean discharge rates and CVs of the ISIs are shown in Figure 3.4. Mean motor unit mean discharge rate significantly decreased from 75% to 100% of task duration (P ≤ 0.05, ES = 0.72). Variability of the firing rate, as measured by CV of the ISI, was stable over the first 50% of the fatigue task and increased significantly during the final 25% of the fatigue task (P ≤ 0.05, ES = 0.71).
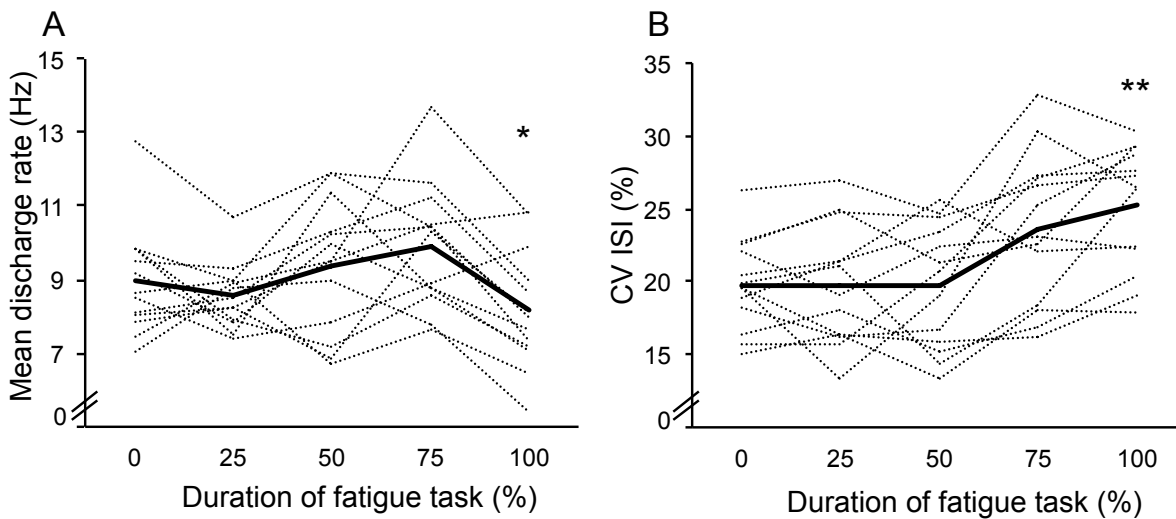
Figure 3.4. Mean (solid line) and the corresponding 13 individual motor unit responses (broken lines) for (A) discharge rate (B) and co-efficient of variation (CV) of the inter-spike interval (ISI), calculated during a submaximal contraction to task failure. * indicates a significant decrease in mean discharge rate over the last 25% of the fatigue task ($P \leq 0.05$). ** indicates a significant increase in CV of ISIs over the last 25% of the fatigue task ($P \leq 0.05$).

3.4.3 Isometric ramp-up, hold, ramp-down contractions following the fatigue task

Maximal voluntary force producing capacity declined to 73.6 ± 4.2% of pre-fatigue MVC value ($P \leq 0.05$, ES = 0.91). Mean recruitment (25.2 ± 14.6 % MVC) and derecruitment (25.7 ± 13.3 % MVC) thresholds during the ramp and hold contractions performed immediately after the fatigue trial were not significantly different to each other (range 8.3 – 51.3% MVC and 6.8 – 52.0% MVC, respectively, P = 0.25). These threshold values were not significantly different to the same measures made over the same type of contraction protocol prior to performing the fatigue task (P = 0.25).

Mean discharge rates at recruitment and derecruitment (5.8 ± 1.5Hz and 6.3 ± 1.7Hz, respectively) for ramp and hold contractions after the fatigue task were not significantly different from each other (range 3.2Hz - 10.1Hz and 4.1Hz - 10.7Hz respectively, P = 0.4). There was also no difference between these values and the pre-fatigue task recruitment and derecruitment discharge rates (P = 0.4). Mean peak discharge rate (13.3 ± 2.3Hz) remained unchanged after the fatigue trial (post fatigue range 7.8Hz - 18.5Hz, P = 0.12) and was significantly higher than recruitment and derecruitment discharge rates (both P ≤ 0.05). A moderate positive linear correlation was still evident between recruitment threshold and recruitment discharge rate during this task (r = 0.47, P ≤

0.05, Fig 3.3A). A moderate negative linear correlation existed between peak discharge rate and recruitment force threshold for ramp and hold contractions after the fatigue task, with higher threshold motor units discharging at slower peak rates after completion of the fatigue trial (r = -0.43, P ≤ 0.05, Fig 3.3B).

3.5 Discussion

We describe the recruitment and discharge characteristics of motor units in AH, a muscle with a postural function (Kelly *et al.*, 2012) which also possesses a low number of motor units (Johns & Fuglevand, 2011). Similarly to other postural muscles (Macefield *et al.*, 2000; Oya *et al.*, 2009; Dalton *et al.*, 2009) motor units in AH displayed low peak discharge rates and were resistant to fatigue. The anatomical configuration of a low number of motor units, relative to PCSA (Johns & Fuglevand, 2011) that are also fatigue resistant, may allow this muscle to generate and sustain moderate to large amounts of force for prolonged periods of time, in order to provide postural support for the foot.

Recruitment threshold and discharge characteristics

In the current study we did not observe any difference between recruitment and derecruitment thresholds, or discharge rates at recruitment and derecruitment for AH motor units. While similar findings have been reported previously (Oya *et al.*, 2009; Jesunathadas *et al.*, 2010) during isometric ramp up-down contractions, derecruitment generally occurs at higher force levels and at lower discharge rates (Adam, 2005; Moritz *et al.*, 2005; Riley *et al.*, 2008*b*; Oya *et al.*, 2009). It is suggested that this is due to the amplifying effects of persistent inward currents (PIC) (Gorassini *et al.*, 2002; Heckman *et al.*, 2008) as well as late adaptation of the motoneurone . Our finding may indicate that similar to another lower limb postural muscle, the soleus (Oya *et al.*, 2009) the effects of PICs and late adaptation are minimal within AH. However, an alternative explanation for the lack of difference between recruitment and derecruitment thresholds, or discharge rates at recruitment and derecruitment, relates to the accuracy of force development and relaxation in the ramp-up and ramp-down phases of the isometric contractions. In our study, despite extensive task familiarization, the accuracy of force tracking during force production was significantly greater than that during force relaxation. Thus, it is possible that a less accurate relaxation of force may have influenced both the threshold and discharge rate at derecruitment.

Discharge rate at recruitment was positively associated with recruitment threshold over the range of force tested. This result is in contrast to the "onion skin" hypothesis, which describes lower threshold motor units discharging at higher initial and peak discharge rates in muscles such as

vastus lateralis and tibialis anterior (Erim *et al.*, 1996; Adam, 2003; De Luca & Hostage, 2010). However, the positive correlation between recruitment threshold and recruitment discharge rate has previously been demonstrated in other muscles such as soleus (Oya *et al.*, 2009), muscles of the hand (Moritz *et al.*, 2005), biceps brachii (Riley *et al.*, 2008*a*) and adductor pollicis (Kukulka & Clamann, 1981). The finding that lower threshold motor units discharge at lower initial rates fits with the theoretical organizational properties of a motoneurone pool, as these motor units possess longer contraction and half relaxation times (Bakels & Kernell, 1993; Kernell *et al.*, 1999) and would therefore summate and fuse at lower firing rates compared to higher threshold units with shorter contraction and half relaxation times (Grimby *et al.*, 1979). It is has been hypothesised previously that this level of organization helps to achieve efficient gradation of force across a wide variety of contraction strengths (Moritz *et al.*, 2005; Oya *et al.*, 2009).

Peak Discharge rate

The peak discharge rates reported in our study are at the lower end of the range of peak discharge rates (between 10 to 25Hz) described in other lower limb muscles (Connelly *et al.*, 1999; Roos *et al.*, 1999; Dalton *et al.*, 2009) during isometric contractions at similar contraction intensities. Our observed low peak discharge rates may be related to the postural function of this muscle (Kelly *et al.*, 2012), as some postural muscles are known to discharge at relatively low rates (Oya *et al.*, 2009; Dalton *et al.*, 2009) for sustained periods in order to resist gravitational forces and maintain upright posture (Sherrington, 1915).

Previous studies have reported both positive (Gydikov & Kosarov, 1974; Moritz *et al.*, 2005; Oya *et al.*, 2009) and negative (De Luca & Hostage, 2010; Stock *et al.*, 2012) linear relationships between recruitment threshold and peak discharge rate. However in AH we found no relationship between peak discharge rate and recruitment threshold, with all motor units converging to similar peak discharge rates, regardless of recruitment threshold. When considering this finding, it must be recognized that we have only recorded data from contractions up to 60% of MVC. Thus it is possible that our latter recruited motor units may have eventually attained higher discharge rates, if the contraction force was increased to levels beyond 60% MVC. Our finding that higher threshold motor units obtained peak discharge rate more rapidly supports this suggestion. Regardless, the relatively small increase in discharge rate after recruitment for all motor units, suggests that rate coding as a method of force gradation may be somewhat limited in AH. Thus recruitment may be the dominant factor in force generation (De Luca *et al.*, 1982; Bellemare *et al.*, 1983), despite the fact that AH has relatively few motor units (Johns & Fuglevand, 2011). This suggestion is further supported by the continued recruitment of motor units during the fatigue task, despite a minimal

change in discharge rate. Due to its postural function, AH is required to generate and sustain relatively large forces to support bodyweight. The organization of a low number of large motor units relative to its PCSA may allow for generation of substantial forces, whilst maintaining fatigue resistance (Gordon *et al.*, 1990; Sirca *et al.*, 1990).

Motor Unit discharge properties during the fatigue task

During the fatigue task an increase in central drive to the motoneurone pool was evidenced by recruitment of eight additional motor units. Despite this increase in central drive, only two of these motor units displayed an increase in discharge rate during the fatigue task. During the final 25% of the task we observed a decrease in motor unit discharge rate in 11 of the 13 motor units. This anomalous decrease in SMU discharge rate observed concurrently with an increase in central drive has been observed previously in upper (Carpentier *et al.*, 2001; Mottram, 2004; Riley *et al.*, 2008*a*) and lower (Kuchinad *et al.*, 2004; Christie & Kamen, 2009; Dalton *et al.*, 2010) limb muscles and is possibly due to reduced spinal motoneurone responsiveness, which impairs the ability to integrate increased cortical input (McNeil *et al.*, 2011*a*; 2011*b*). Reduced spinal motoneurone responsiveness may occur as a result of intrinsic motoneurone adaptation (due to repetitive discharge) (Kernell & Monster, 1982; McNeil *et al.*, 2011*b*) and reflex inhibition by Group III and IV afferents (Rotto & Kaufman, 1988). We must also recognize motor units recruited during the later stages of the fatigue may have actually increased their discharge rates, in order to compensate for the decrease in discharge rate of the existing motor units. Regardless, it is worthy to note that AH motor units were able to maintain moderate to high levels of force (40% MVC for 233 s) for similar periods and intensities (40-60% MVC for 292 s) (Kuchinad *et al.*, 2004) to the fatigue resistant soleus and for considerably longer than the biceps brachii (17% MVC for 117 s) (Riley *et al.*, 2008*a*).

Despite increasing central drive, discharge rate variability also remained relatively unchanged until late in the fatigue contraction, when it was observed to increase significantly in the final 25% of the task. Discharge variability arises as a result of fluctuations in synaptic noise due to an increase in both excitatory and inhibitory input (Berg *et al.*, 2008), causing variability in the motoneurone membrane potential (Calvin & Stevens, 1968). Our findings that both discharge rate and discharge rate variability of AH motor units remains relatively stable until just prior to task failure, indicates that AH is able to sustain a relatively constant and moderate output for prolonged periods. It appears that it is only in the late phase of a sustained contraction that significant alterations in synaptic input and intrinsic motoneurone properties occur, disturbing the balance of repetitive discharges.

Maximal voluntary force production was reduced by 27% following the fatigue tasks. However, recruitment thresholds of the recorded units during ramp and hold contractions following the fatigue task were not significantly different from those pre-fatigue. Our finding of no change in recruitment thresholds following the fatigue task suggests that additional motor units, other than those detected by our fine wire electrodes may have been recruited in order to generate 60% of pre-fatigue MVC (equivalent to 83% post-fatigue MVC). However this suggestion cannot be quantified in the current study, as we have not collected surface EMG data. Regardless, the 27% decline in MVC following a sustained moderate to high intensity fatigue task is similar to that of the fatigue resistant soleus (Kuchinad *et al.*, 2004), highlighting the fatigue resistance properties of this muscle.

Following the fatigue trial we observed a moderate negative correlation between recruitment threshold and peak discharge rate. This relationship was not evident prior to the fatigue task, when all motor units attained similar peak discharge rates, thus indicating a fatigue related alteration in the discharge behaviour of higher threshold motor units. The divergence in discharge behaviour between lower and higher threshold motor units may be explained by the fact that higher threshold motor units generally innervate faster twitch muscle fibres, which are less fatigue resistant (Bakels & Kernell, 1993).

3.6 Conclusion

We have described the discharge characteristics of motor units from AH, a postural muscle in the foot that is known to have relatively few motor units. This muscle is comparatively fatigue resistant and appears to rely predominantly on recruitment to generate force, optimizing the use of slow twitch, fatigue resistant fibres to generate moderate to large amounts of force for sustained periods of time.

3.7 Acknowledgements

3.8 Disclosures

The authors have no conflict of interest to report.

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CHAPTER FOUR – INTRINSIC FOOT MUSCLES HAVE THE CAPACITY TO CONTROL DEFORMATION OF THE LONGITUDIUNAL ARCH

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4.1 Summary

The human foot is characterised by a pronounced longitudinal arch that compresses and recoils in response to external load during locomotion, allowing for storage and return of elastic energy within the passive structures of the arch, contributing to metabolic energy savings. Here we examine the potential for active muscular contribution to the biomechanics of arch deformation and recoil, testing the hypotheses that activation of the three largest plantar intrinsic foot muscles, abductor hallucis, flexor digitorum and quadratus plantae is associated with muscle stretch in response to external load on the foot and that activation of these muscles (via electrical stimulation) will generate sufficient force to counter the deformation of longitudinal arch caused by the external load. We found that recruitment of the intrinsic foot muscles increased with increasing load, beyond specific load thresholds. Interestingly, LA deformation and muscle stretch plateaued towards the maximum load of 150% body weight, when muscle activity was greatest. Electrical stimulation of the plantar intrinsic muscles countered the deformation that occurred due to the application of external load by reducing the length and increasing the height of the LA. These findings

demonstrate that these muscles have the capacity to control foot posture and LA stiffness and may provide a buttressing effect during foot loading. This active arch stiffening mechanism may have important implications for how forces are transmitted during locomotion and postural activities as well as consequences for metabolic energy saving.

4.2 Introduction

The human foot is a flexible structure, capable of conforming to variations in surface and load to maintain effective force transmission between the lower limb and the ground. This functionality is achieved via an intricate interaction of movements occurring in a series of small joints, which allows the longitudinal arch (LA) to lengthen and lower during stance (Leardini *et al.*, 2007) and absorb loading forces as elastic strain energy (Ker *et al.*, 1987; Erdemir *et al.*, 2004). Later in the stance phase, passive elastic recoil of the plantar aponeurosis contributes to positive work generation for propulsion, aided by the windlass mechanism, which effectively stiffens the LA during toe extension (Hicks, 1954; Ker *et al.*, 1987; Erdemir *et al.*, 2004). This process allows for a highly efficient bipedal gait that is unique to humans (Vereecke & Aerts, 2008).

The plantar aponeurosis along with the windlass mechanism are considered the key contributors to foot stiffness during human gait (Hicks, 1954; Ker *et al.*, 1987). It is proposed that extension of the toes in mid- to late-stance, creates increased tension in the plantar aponeurosis, resulting in shortening of the LA via flexion and adduction of the metatarsals in combination with supination of the rear-foot (Hicks, 1954; Caravaggi *et al.*, 2009). These alterations in bony alignment act to stiffen the foot and transform it from a compliant attenuator to a rigid lever, allowing ankle plantar flexor torque to be efficiently transmitted to the ground (Donatelli, 1985). Recent studies investigating the biomechanics of LA deformation during locomotion have confirmed that the plantar aponeurosis has a critical influence on the stiffness of the LA (Caravaggi *et al.*, 2009; 2010). However these studies (Caravaggi *et al.*, 2010) and others by Pataky *et al* (Pataky *et al.*, 2008) and Bates *et al* (Bates *et al.*, 2013) have also highlighted the potential contribution of an active stiffening mechanism, possibly produced by muscles such as the plantar intrinsic foot muscles.

The plantar intrinsic foot muscles possess origins and insertions that are contained within the foot with the three largest muscles, abductor hallucis (AH), flexor digitorum brevis (FDB) and quadratus plantae (QP), having muscle-tendon units that span the length of the LA (Kura *et al.*, 1997; Ledoux *et al.*, 2001; Tosovic *et al.*, 2012). The function of these muscles during stance and gait has been the subject of speculation for many years and remains an area of intense interest. Anatomy texts describe these muscles as accessory toe flexors, which may also aid in forefoot stabilization during the push-off phase of gait (Thibodeau & Patton, 2007). It appears however, that a disparity exists between the mechanical action proposed by textbooks and the electromyography (EMG) profiles described in the literature. Early EMG studies suggest these muscles may play a role in stabilization of the LA, with muscle recruitment occurring in response to increased loading (Basmajian & Stecko, 1963; Mann & Inman, 1964). Further supporting this hypothesis, individuals with a lower LA height in stance (i.e., greater LA deformation) were shown to display greater levels of intrinsic muscle activity (Gray & Basmajian, 1968). Recent studies from our own laboratory using intra-muscular EMG have reported that the plantar intrinsic muscles act in a synchronous manner to provide postural support for the foot, with activation amplitude and timing being correlated with postural task difficulty and medial postural sway, respectively (Kelly *et al.*, 2012).

Despite some evidence suggesting that the plantar intrinsic foot muscles may actively contribute to regulation of foot stiffness during stance and gait (Pataky *et al.*, 2008; Caravaggi *et al.*, 2010), the specific mechanical functions of these muscles are yet to be described. It is also unknown whether these small muscles are able to generate enough force to produce a significant alteration in foot biomechanics under loaded conditions, in order to influence LA biomechanics. Here we tested two hypotheses, firstly, that the LA would deform under increasing load, producing stretch of the plantar intrinsic foot muscles (AH, FDB and QP) and an increase in involuntary activity. Secondly, we tested the hypothesis that these same muscles are capable of generating sufficient forces to attenuate LA deformation produced by the load, effectively increasing LA stiffness. Activation of these muscles with load and their ability to generate sufficient force to counter LA deformation may have important implications for how the foot can absorb and generate energy during gait.

4.3 Methods

4.3.1 Participants

Nine healthy males with no history of neuromuscular disorder or lower limb injury in the previous six months volunteered to participate in the study (mean ± standard deviation (SD) for age, height and body mass were 30 ± 4yrs, 179 ± 7cm and 80 ± 6kg, respectively). All participants were

informed of the study requirements, benefits and risks before giving written informed consent. The procedures were approved by the local scientific ethics committee and performed according to the Declaration of Helsinki. Two discrete experiments with similar experimental setups were performed on the same group of participants during the one test session, in order to address our two hypotheses.

4.3.2 Experiment 1 – Foot loading

The aim of this experiment was to examine the relationship between mechanical loading of the foot and both deformation of the foot and also muscle activity of the intrinsic foot muscles (AH, FDB and QP). Loads were incrementally applied to the thigh via a loading rig described in detail below (Figure 4.1). Loads ranged from 0% body mass to 150% body mass with 25% increments. A period of approximately 5-s was maintained at each loading increment, during which time intramuscular EMG, kinematic and force plate data were recorded. Subjects were advised to remain still and refrain from any voluntary movement throughout the trial.
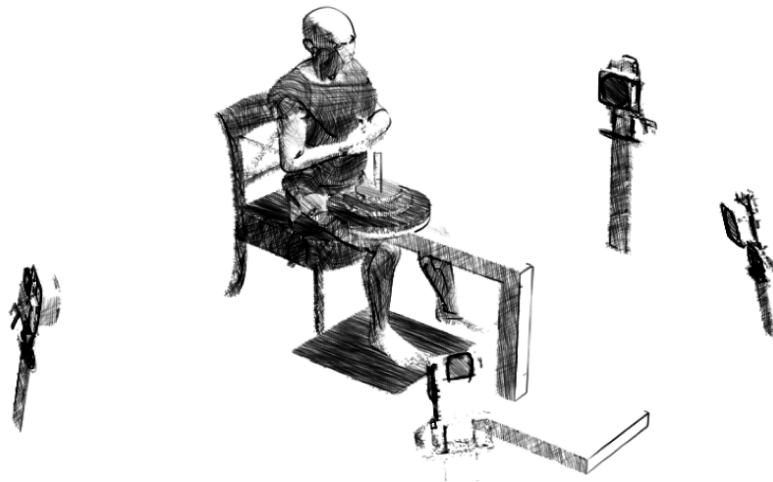
Figure 4.1. Experimental set up. Foot motion, ground reaction forces and intramuscular electromyography were recorded during incremental loading (Experiment one) and independent electrically evoked contractions of the three major plantar intrinsic foot muscles (Experiment two). Loads ranging from 0-150% of body mass were added to a loading device, which was secured to the distal aspect of the participants right thigh. The participant's foot was placed on the centre of a force plate and four motion analysis cameras were positioned to record three-dimensional motion of the shank and two individual foot segments during each task.

4.3.3 Experiment 2 - Electrically evoked muscle contractions

The aim of this experiment was to determine the mechanical response of the foot to stimulation of the individual intrinsic foot muscles (AH, FDB and QP) under different loading conditions. Loads corresponding to 50% and 100% of body mass were applied using the same loading rig described above while the each individual muscle was electrically stimulated. One experimental trial consisted of three electrically evoked contractions, each separated by 15s, for each muscle. The trial was completed for each of the three muscles under the two loading conditions, which were undertaken in a randomized in order. As such, a total of 6 trials were completed for each participant.

4.3.4 General experimental setup

Each participant was seated with their right foot placed flat on a marked area in the centre of a force plate (Kistler 9286A, Zurich, Switzerland). The shank was positioned at approximately 10 degrees of flexion (relative to vertical) with the femur positioned parallel to the floor. Loads of up to 150% of body mass could be applied to the distal aspect of thigh using a custom built rig (Figure 4.1) so that the vertical force was located slightly anterior to the ankle joint axis, similar to where it occurs during quiet standing (Tokuno *et al.*, 2007).

4.3.5 Data Collection

Muscle activation and stimulation

Paired, fine wire, intramuscular electrodes (0.051mm stainless steel, Teflon coated, Chalgren, USA) were inserted into both the proximal and distal ends of the AH, FDB and QP muscles in the right foot (Figure 4.2) of each subject using delivery needles (0.5mm x 50mm) under B-mode ultrasound guidance (12MHz, 38mm linear array, Siemens Acuson Antares, USA)(Kelly *et al.*, 2012). After removal of the delivery needles, the muscles were imaged once more to determine that the ends of the fine wire electrodes remained within the relevant muscle after needle removal. The most proximal pair of fine wire electrodes was used for measuring EMG activity during foot loading (Experiment 1 only). The electrodes had a detection length of 2 mm and were separated by approximately 2 mm. A surface ground electrode was attached to the medial malleolus of the right ankle and secured with adhesive tape. All signals were amplified 1000 times, band-pass filtered from 30Hz to 1kHz (Delsys Bagnoli, Boston, USA) and subsequently analogue to digitally converted (Power 1401, Cambridge Electronic Design, Cambridge, UK) at a sampling rate of

10kHz and collected using Spike2 software (Cambridge Electronic Design, Cambridge, UK). All data was manually inspected to ensure that muscle electrical activity could be clearly distinguished from that of background noise or artefact. In the case where recordings were contaminated by artefact, or muscle electrical activity appeared absent, the location of the fine wire electrodes were slightly adjusted and the loading task was repeated. If clear signals could not be obtained following this procedure, the data from that individual was excluded from further analysis.
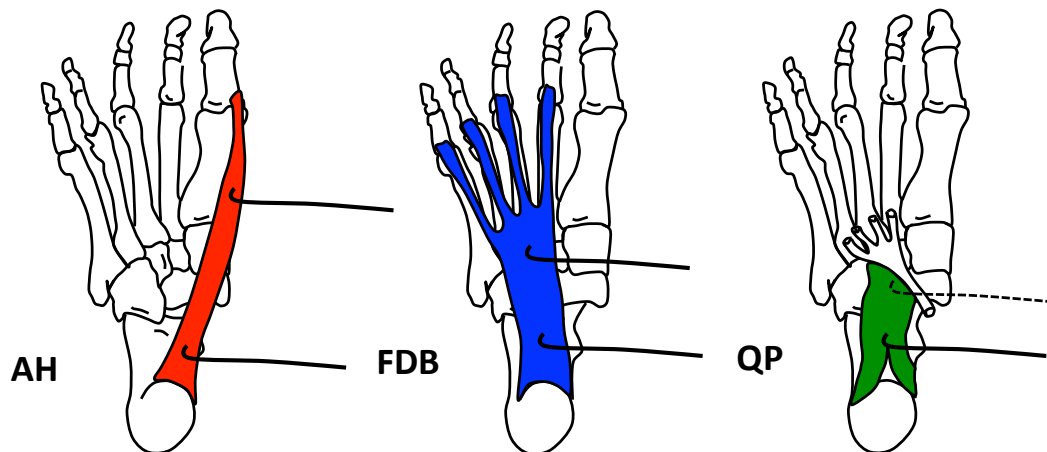
Figure 4.2. Location of electrodes within the intrinsic foot muscles. Schematic depiction of the anatomical location of abductor hallucis (AH), flexor digitorum brevis (FDB) and quadratus plantae (QP) from the plantar aspect of a right foot. Fine wire pairs of electromyography (EMG) electrodes (black lines with hooked ends) were inserted under ultrasound guidance, with one pair being inserted proximally and one pair distally to the muscle belly. The proximal electrode pair was used for the EMG recordings in Experiment 1, while one wire from each of the proximal and distal pairs were connected to a constant current electrical stimulator, which delivered trains of electrical stimulation to each muscle independently in Experiment 2.

For experiment 2, a constant current electrical stimulator (Digitimer DS7AH, Digitmer, Herfordshire, UK) was connected to one of each pair of intra-muscular electrodes with the cathode connected to the proximal electrode and anode to the distal electrode. The electrical stimulator was programmed using Spike 2 software (Cambridge Electronic Design, Cambridge, UK) to deliver trains of current pulses (400V, 20 rectangular pulses, 10µs pulse width, 40 Hz frequency) across the motor point of the muscle. A submaximal level of stimulating current was determined prior to data collection by delivering a train of pulses commencing at 1mA and increasing incrementally by 1mA until a mechanical response was observed as a minimum change of 10N in the vertical ground reaction force. The 10N vertical force threshold was chosen so as to elicit a clear mechanical response while minimizing subject discomfort. The above task was undertaken with a mass of 20kg

applied to the thigh using the loading rig, in order to ensure consistent foot position on the force plate during the stimulations. Mean stimulation intensities were $6 \pm 1mA$ for all muscles.

Foot motion and force measurements

Three-dimensional (3D) motion-capture and force plate data were collected in order to quantify the magnitude and direction of the biomechanical responses due to loading and/or muscle stimulation. Fourteen retro-reflective markers (diameter 9.0 mm) were placed on the skin of the right foot and ankle according to a multi-segment foot model developed to describe rear-, mid- and fore-foot motion (Leardini *et al.*, 2007) (Figure 4.3). This model (Leardini *et al.*, 2007) has been designed to describe motion of the LA and has been shown to have a high inter and intra-tester repeatability healthy adults (Caravaggi *et al.*, 2011). Marker trajectory and force data were collected synchronously at 200Hz using a four camera motion-capture system (Vicon MX, Vicon motion systems, Oxford, UK) and the previously described force platform. All marker trajectories and force plate data were processed using Visual 3D (C-Motion Inc., Germantown, USA) with the marker trajectories filtered using a 6Hz, low pass, fourth order Butterworth filter. Assumed rigid segments were created according to the previously described multi segment foot model (Leardini *et al.*, 2007) including the calcaneus, mid-foot and metatarsals.

Figure 4.3. Retroflective skin marker locations. Retro-reflective skin markers were applied to the right foot of each subject in order to create a multi-segment foot model. Views from the anterior (top), medial (middle) and lateral (bottom) aspects of the right foot. Markers are attached to rigid plastic disks and are secured to the skin with double-sided adhesive tape.

4.3.6 Data analysis

Muscle activation

Root mean square (RMS) signal amplitude of the EMG data was calculated over the middle 3-s epoch of each 5-s loading increment in experiment 1. RMS amplitudes were normalised to the maximal occurring RMS amplitude recorded over a 1-s epoch for each muscle across all loading trials.

Arch deformation and muscle lengths

The LA height was defined from the 3D-motion data as the vertical height of the navicular marker from the floor (Nielsen *et al.*, 2009; Hageman *et al.*, 2011). LA length was defined as the straight-line distance between the markers located on the medial calcaneus and the head of the first metatarsal.

For experiment 1 LA height and MTU lengths were calculated over the same 3-s epochs as the EMG data, corresponding to each 25% loading increment. These values were normalised to the values recorded prior to any loading being applied to the rig. Thus LA length and height and MTU length were expressed as changes relative to the unloaded posture.

For experiment 2, LA length and height prior to electrical stimulation (loading condition) and that occurring during stimulation (stimulated condition) were calculated for each loading condition (50% and 100% body mass). The peak values for the three stimulations recorded during each trial were averaged for each condition and normalized to the LA length and height recorded prior to the application of any load to determine the effect of load and stimulation.

Muscle tendon unit (MTU) lengths for AH, FDB and QP were determined based on a geometrical model according to the multi-segment 3D-motion data, by defining virtual markers corresponding to the origin, tether and insertion points for AH and FDB, in accordance with previous cadaveric descriptions for these muscles (Kura *et al.*, 1997; Ledoux *et al.*, 2001; Tosovic *et al.*, 2012). Origin, tether and insertion points were expressed as fixed locations on the bony segment to which they were attached, allowing estimation of changes in MTU length according to the motion of the rigid foot segments. A tether point (a point that the line of action of the muscle is constrained to pass through) was created for the AH muscle to represent the fascial encapsulation of this muscle that occurs posterior to the navicular bone, extending from the deltoid ligament (Wong, 2007). This encapsulation serves as a pulley, changing the anatomical pathway for this muscle. Each MTU length was defined as the straight-line distance from the origin to the insertion, via any tether points.

In order to provide detailed insight to the contribution of individual foot segments to the biomechanics of the longitudinal arch due to the application of load and muscle stimulation, segment angles for the calcaneus and metatarsals were calculated in the sagittal, frontal and transverse planes (experiment 2 only). Angular rotations of these segments were defined relative to the laboratory co-ordinate system (+x-lateral, +y-anterior, +z-up) and according to an x-y-z cardan sequence of rotations ie. rotation about the x-axis - sagittal plane motion; rotation about the y-axis –

frontal plane motion; rotation about the z-axis – transverse plane motion. For the purpose of aligning our findings with previous cadaveric and in-vivo data, we termed rotation about the x-axis as extension (positive) and flexion, rotation about the y-axis as inversion (positive) and eversion, and z-axis rotations as adduction (positive) and abduction. Segment angles were normalised to unloaded segment angles that were recorded in the experimental position prior to the application of load, so that zero degrees about all axes represented the segment angle when the foot was unloaded. For each participant, mean angular rotations were calculated within the sagittal, frontal, and transverse planes by creating an average of the angular path associated with the three stimulations in each task across a 2-s window from the onset of stimulation and continuing for 1.5 s following the cessation of the stimulation train. Joint angles were normalized and calculated for loading and stimulation conditions by applying the same method described for LA length and height.

Force measurements

Vertical ground reaction force (Fz) and centre of pressure (COP) in the antero-posterior (COP_{AP}) and medio-lateral (COP_{ML}) directions were calculated from the ground reaction force and moment data which were low pass-filtered with a fourth order 6Hz Butterworth filter. During experiment two, the COP position and Fz values were calculated prior to and the peak value occurring during muscle stimulation. Centre of pressure and Fz values were averaged over the three stimulations for each muscle and condition using the same procedure described for the kinematic data.

4.3.7 Statistics

Group means for LA height, MTU length and EMG RMS activity were calculated at each loading increment in order to describe how these variables change as loading increased (Experiment 1). A two-way repeated measures ANOVA was used to determine the effect of loading (50% versus 100% body mass) and muscle stimulation on LA length, LA height, segment angles, COP and Fz for AH, FDB, and QP muscles (Experiment 2). Multiple comparison tests including Bonferroni corrections were applied as post-hoc analysis between conditions when significant main effects were reported. Statistical differences were established at $P \leq 0.05$. Results are presented as mean ± standard error unless otherwise stated.

4.4 Results

4.4.1 Experiment 1 – Response to loading

Intramuscular EMG data for the AH and FDB muscles was obtained from all nine participants, however QP data was only obtained from five participants due poor signal to noise quality. Mean unloaded lengths for the AH, FDB and QP MTU's were 168.8 ± 6.9mm, 153.3 ± 4.5mm and 65.5 ± 3.9mm respectively.

The relationship between the external load applied to the leg and foot, and i) change in LA height, ii) change in AH, FDB and QP length and iii) AH, FDB and QP normalised EMG RMS activity are shown in Figure 4.4. With an increase in load there was a reduction in LA height and a subsequent stretch in the MTU's of AH, FDB and QP. The load under which muscle activity could first be detected, or load threshold, was different for each muscle. Despite MTU lengthening, muscle activity was first evident when loading reached 50, 75 and 100 % of body mass for FDB, QP and AH respectively. Beyond these individual muscle thresholds there was a progressive increase in activation with increasing load for all muscles. Longitudinal arch height and the lengths of the AH, FDB and QP MTU's appeared to plateau around 125% body mass, while muscle activation continued to increase up to the highest load tested (150% body mass).
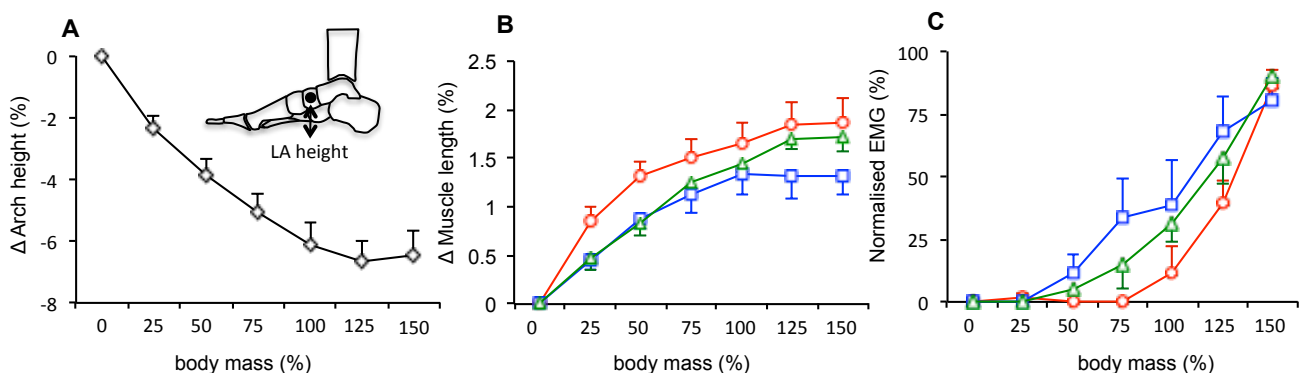
Figure 4.4. Group means ± standard deviation for (A) change in longitudinal arch (LA) height, (B) change in muscle tendon unit length and (C) normalized electromyographic (EMG) root mean square (RMS) plotted as a function of load applied to the thigh during the incremental loading task. For each participant, muscle length and arch height were normalised to the resting unloaded values. The EMG RMS amplitude was normalised to the maximal value recorded during the 150% body mass trial. Open circles (red) represent abductor hallucis, open squares (blue) represent flexor digitorum brevis and open triangles (green) represent quadratus plantae muscle.

4.4.2 Experiment 2 – Response to stimulation

Mean unloaded LA length and height were 156.7 ± 18.2mm and 53.5 ± 4.7mm respectively. The height and length of the LA was significantly influenced by loading and muscle stimulation for all muscles (all P ≤ 0.05). The LA was significantly longer and lower when loaded with 100%, compared to 50% body mass (P ≤ 0.05, Figure 5). Individual stimulation of AH, FDB and QP muscles countered the LA deformation produced by the load, by reducing the length and increasing the height of the LA when loaded with both 50% and 100% body mass (all P ≤ 0.05, Figure 4.5).
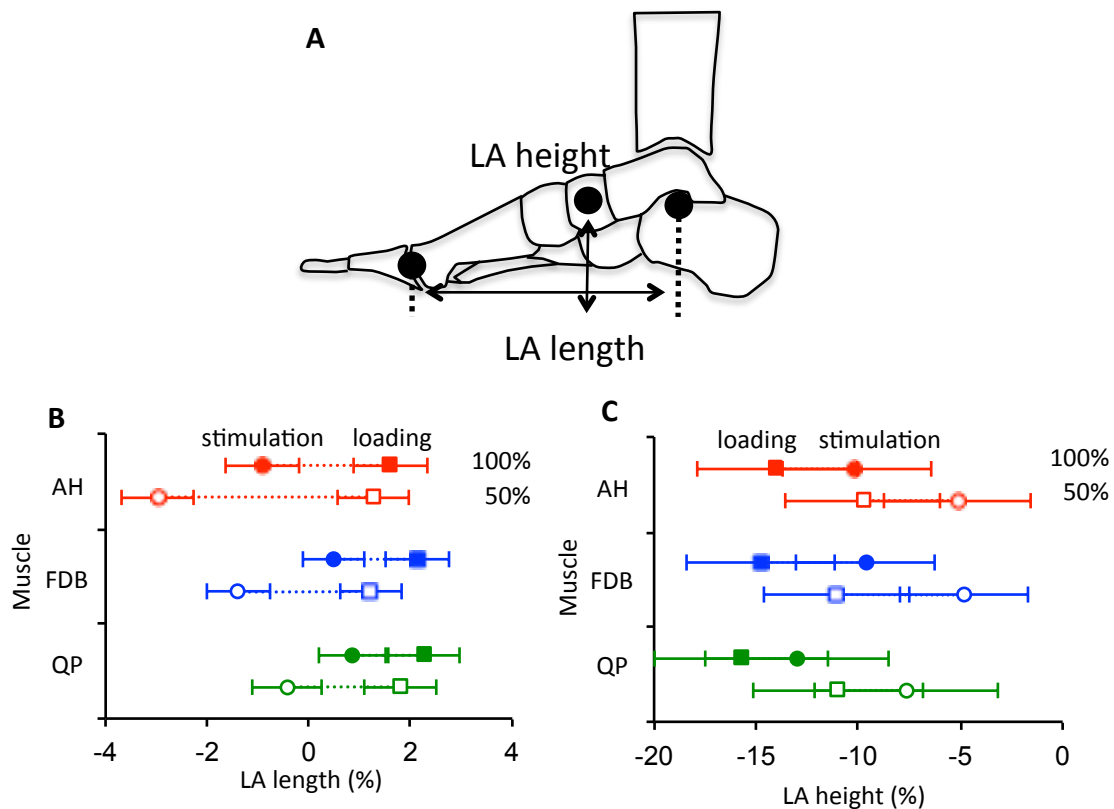
Figure 4.5. (A) Diagram of the measurements of longitudinal arch (LA) length and height. (B) Group mean ± standard error for LA length and height with 50% (open) and 100% (filled) body mass loading for abductor hallucis (AH, red), flexor digitorum brevis (FDB, blue) and quadratus plantae (QP, green) muscles. LA length and height values are shown in response to loading (squares) and stimulation (circles). Length and height of the LA are presented as a percentage change from the resting unloaded LA values (mean unloaded LA length = 156.7 ± 18.2mm, mean unloaded LA height = 53.5 ± 4.7mm). Stimulation of AH, FDB and QP resulted in a significant reduction in LA length and increase in LA height for all conditions (all P ≤ 0.05).

The alterations in LA length and height described above occurred as a result of a series of rotations occurring in multiple segments of the foot. In order to provide additional insight to the biomechanics of LA deformation and the impact of the plantar intrinsic foot muscles on this process, we have described the motion of the calcaneus and metatarsal segments during the loading and stimulation tasks. These findings are explained below and a visual depiction can be found in Figure 4.6.
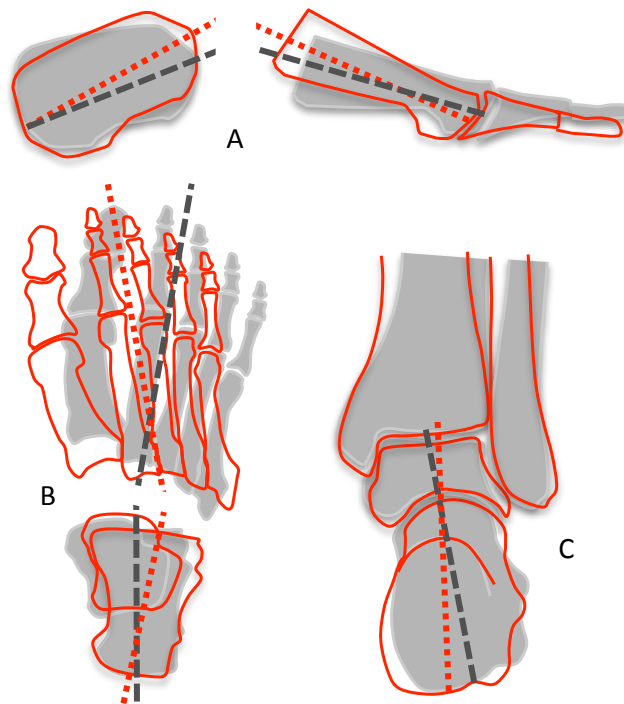
Figure 4.6. Depiction of foot motion changes occurring due to stimulation of abductor hallucis (AH). The position of the foot segments under load is represented by the grey shaded image and the stimulated position is represented by the red outlined image. The movements include (A) calcaneal extension and metatarsal flexion in the sagittal plane (B) calcaneal abduction and metatarsal adduction in the axial plane and (C) calcaneal inversion in the frontal plane. This combination of segment movements lead to a reduction in length and an increase in height of the longitudinal arch.

Calcaneus motion

When loaded with 50% body mass, angular displacements of the calcaneus were observed in the sagittal (extension), frontal (eversion) and transverse (adduction) planes, with the orientation of the calcaneus remaining similar when load was increased to 100% of body mass (all $P > 0.05$, Figure 4.7). Stimulation of AH produced extension, inversion, and abduction of the calcaneus in the 50%

body mass condition (P ≤ 0.05) and inversion and abduction of the calcaneus in the 100% body mass condition (P ≤ 0.05). Stimulation of FDB produced inversion and abduction of the calcaneus in both 50% and 100% body mass conditions (all P ≤ 0.05) while stimulation of QP produced abduction of the calcaneus in both 50% and 100% loading conditions (both P ≤ 0.05).

Metatarsal motion

Under loads equivalent to 50% body mass, the metatarsal segment flexed (sagittal plane) and abducted (transverse plane), with these rotations increasing significantly when load was increased to 100% of body mass (all P ≤ 0.05, Figure 4.7). Individual stimulation of AH, FDB and QP significantly changed the orientation of the metatarsal segment, in the opposite direction to that observed with the application of load (all P ≤ 0.05). Stimulation of AH produced flexion and adduction of the metatarsals while stimulation of FDB and QP produced adduction of the metatarsals under loads of 50% and 100% of body mass (all P ≤ 0.05).
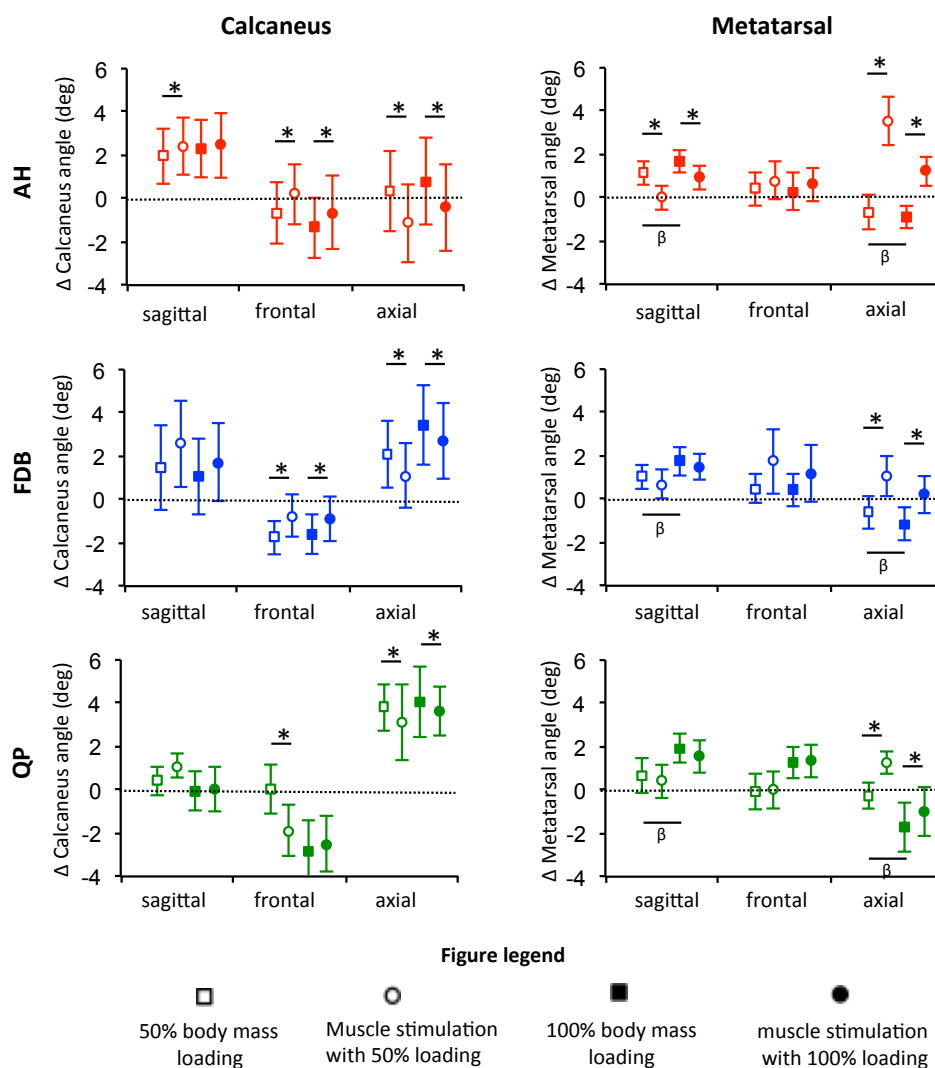
Figure 4.7. Changes in calcaneal and metatarsal segment angles due to passive loading and intrinsic foot muscle stimulation. Group means ± standard error for changes in calcaneal and metatarsal segment angles due to loading, 50% (open) and 100% (closed) body mass, as well as the subsequent changes in segment angles occurring with stimulation of abductor hallucis (AH, red), flexor digitorum brevis (FDB, blue) and quadratus plantae (QP, green) muscles. Segment angles are shown in response to loading (squares) and stimulation (circles). Angular rotations are defined relative to the laboratory co-ordinate system (x-lateral, y-anterior, z-upward) and according to an x-y-z cardan sequence of rotations, with extension-flexion (positive extension) as the rotation about the x-axis, inversion-eversion (positive inversion) as the rotation about the y-axis and abduction-adduction (positive adduction) as the rotation about the z-axis. Segment angles are normalised to the seated, unloaded segment angle, such that zero degrees equals the unloaded segment angle for all axes. $^\beta$ indicates significant effect of load (100% versus 50% body mass) on segment angle. * indicates significant change in segment angle due to muscle stimulation.

Force measurements

The location of COP_{ML} or COP_{AP} remained unchanged in both loading conditions ($P > 0.05$). Stimulation of AH shifted the COP posteriorly and laterally for both 50% and 100% loading conditions (both $P \leq 0.05$), while stimulation of FDB and QP produced a significant posterior shift in the location of the COP for both loading conditions (both $P \leq 0.05$, Figure 4.8).

Individual stimulation of AH, FDB, and QP produced an increase in vertical force, in both the 50% (AH: 23.09 ± 8.7 N, FDB: 21.89 ± 13.2 N, and QP: 20.43 ± 11.4 N, all $P \leq 0.05$) and 100% (AH: 22.73 ± 12.1 N, FDB: 20.97 ± 21.5 N, and QP: 20.36 ± 21.8 N, all $P \leq 0.05$) body mass loading conditions.
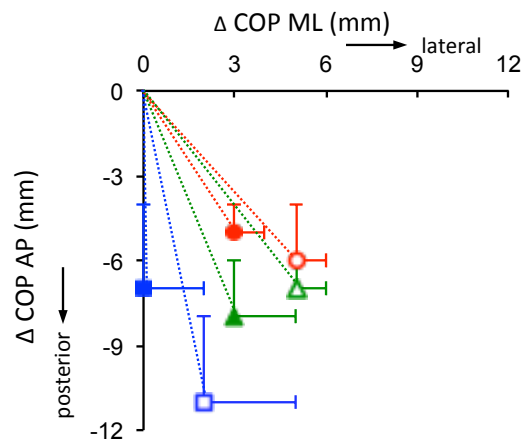
Figure 4.8. Changes in centre of pressure (COP) position due to intrinsic foot muscle stimulation. Mean ± standard error for COP in the medio-lateral (COP_{ML}, X co-ordinate) and antero-posterior (COP_{AP}, Y co-ordinate) directions occurring due to electrically evoked contractions in abductor hallucis (red circle), flexor digitorum brevis (blue square) and quadratus plantae (green triangle) with both 50% (open) and 100% (filled) loading conditions. Changes in COP position were calculated by subtracting the COP position immediately prior to stimulation from the subsequent maximum COP displacement that occurred during muscle stimulation, such that 0,0 (X,Y) represents the COP position prior to muscle stimulation, for all conditions. Stimulation of AH, FDB and QP produced significant changes in COP position in both loading conditions (all $P \leq 0.05$).

4.5 Discussion

Our results demonstrate the importance of the intrinsic foot musculature in contributing to foot arch

posture under physiological loads that would be exerted during tasks like walking. We have shown that increased vertical loading resulted in significant LA length and height deformations, stretching of the arch musculature and increased electrical activity of the intrinsic foot muscles beyond specific load thresholds. This indicates that the intrinsic foot muscles respond to loading of the foot, however their onset seems not to be mediated by stretch as MTU length increases were evident while EMG activity was notably absent at the lowest loading condition. Interestingly, foot deformation and muscle stretch plateaued at the highest loads; when muscle activity was still increasing. Our second experiment demonstrated that electrically induced contractions of individual intrinsic foot muscles (AH, FDB and QP), over and beyond their natural activity, can attenuate and even reverse LA arch deformation. Hence these muscles have the capacity to stiffen the LA under load and could potentially account for the plateau in arch deformation observed at higher loads.

The capacity for the arch of the human foot to compress when loaded, allowing for storage of elastic strain energy, was dubbed the "foot spring" mechanism by Ker and colleagues (Ker *et al.*, 1987). They reported that energy was stored as elastic strain in the passive ligamentous structures located within the LA, such as the plantar aponeurosis and plantar ligaments. This process was shown to provide metabolic energy savings, as well as structural support countering compression of the LA. The results of our initial experiment confirm that the intrinsic foot muscles also stretch in response to LA deformation, with activation of these muscles increasing at higher loads. Results from experiment 2 suggest that these muscles have the capacity to contribute and attenuate arch deformation during loading. Therefore activation of the intrinsic foot muscles with load may have the potential to provide a buttressing effect in parallel to that provided by the plantar aponeurosis. It appears that regulation of muscle activation may be contingent on loading demands, allowing forces generated from the intrinsic foot muscles to augment the contributions of the plantar aponeurosis once specific force or deformation thresholds are exceeded and potentially assisting in providing stabilisation of the arch when encountered with excessive load.

A novel aspect of our study was the use of intra-muscular electrical stimulation in addition to vertical loading to provide detailed insight to the biomechanical capability of the three largest plantar intrinsic foot muscles, AH, FDB, and QP. Our data revealed that individual activation of AH, FDB, and QP was sufficient to produce forces large enough to induce angular displacement of the calcaneus (extension, inversion and abduction) and metatarsals (flexion and adduction), which reduced the initial loading deformation by reducing LA length and increasing LA height. A

conceptual figure demonstrating the general movement that occurs when the AH muscle is stimulated is shown in Figure 4.6.

Despite the similar effect that individual muscle stimulations had on overall LA motion, differences did exist between muscles and the axis in which each muscle exerted mechanical influence on the calcaneal and metatarsal segments. The AH has the largest physiological cross sectional area (PCSA) of the plantar intrinsic foot muscles (Kura *et al.*, 1997; Ledoux *et al.*, 2001) and stimulation of this muscle produced the most pronounced alterations in segment angles in all anatomical planes, including extension, inversion and abduction of the calcaneus, with flexion and adduction of the metatarsals. The FDB and QP have smaller PCSA's than AH (Kura *et al.*, 1997; Ledoux *et al.*, 2001) and, for the submaximal stimulation intensity used here, only exerted significant influence in the frontal (calcaneal inversion) and transverse (calcaneal abduction and metatarsal adduction) planes. The AH is also the most medially located of the three muscles investigated (Tosovic *et al.*, 2012), therefore compared to FDB and QP it may possess a greater moment arm over the joints of the LA, thereby giving it the possibility to produce larger torques and therefore greater segmental motion.

Stimulation of the individual plantar intrinsic foot muscles produced angular displacement of the calcaneus and metatarsal segments which led to a reduction in arch length and an increase in arch height. Given that the applied downward load was constant during our muscle stimulations, a reduction in length of the LA indicates an overall increase in LA stiffness (reduced deformation for the same load). This may provide an explanation for the findings of Carravaggi (Caravaggi *et al.*, 2010), Bates (Bates *et al.*, 2013) and Pataky (Pataky *et al.*, 2008) who have suggested that active contractile mechanisms may provide substantial contributions to regulation of the stiffness of the LA. The presence of an active force generating element in parallel with a passive elastic element may help in both attenuation of impact forces and the generation of sufficient stiffness to transmit forces from the leg for effective forward propulsion (Vereecke & Aerts, 2008). Active stiffening of the LA may occur in a feedback or feed-forward manner in response to known or unknown variations in surface or loading demand, with the intrinsic foot muscles contributing either negative or positive work in order to provide transient adjustments in stiffness, in addition to that provided by the passive structures (Hicks, 1954; Ker *et al.*, 1987; Erdemir *et al.*, 2004; Caravaggi *et al.*, 2009). This mechanism may contribute additional positive work, as required to provide postural stability (Kelly *et al.*, 2012) and aid in the transfer of ankle plantar flexion moments during gait and

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possibly generate additional positive power during propulsion (Zelik & Kuo, 2010).

A recent paper by Kelly et al. (Kelly *et al.*, 2012) used intra-muscular EMG to describe the activation patterns of the plantar intrinsic foot muscles during various standing balance tasks and reported highly correlated inter-muscular activation with medial postural sway. This study was unable to determine whether these relatively small muscles were capable of generating sufficient force to alter COP position and thus influence posture. In our current study we have extended the findings of Kelly et al. (Kelly *et al.*, 2012) by confirming that even individual activation of these muscles is capable of shifting the COP location, and as such could play a part along with other lower limb muscles in balance control. An interesting finding from the current study was that stimulation of the intrinsic foot muscles resulted in a posterior shift in COP. This may be due to the shortening of the LA, predominantly arising from its distal end, and thus a posterior displacement in COP. In the current study we have largely eliminated postural influences by recording data from subjects in a seated position with weights loaded on to their knees, in order to simulate the loads applied during standing, in the absence of postural sway. This may help to explain the divergence in results between the current study and that of Kelly et al (Kelly *et al.*, 2012) who found no correlation between COP_{AP} and intrinsic foot muscle activation, as any relationship between COP_{AP} and muscle activity may have been hidden by the moments produced by the significantly larger soleus and gastrocnemius muscles.

There are some limitations to the approach employed here in attempting to understand the capacity of the intrinsic foot muscles to adapt foot stiffness under load. During the incremental loading task, QP muscle activation was not able to be collected from all participants. In four participants, muscle activation could not be distinguished from background noise. This may have been due to the unstable nature of recordings from this small muscle, or conversely, it may also be due to a lack of activation within QP under the loading conditions produced in this study. Additionally, for Experiment 2 we have not made direct statistical comparison between muscles, as we are uncertain if all muscles were contracting with the same relative intensity. Normalisation of the stimulation intensity across muscles could be achieved by evoking a supra-maximally stimulated contraction, however, this was not attempted due to the risk of damage to muscle tissue, discomfort and the increased risk of the stimulation current spreading to other nearby muscles which would confound the results. It is also difficult to ascertain what the summative effect of muscle activation might be in terms of both kinematics and kinetics as we did not simultaneously stimulate all three muscles.

Our prediction is, however, that simultaneous activation (which is likely to be the physiological normality in walking and running) would increase the overall effect with an even greater increase in LA height and reduction of LA length. It must also be acknowledged that as we did not record EMG from these muscles during the evoked muscle stimulations, we cannot verify that they were quiescent during these tasks. In fact, based on the results of Experiment 1, it is likely that these muscles may been active in the 100% body mass loading condition and as such our measures may have been influenced by a low level of background activation. Finally, we relied on skin-mounted markers to determine changes in LA height and length as well as movement of calcaneus and metatarsal segments. This approach is likely to underestimate some of the motion of the mid-foot during walking (Nester *et al.*, 2014), however we are confident that the general movement directions measured are consistent with what actually occurred during loading and muscle stimulation. The model we have used has been specifically designed to examine LA biomechanics, and has been shown to have high repeatability (Caravaggi *et al.*, 2011). In our measures, the movement of the foot segments is limited compared to walking and hence the contribution of factors such as skin movement relative to the foot segments is also more limited and changes in marker position are likely to represent motion of foot rather than that of the skin.

In summary, our initial experiment has shown that the intrinsic foot musculature stretched in a similar manner to that of the plantar aponeurosis in response to LA deformation, while muscle activation increased considerably as loads increased beyond certain threshold loads for each muscle. Our following experiment has shown that activation of the plantar intrinsic foot muscles under load produced significant alterations in metatarsal and calcaneus segment angles, which countered the deformation occurring due to the initial load and ultimately increased LA stiffness. This active arch buttressing mechanism may have important implications for how forces are transmitted during locomotion and postural activities. Future studies should examine the influence of the plantar intrinsic foot muscles on LA biomechanics during dynamic activities such as walking and running.

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CHAPTER FIVE – ACTIVE REGULATION OF LONGITUDINAL ARCH DEFORMATION AND RECOIL DURING WALKING AND RUNNING

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5.1 Summary

The longitudinal arch (LA) of the human foot compresses and recoils in response to being cyclically loaded. This has typically been considered a passive process, however it has recently been shown that the plantar intrinsic foot muscles have the capacity to actively assist in controlling LA motion. Here we tested the hypothesis that intrinsic foot muscles, abductor hallucis (AH), flexor digitorum brevis (FDB) and quadratus plantae (QP), actively lengthen and shorten during the stance phase of gait in response to loading of the foot. Nine participants walked at 1.25 ms^{-1} and ran at 2.78 and 3.89 ms^{-1} on a force-instrumented treadmill while foot and ankle kinematics were recorded according to a multi-segment foot model. Muscle tendon unit (MTU) lengths, determined from the foot kinematics, and intra-muscular electromyography (EMG) signals were recorded from AH, FDB and QP. Peak EMG amplitude was determined during the stance phase for each participant at each gait velocity. All muscles underwent a process of slow active lengthening during LA compression, followed by a rapid shortening as the arch recoiled during the propulsive phase. Changes in MTU length and peak EMG increased significantly with increasing gait velocity for all muscles. This is the first in-vivo evidence that the plantar intrinsic foot muscles function in parallel to the plantar aponeurosis, actively regulating the stiffness of the foot in response to the magnitude of forces encountered during locomotion. These muscles may therefore contribute to power absorption and generation at the foot, limit strain on the plantar aponeurosis and facilitate efficient foot ground force transmission.

5.2 Introduction

The human foot is a unique structure characterized by the presence of a pronounced longitudinal arch (LA) that provides considerable stiffness to enable forward propulsion, whilst also retaining sufficient flexibility to adapt and conform to alterations in surface and loading demand (Hicks, 1954; Vereecke & Aerts, 2008). When encumbered with load, the LA lengthens and lowers, subsequently recoiling as the load is removed (Ker *et al.*, 1987; Erdemir *et al.*, 2004). This compression – recoil process has been termed the "foot spring" mechanism and allows mechanical energy to be stored and subsequently released during each foot contact, which may improve the metabolic efficiency of gait (Ker *et al.*, 1987). The contribution of the passive ligamentous structures to this mechanism have been well established (Ker *et al.*, 1987; Erdemir *et al.*, 2004) however, to date very little attention has been paid the potential contributions of the contractile tissues of the LA in this mechanism.

The plantar intrinsic foot muscles are a group of muscles that contain both origin and insertion within the foot. The three largest of these muscles, abductor hallucis (AH), flexor digitorum brevis (FDB) and quadratus plantae (QP) have muscle tendon units (MTU) that span the length of the LA and follow similar anatomical pathways to the medial and central slips of the plantar aponeurosis (Kura *et al.*, 1997; Ledoux *et al.*, 2001; Tosovic *et al.*, 2012). Recent work from our own laboratory has shown that similar to the plantar aponeurosis, these muscles stretch in response to controlled LA compression, with muscle activation increasing in response to the magnitude of encumbering load (Kelly *et al.*, 2014). Furthermore, we have shown that additional activation of these muscles counteracts LA compression under load and subsequently increases the stiffness of the LA (Kelly *et al.*, 2014).

During human locomotion, the muscles and tendons of the lower limb perform positive and negative work on the body (Cavagna & Kaneko, 1977). Active MTU lengthening is achieved through the application of an external load to forcibly extend muscles as they actively generate tension. This muscle action acts to absorb mechanical energy (power). Conversely, active MTU shortening (or contractions) generates mechanical power (Cavagna & Kaneko, 1977; Ito *et al.*, 1983; Winter, 1983; Donelan *et al.*, 2002). Early electromyographic measurements from the intrinsic foot muscles suggest that these muscles are active during the stance phase of gait (Mann &

Inman, 1964), however it is unclear whether this activation occurs relative to lengthening or shortening of the MTUs.

Previous experiments from our laboratory have shown that the MTU's of AH, FDB and QP activate in response to being forcibly lengthened due to LA compression during loading of the foot (Kelly *et al.*, 2014). During locomotion it is likely that these MTU's will also activate in response to LA compression that occurs during early stance phase. Based on our previous data (see Chapter four), activation of the intrinsic foot muscles would stiffen the LA during early stance while also contributing to absorption of power within the stretched MTU's, effectively reducing the total load encumbered by the passive ligamentous structures. De-activation of these muscles during late stance, during which time the MTU's presumably shorten, may also contribute to power being delivered through muscle contraction or elastic recoil of the elastic structures within the MTU's. Given that we have previously found that the magnitude of activation of these muscles is dependent on the load encountered (Kelly *et al.*, 2012; 2014), we expect to see an increase in the activation with speed of locomotion. An active contribution of the plantar intrinsic foot muscles could potentially enhance the capacity of the foot to adapt to the variations in external load as they are encountered, allowing efficient force transmission between the foot and the ground during tasks such as walking and running, when the magnitude of forces encountered are constantly changing. This may also reduce the total load, and hence strain, experienced by the passive ligamentous structures of the foot (plantar aponeurosis).

As such, we tested the hypothesis that the MTU's of AH, FDB and QP undergo an active stretch and shortening process in response to LA deformation during the stance phase of gait, and therefore are capable of contributing positive and negative power at the foot. Furthermore we hypothesised that the magnitude of MTU deformation and muscle activation would increase with the increasing loads that are encountered when gait velocity is increased during walking and running.

5.3 Methods

5.3.1 Participants

Nine healthy male subjects (mean ± standard deviation for age 32 ± 5 years; height: 181 ± 8 cm; mass: 81 ± 11 kg) with no history of lower limb injury in the previous six months or known neurological impairment volunteered to participate in the study. Written informed consent was obtained from each subject. The study protocol was approved by the institutional human research ethics committee and conducted in accordance with the Declaration of Helsinki.

5.3.2 Experimental Procedures

Subjects performed walking trials at 1.25 m.s^{-1}, as well as running trials at 2.78 and 3.89 m.s^{-1} on a force-instrumented treadmill (AMTI, force-sensing tandem treadmill, Watertown, MA, USA). To ensure familiarity with the treadmill and each gait velocity, subjects were allowed 1-minute to adapt and familiarise themselves to each speed, prior to the commencement of data capture. Kinetic, kinematic and EMG data were collected simultaneously during all walking and running trials, with approximately 15-20 strides (toe-off to ipsilateral toe-off) being recorded at each gait velocity for subsequent data analysis.

5.3.2 Data Acquisition

Kinematic and kinetic measurements

Three-dimensional (3D) motion-capture of the foot and shank, and ground reaction force data were collected during each walking and running trial. Fourteen retro-reflective markers (diameter 9.0 mm) were placed on the skin of the right foot and ankle according to a multi-segment foot model developed to describe rear-, mid- and fore-foot motion (Leardini *et al.*, 2007). Two additional markers were applied to the skin over the second and fourth toes, at the level of the middle phalanx, in order to track the movement of the lesser toes.

Kinematic data was captured at 200 Hz using an eight camera 3D optoelectronic motion capture system (Qualysis, Gothenburg, Sweden) while ground reaction force and EMG data were synchronously captured at 2000 Hz through an analogue to digital converter. Kinematic, force and EMG data were collected simultaneously and synchronized using the Qualysis Track Management software from the same company.

Electromyography

Identification of the AH, FDB and QP muscles was conducted using real-time B-mode ultrasound imaging (10 MHz linear array, Ultrasonix RP, USA) in the right foot of each subject. Subsequently, bi-polar fine wire electrodes (0.051 mm stainless steel, Teflon coated, Chalgren, USA) with a detection length of 2 mm and inter-electrode distance of 2 mm were inserted using delivery needles (0.5 mm x 50 mm) into the muscle tissue of AH, FDB and QP under ultrasound guidance, in accordance with previously described methods (Kelly *et al.*, 2012). The size of the active area and separation between sites was chosen to give the best chance of recording representative activity from each muscle, while reducing the possibility of cross-talk from nearby muscles. Once the wires

were positioned appropriately in each muscle the delivery needles were removed and the muscle was imaged once more to determine that the electrode sensitive ends of the wires remained within the muscle tissue. Sterile techniques were used for the insertion of all wires.

All EMG signals were amplified 1000 times and recorded with a bandwidth of 30 -1000 Hz (MA300, Motion Labs, LA, USA). In order to prevent movement artefacts, the fine wire electrodes, connectors, cabling and pre-amplifiers were secured with cohesive bandage around the distal part of the shank. A surface ground electrode (Ag-AgCl electrode, 24 mm diameter; Tyco Healthcare Group) was secured to the skin overlying the fibula head.

Prior to data collection, the participant was asked to perform foot manoeuvres known to activate each muscle separately. When predicted EMG patterns could be detected, it was concluded that the electrodes were in the correct position. If not, the electrodes were withdrawn approximately 1mm until appropriate activation patterns could be detected and possible crosstalk excluded. A Velcro strap was secured around the participant's waist, which enabled the EMG amplifier box to be secured to the subject without interfering with their gait. A lightweight optical cable connected the amplifier box to the analogue to digital converter.

5.3.3 Data analysis

Kinetic, kinematic and EMG data files were exported to Visual3D (C-motion Inc., Germantown, MD, USA) for analysis. A vertical ground reaction force threshold was set to define each toe-off as occurring when vertical ground reaction force fell below 50 N, while foot contact was defined as occurring when vertical force subsequently rose above 50 N. Swing phase was defined as the period from right toe-off to right foot contact, while stance phase was defined as occurring between right foot contact and right toe-off. One gait cycle was considered as right toe-off to the subsequent ipsilateral toe-off.

Force plate data recorded during each experimental trial was digitally filtered with a 20 Hz low pass, fourth order Butterworth filter. Subsequently the vertical component of the ground reaction force was calculated for each gait velocity and normalised to bodyweight for each participant.

Marker trajectories were digitally filtered with a 6 Hz low pass, fourth order Butterworth filter. Assumed rigid segments were created according to a previously described multi segment foot model (Leardini *et al.*, 2007) including the shank, foot, calcaneus, mid-foot and metatarsals. Joint rotations were calculated in accordance with International Society of Biomechanics

recommendations (y-up, z-lateral, x-anterior) with rotation about the z-axis - sagittal plane motion, rotation about the x-axis – frontal plane motion and rotation about the y-axis – transverse plane motion (Wu & Cavanagh, 1995). The LA angle was defined as rotation of the metatarsals relative to the calcaneus, about the z-axis, with metatarsal extension being positive and flexion negative (Leardini *et al.*, 2007). Thus an increase in LA angle is indicative of a reduction in LA height (Figure 5.1). For each gait velocity, LA compression was calculated by subtracting the LA angle at foot contact in the 1.25 m.s^{-1} condition from the maximal LA angle recorded during each stance phase. Mean peak LA compression was calculated for each gait velocity by averaging the LA compression occurring over a minimum of 10 gait cycles.

161 ± 6°	173 ± 6°	148 ± 4°
Foot contact	Peak	Toe-off
A	B	C
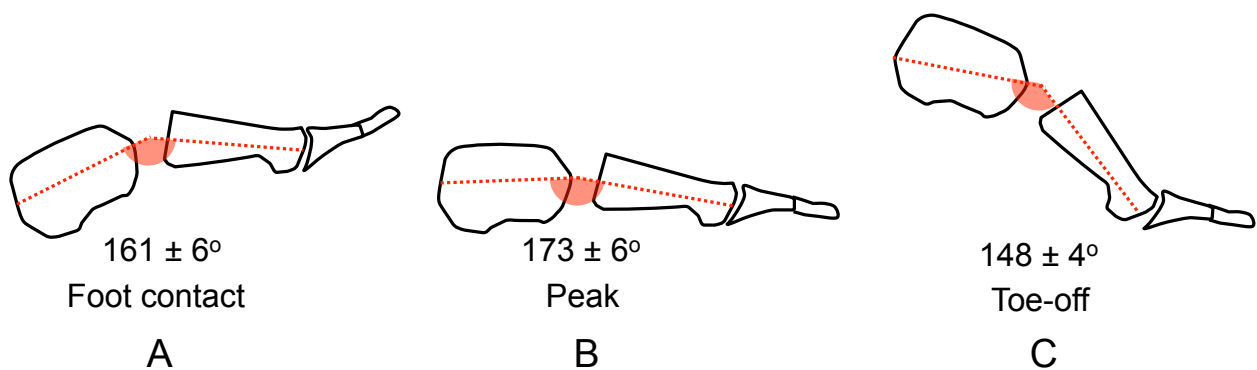
Figure 5.1. Compression and recoil of the longitudinal arch (LA). The LA angle is defined as the sagittal plane rotation of the metatarsals relative to the calcaneus. An increase in LA angle indicates compression of the LA which is calculated by subtracting LA angle at foot contact from peak LA angle, which generally occurred at mid-stance. Group mean LA angles are presented at foot contact (A), peak LA angle (B) and toe-off (C) when running at 3.89m.s^{-1} with data indicating that the LA compresses and recoils during stance phase.

Muscle tendon unit lengths for the AH, FDB and QP muscles were determined based on a geometrical model according to the multi-segment kinematic data by defining virtual markers corresponding to the origin, tether and insertion points for each individual muscle in accordance with previous cadaveric descriptions (Kura *et al.*, 1997; Ledoux *et al.*, 2001; Tosovic *et al.*, 2012). The points were expressed as fixed locations on the bony segment to which they were attached, allowing estimation of changes in MTU length according to the motion of the rigid foot segments. MTU length was defined as the straight-line distance from the origin to the insertion, via any tether points. Tether points were created at the distal end of the metatarsal segments for AH and FDB, representing the point where each MTU wraps around the metatarsophalangeal joints (Figure 5.2).

Additionally, a second tether point was created for the AH MTU, representing the fascial encapsulation of this muscle that occurs posterior to the navicular bone, extending from the deltoid ligament (Wong, 2007). This encapsulation serves as a pulley, changing the anatomical pathway of AH. Within this geometric model, any length changes observed for the AH and FDB MTUs will be due to a combination of rotations about the LA and metatarsophalangeal (MTP) joints, while QP MTU length changes will be due to rotation about the LA only (Figure 5.2). Peak MTU strain was calculated during stance phase at each gait velocity by dividing the change in MTU length (Peak MTU length minus MTU length at foot contact) during stance phase by the MTU length at foot contact.

AH **FDB** **QP**
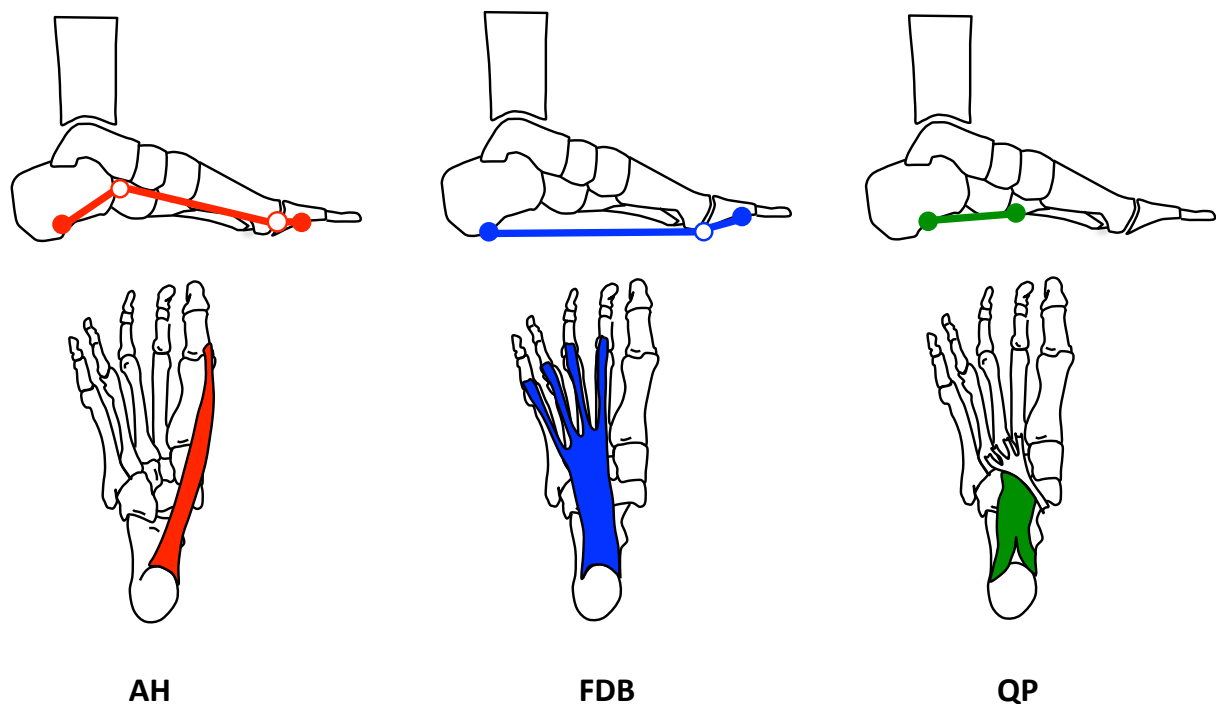
Figure 5.2. Depiction of the muscle tendon unit (MTU) pathways (top row) and anatomical pathways (bottom) for abductor hallucis (AH, red), flexor digitorum brevis (FDB, blue) and quadratus plantae (QP, green). Filled circles indicate origin and insertion points for each MTU, while open circles indicate tether points. The MTU length changes for AH and FDB will be due to a combination of rotations occurring about the longitudinal arch and metatarsophalangeal joints, while QP MTU length changes will occur due to changes in the longitudinal arch angle.

Raw EMG signals were visually inspected in order to identify data that may have been contaminated by movement artefact, which was defined as an abnormal spike in the signal associated to foot contact. In the event that movement artefact was identified in the EMG signal, data from that particular stride was excluded from the analysis. Following removal of any DC offset

from each EMG signal, root mean square (RMS) signal amplitude was calculated using a moving window of 50 ms. Subsequently for each muscle, peak EMG RMS amplitude was selected during the stance phase for each stride cycle, allowing comparisons in magnitude of activation occurring at each gait velocity. EMG data for each muscle was normalised to the peak RMS amplitude recorded across all gait velocities for each muscle.

For each individual, the kinetic, kinematic and EMG data from each gait cycle were time normalised to 100 points and a minimum of 10 gait cycles were averaged from a single velocity to form an individual mean for each variable, at each gait velocity. This process allows for comparison of data across gait cycles at varying velocities.

5.3.4 Statistics

A one-way repeated measures analysis of variance (ANOVA) was used to describe the effects of gait velocity on mean maximum vertical ground reaction force, LA compression, peak MTU strain, and peak stance phase EMG RMS amplitude for each muscle. Post-hoc multiple comparison tests including Sidak corrections were performed between each gait velocity (1.25 v 2.78 v 3.89 m.s^{-1}). Statistical differences were established at $P \leq 0.05$. Results are presented as mean difference ± standard error of the mean (SEM) unless otherwise stated.

5.4 Results

A representative example of raw kinetic, kinematic and EMG data from a representative individual running at 3.87 m.s^{-1} is presented in Figure 5.3. The data shows a high degree of similarity between the five sequential strides. The prominent peaks in the vertical ground reaction force indicate stance phase, which is approximately divided equally into deceleration and propulsion phases as shown by the horizontal ground reaction force. The change in LA angle for this subject at this running velocity was cyclic and highly reproducible. A process of LA compression and recoil is shown by the rapid increases in LA angle occurring during early stance, followed by a rapid decrease in LA angle occurring in late stance, associated with propulsion. While small variations in muscle activity were observed between the three intrinsic foot muscles, for the most part their activity was similar with significant periods of activity during stance and silence during swing, except for AH.
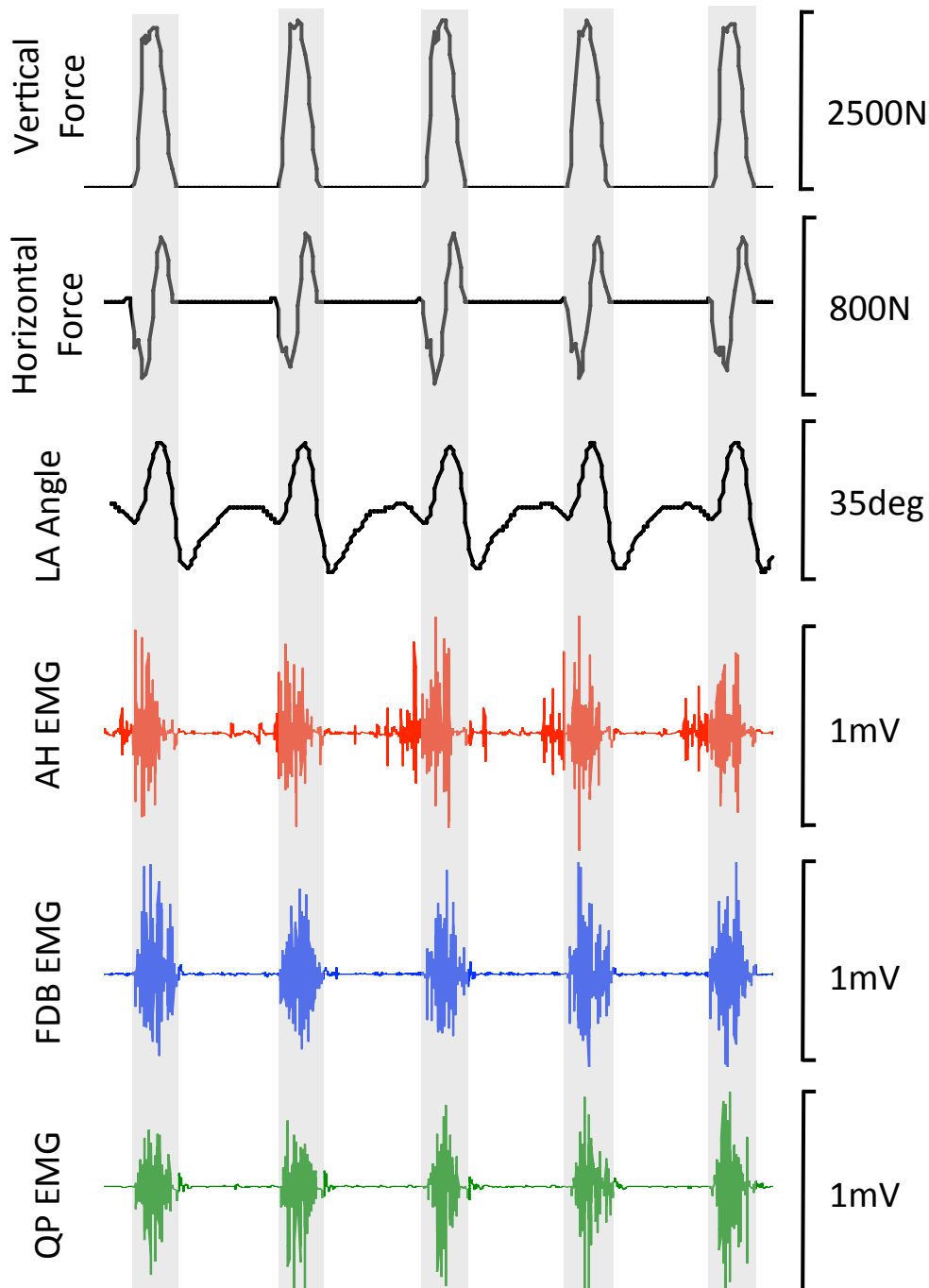
Figure 5.3. Raw data collected from a representative participant while running at 3.87m.s^{-1}. Vertical and horizontal forces are calculated from the force instrumented treadmill. Longitudinal arch (LA) angle is calculated based on multi-segment foot kinematics and intramuscular electromyography (EMG) recordings are collected from the abductor hallucis (top), flexor digitorum brevis (middle) and quadratus plantae (bottom). Shaded areas indicate stance phase.

5.4.1 Vertical force, LA compression and MTU strain

During early to mid-stance LA compression occurred (Figure 5.1) and the MTU's of AH, FDB and QP lengthened as vertical force increased. From mid-stance to late-stance, as vertical force decreased, the LA recoiled and the MTU's of AH, FDB and QP rapidly shortened (Figure 5.3). It was observed that vertical force, LA compression and peak MTU strain all increased significantly with increasing gait velocity (all $P \leq 0.05$, Figure 5.4).
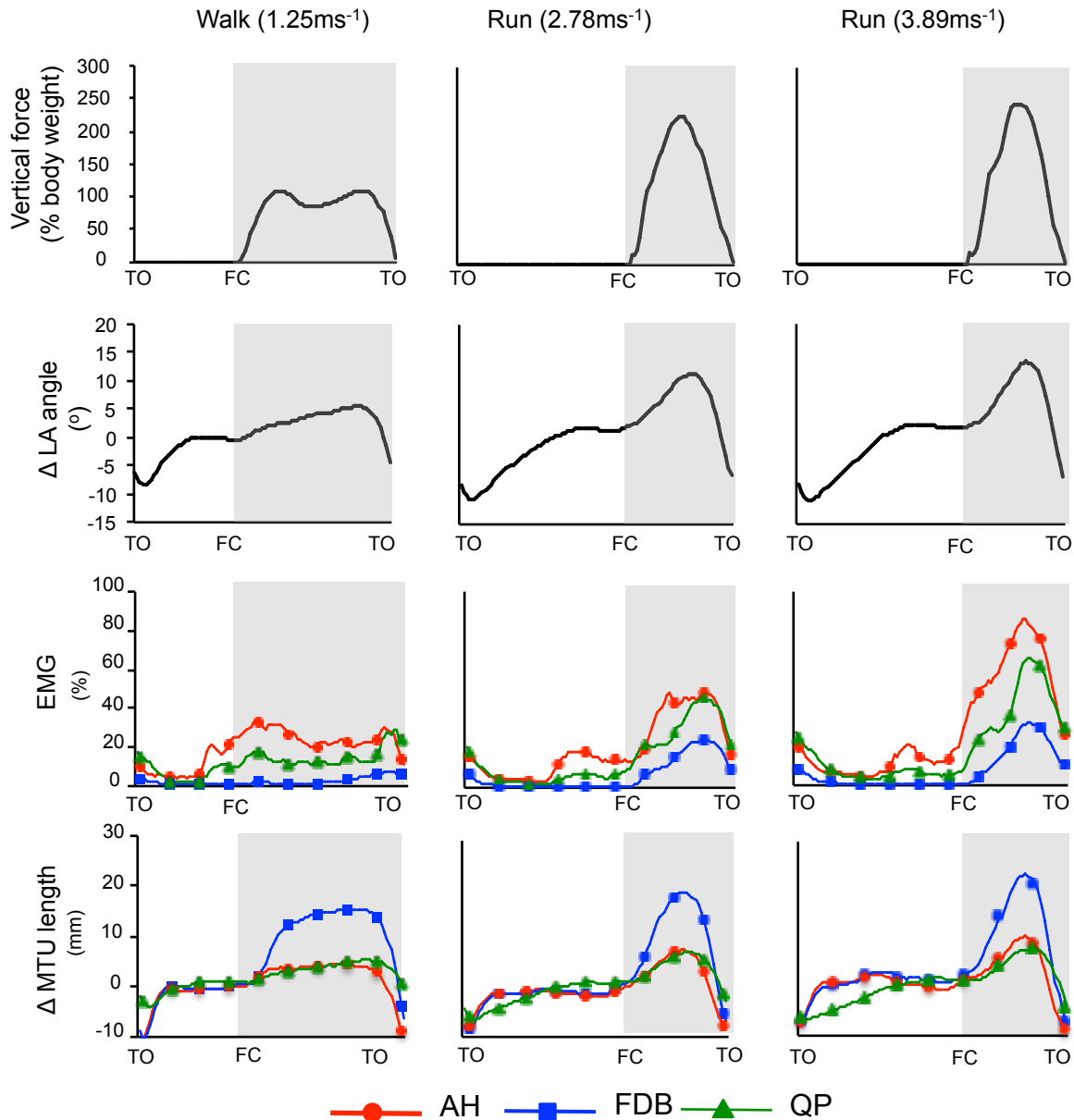
Figure 5.4. Group mean ensembles $\pm$ standard error of the mean for vertical ground reaction force, longitudinal arch (LA) angle (degrees, ^{o}), electromyography (EMG) root mean square signal amplitude and changes (Δ) in muscle-tendon unit (MTU) length for abductor hallucis (AH, red circles), flexor digitorum brevis (FDB, blue squares) and quadratus plantae (QP, green triangles). Group mean ensembles are defined from toe off (TO) to ipsilateral toe off for the right foot. Data recorded during walking at 1.25 m.s^{-1} and running at 2.78 and 3.89 m.s^{-1}.

For each muscle EMG data is normalised to the maximal amplitude recorded for all trials. Change in MTU length and LA angle is calculated by offsetting the MTU length and LA angle at heel contact in the 1.25 ms^{-1} condtition, respectively. Vertical ground reaction force (GRF) data is normalised to body mass. FC, foot contact

5.4.2 Muscle activation

All muscles displayed EMG patterns that were similar in nature, highlighted by substantial bursts of activation during stance and periods of relative inactivity during early swing phase (Figure 5.3). For all muscles stance phase activation increased with increasing gait velocity and the associated increase in ground reaction force.

The AH activation pattern consisted of two discrete bursts, with the initial burst occurring during late swing phase, prior to foot contact (Figures 5.3 & 5.4). The second more substantial burst of AH activity occurred during stance for both walking and running. Peak activation generally coincided with peak vertical ground reaction force with de-activation occurring during late-stance (propulsion phase), as AH underwent shortening (cf. Figures 5.3 & 5.4). Peak AH activation during stance increased significantly with increasing gait velocity (P ≤ 0.05) as did AH total EMG activity over the stride cycle (P ≤ 0.05, Figure 5.5).

FDB displayed a burst of activity commencing at foot contact and continuing throughout stance during running and to a lesser extent during walking. Peak activation occurred at mid to late stance (Figure 5.4). De-activation occurred during the later part of stance usually associated with the propulsion phase (cf. Figure 5.3). FDB activity during stance significantly increased with increasing gait velocity (P ≤ 0.05, Figure 5.5).

Quadratus plantae displayed a small increase in activation during late swing that continued into early-stance, followed by a second larger burst of activity in mid-stance during running and late-stance during walking (Figures 5.3 & 5.4). Peak stance phase activity increased with gait velocity (P ≤ 0.05, Figure 5.5).
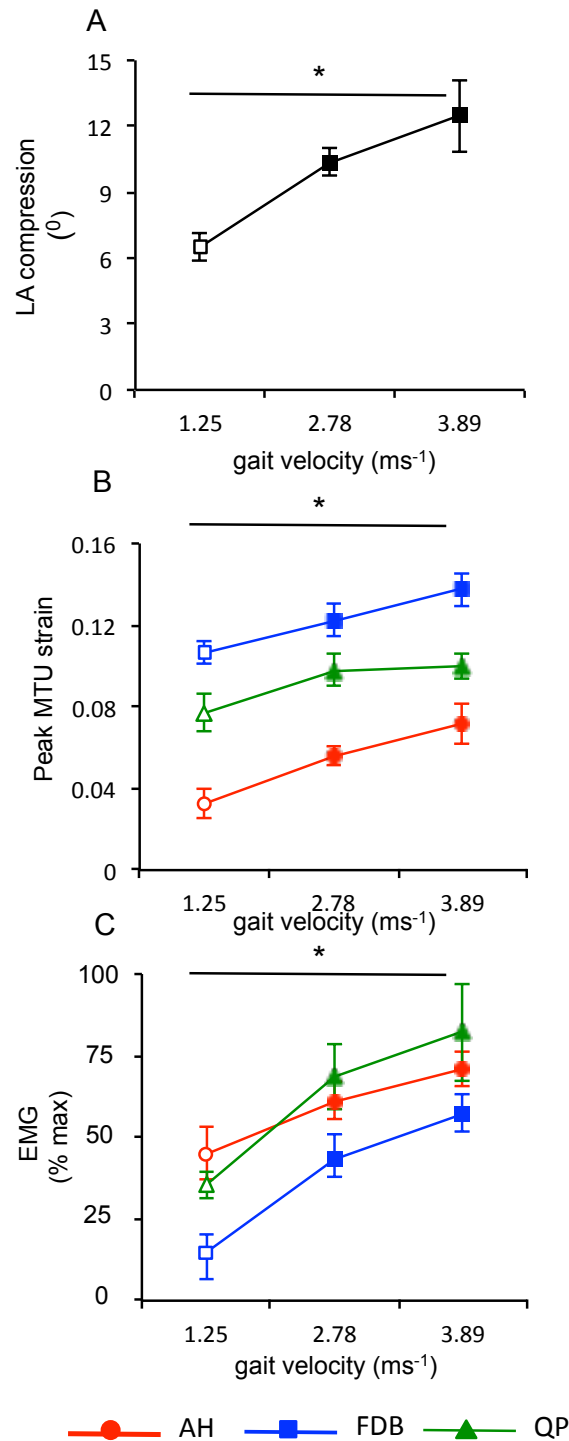
Figure 5.5. Group mean data for longitudinal arch (LA) compression (A), peak muscle-tendon unit (MTU) strain (B) and electromyography (EMG) root mean square amplitude (C) during stance for abductor hallucis AH (red circles), flexor digitorum brevis (FDB, blue squares) and quadratus plantae (QP, green triangles). LA compression is calculated by subtracting the LA angle at heel strike in the $1.25 ms^{-1}$ condition from the peak angle occurring during stance, at each gait velocity. EMG RMS values are normalized to the maximal amplitude recorded during all trials. *denotes significant difference, with all values increasing with increasing gait velocity (all $P \leq 0.05$).

5.5 Discussion

This study provides unique insight into the neuromechanical function of the plantar intrinsic foot muscles during walking and running at different velocities. These novel findings provide the first in-vivo evidence that the plantar intrinsic foot muscles actively lengthen during early stance, absorbing mechanical power and stiffening the arch in response to increasing ground reaction force. Subsequently in late stance as ground reaction force subsides, shortening of the MTU's allow mechanical power to be returned, presumably aiding forward progression during propulsion. We suggest that this mechanism to actively adapt the stiffness of the foot in response to the magnitude of load encountered may enhance foot ground force transmission and also reduce strain experienced by passive ligamentous structures of the foot.

The foot is the conduit for force transmission between the body and the ground during locomotion. The presence of a pronounced LA gives the foot the capacity to compress and conform in response to load, whilst retaining sufficient stiffness to enable forward propulsion (Donatelli, 1985; Vereecke & Aerts, 2008). The ligamentous plantar aponeurosis is known to stretch during early stance, providing some resistance to LA compression, while in late stance the windlass mechanism increases LA stiffness in preparation for propulsion (Hicks, 1954; Caravaggi *et al.*, 2009). While the plantar aponeurosis has been considered the primary contributor to LA stiffness, this passive structure is limited in its ability to respond and adapt to the loading variations that are commonly encountered during locomotion. Additionally, the suggestion that the regulation of foot stiffness is entirely passive does not completely account for the highly adaptable nature of the LA (Pataky *et al.*, 2008), which is known to display increased stiffness when encumbered with higher loads in the absence of increased plantar aponeurosis tension (Caravaggi *et al.*, 2010). Recently we have shown that the plantar intrinsic foot muscles also possess the capacity to stiffen the LA (Kelly *et al.*, 2014). When considering this knowledge in light of the current findings that plantar intrinsic foot muscle activation increases with increasing gait velocity, we suggest that these muscles are recruited in order to stiffen the LA, countering the LA compression that occurs due to higher ground reaction forces. The ability of the plantar intrinsic foot muscles to provide force dependent alterations in LA stiffness may facilitate effective foot ground force transmission, enabling higher ground reaction forces to be transmitted over a shorter period of time, as required at higher gait velocities (Nilsson & Thorstensson, 1989).

Compression and recoil of the LA in response to load during stance allows mechanical energy to be both absorbed and returned during each foot contact and may provide metabolic energy savings

(Alexander, 1984; Ker *et al.*, 1987). This process has traditionally been considered passive in nature, with energy being stored and released via elastic stretch and recoil of the plantar aponeurosis (Ker *et al.*, 1987; Erdemir *et al.*, 2004). However, if activation of the plantar intrinsic foot muscles provides the capacity to actively absorb and generate mechanical power at the foot during locomotion, then this may change our interpretation of the mechanical function of the foot. Stiffening the LA will essentially reduce compression, effectively reducing the strain experienced by the plantar aponeurosis and other ligamentous structures that would otherwise stretch further in the absence of muscular intervention. While this may provide some protection to the plantar aponeurosis and other structures, it also reduces the amount of energy storage and return from these structures. However, as the intrinsic foot muscles have relatively short muscle fibres (~ 23 mm) relative to the MTU length (~116 mm), the elastic structures of these muscles (tendon and aponeurosis) are well suited for storing the energy that is absorbed by the muscle during early stance and returning it to generate power during deactivation of the muscle in the shortening phase (push-off) (Alexander, 1984). The extent to which these muscles might be able to store and return the energy as well as tuning the stiffness of the foot is yet to be explored.

It is important to note that within the current experimental design we were unable to separate the individual contribution of the plantar aponeurosis and plantar intrinsic foot muscles to the foot spring mechanism, as these two structures act in parallel to regulate LA stiffness during locomotion. Based on the EMG profiles of these muscles during walking, it is apparent that at lower gait velocities the majority of energy absorption and return may occur in the passive plantar aponeurosis with some contribution from the active intrinsic foot muscles. However, as gait velocity increases and the magnitude of force required to be transmitted between the foot and ground also increases, it is likely that the contribution from the intrinsic foot muscles increases substantially, as noted by the significant increase in muscle activation. Caravaggi and colleagues (Caravaggi *et al.*, 2010) have previously reported that the compression of the arch during fast walking is significantly less than that which would be expected based on the passive stiffness of the arch reported by Ker et al. [3]. We suggest that this is due to the role of the intrinsic foot muscles in increasing the stiffness of the arch with increased force demand. This force dependent contribution from the intrinsic foot muscles may serve to stiffen the foot at higher velocities, allowing ankle plantar flexion torque to be transmitted to the ground rapidly, while also serving to modulate the amount of energy that is stored within the elastic element of the MTU. Further research exploring the relative contribution of these structures to the energetics of locomotion may provide valuable insight to human locomotor function.

The role of the foot in generating or absorbing power at the level of the body centre of mass also deserves consideration. Recently, Zelik and Kuo (Zelik & Kuo, 2010) compared measures of total joint work from the ankle, knee and hip against work performed on the centre of mass during constant velocity locomotion with the aim of quantifying the magnitude of mechanical energy dissipation performed by soft tissue. They reported a substantial disparity in total joint work when compared to the total work performed on the centre of mass, with most of this disparity being dissipatory in nature and occurring during the first half of stance. Because Zelik and Kuo (2010) assumed a rigid foot segment in their inverse dynamics analysis, they attributed the differences in joint work and centre of mass work to the inability of rigid body inverse dynamics to measure dissipative work performed by the soft tissues. They concluded that it is likely that passive soft tissues do play an important role in mechanical energy dissipation (Ker *et al.*, 1987; Pain & Challis, 2001; Gefen *et al.*, 2001). However, when considering their findings in light of the findings from our current study, it is possible that some of this difference may also be due to the role of both the passive and active components contributing to foot stiffness and subsequently contributing to both negative and positive power during stance.

We have provided a detailed description of the activation patterns of AH, FDB and QP recorded from a range of walking and running velocities. An early intramuscular EMG study by Mann and Inman (Mann & Inman, 1964) reported that some plantar intrinsic foot muscles are activated as a functional group during late stance in order to stabilise the forefoot during propulsion. Results from the current study provide evidence that while these muscles may have similar mechanical functions, specific differences in activation patterns exist. For example AH, a muscle that is known to be a slowly discharging, fatigue resistant muscle (Kelly *et al.*, 2012) displayed a substantial amount of late swing and early stance activation, which may indicate that this muscle provides preparatory stiffening of the LA prior to foot contact, as well as mechanical energy absorption during early stance. Recruitment of FDB and QP occurred largely at foot contact, with peak activation occurring in mid-stance and continuing into the propulsive phase, giving FDB a primary function of generating power during propulsion. Despite specific differences in activation patterns between the three muscles, it is apparent that regardless of specific function, activation is regulated in response to the magnitude of vertical force and subsequent LA compression encountered by the foot.

This study has focussed on the behaviour of the AH, FDB and QP MTU's during locomotion. It needs to be acknowledged that in addition to LA kinematics, rotation of the metatarsophalangeal (MTP) joints may also influence length changes of the MTU's of AH and FDB. Extension of the MTP joints that occurs in late stance as the heel rises from the ground would presumably have a

lengthening effect on the MTU as it wraps around the joint. However based on our data this lengthening effect is minimal (Figure 5.6A) with this likely being due to the relatively small moment arm of the FDB and AH MTU's across the MTP joint when compared to their moment arm across the joints of the LA (Figure 5.6B & 5.6C). Thus length changes of the MTU's are closely aligned to the kinematics of the LA, as is reflected by the data in this study.
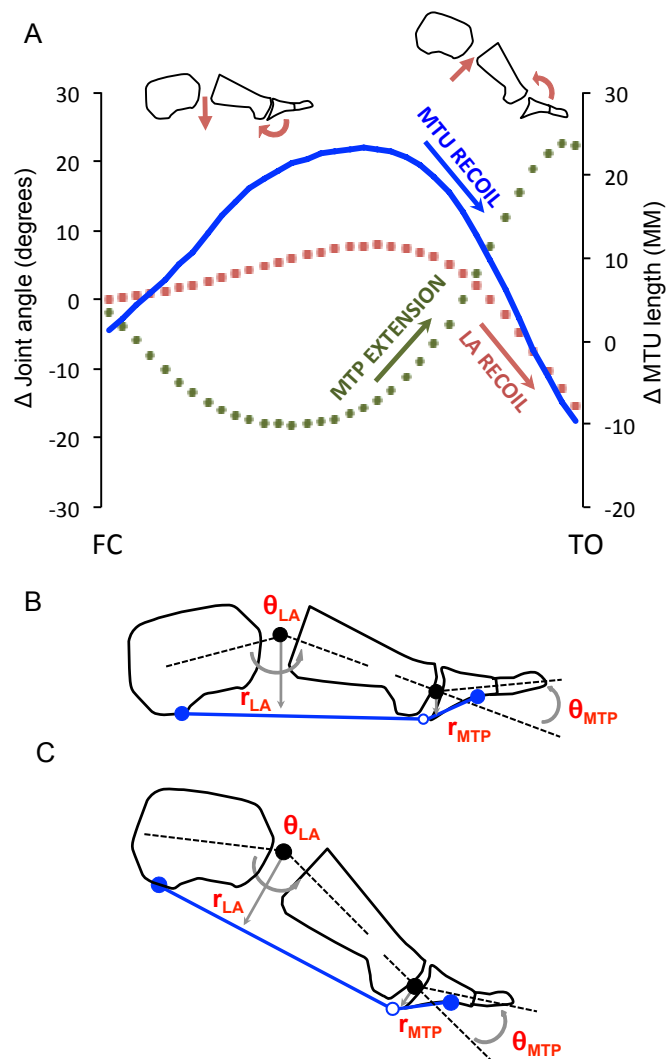
Figure 5.6. A - Changes in FDB muscle tendon unit (MTU) length (blue line), metatarsophalangeal (MTP) joint flexion/extension (green circles) and longitudinal arch (LA) angle (red squares) during stance phase of running at 2.78ms^{-1}. Data shows that MTU length recoils rapidly during late stance in parallel to LA recoil. This recoil happens despite the opposing influence of MTP joint extension occurring at the same time that should presumably lengthen the MTU. Parts B and C show the large moment arm of FDB across the LA, compared to its relatively small moment arm across the MTP joints, thus providing a biomechanical rationale for why MTP extension has minimal effect on overall length changes of the MTU.

There are some methodological limitations within the current experimental design that need to be acknowledged. The use of skin-mounted markers to determine changes in foot segment motion may underestimate some of the motion of the mid-foot (Lundgren *et al.*, 2008; Nester *et al.*, 2014) and therefore may also impact on our modelling of MTU lengths. However we are confident that the general movement directions measured are consistent with what actually occurred during each gait trial and therefore the patterns of MTU lengthening and shortening should be representative of what has occurred. The use of intramuscular fine wire electrodes had the potential to influence running biomechanics of some participants, due to discomfort from the fine wires. In order to address this issue, all participants were asked to acknowledge any pain or discomfort arising from the electrodes. None of our participants experienced pain or discomfort during the experimental task, thus we are confident that this was not the case.

In summary, the plantar intrinsic foot muscles are activated in order to provide dynamic support of the LA during locomotion. These muscles undergo active lengthening and shortening during stance, with muscle activation and stretch increasing in response to increasing vertical load. Thus, these muscles have the capacity to contribute to power absorption in early to mid-stance and power return and generation in late stance. The AH, FDB and QP muscles displayed distinct patterns of activation that may be related to differences in function, however activation of all muscles appears to be regulated in response to the magnitude of loading forces encountered.

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CHAPTER SIX – THESIS SUMMARY

This thesis investigated the in vivo function of the plantar intrinsic foot muscles. The four studies presented provide novel findings pertaining to the neurophysiological properties and biomechanical function of these muscles during postural activity and locomotion. The following chapter integrates the key findings and discussion points, while also discussing the significance of the findings of this thesis as a whole. Finally, this chapter provides an insight to the directions for future research in this field.

6.1 Summary of key findings

6.1.1 Relationship between neurophysiological properties and biomechanical function of the intrinsic foot muscles

The human foot has undergone a number of key structural adaptations as part of the evolutionary transition towards upright bipedal locomotion, including an adducted hallux, enlarged and re-aligned tarsal bones, shortened lateral digits and a pronounced LA (Bramble & Lieberman, 2004; Thorpe *et al.*, 2007; Rolian *et al.*, 2009; Crompton *et al.*, 2010). These important adaptations reflect a change in the functional requirements of the foot from grasping and object manipulation toward the modern human foot that is primarily a load bearing structure, acting as the interface between the body and ground (Li *et al.*, 1996; Bramble & Lieberman, 2004; Wang & Crompton, 2004; Rolian *et al.*, 2009; 2010; Crompton *et al.*, 2012). While these structural adaptations have been well described in the literature, prior to this thesis it had not been established whether the neurophysiological properties of the musculature within the foot is well matched to their function in providing support for the LA during upright stance and locomotion.

Chapters two, four and five highlight the functional importance of the plantar intrinsic foot muscles in providing active support for the LA during postural tasks and locomotion. Given this function, it would seem essential that these muscles have the ability to generate force in response to, or in anticipation of the foot impacting the ground. Furthermore these muscles would also require the capacity to sustain their force generating capacity in a cyclic manner for prolonged periods of time, as is required to provide support for the LA during locomotion. The findings from Chapter three support this suggestion, with AH displaying the hallmarks of a fatigue resistant muscle that has the capacity to generate and sustain moderate force for prolonged periods with little disruption to discharge characteristics or force output.

Evidence that the neurophysiological properties of the intrinsic foot muscles are closely linked to their function in LA support may be observed by comparing the discharge characteristics of AH reported in Chapter three, to similar muscles within the hand. The human hand remains a structure that is specialised for grasping and fine manipulation of objects, in a similar manner to how the pre-human arboreal foot may have functioned. Even though the human hand has also likely undergone further evolutionary divergence towards greater precision of force, the comparison provides valuable insight into how the neurophysiological properties of AH may be well adapted to its role in providing postural support for the foot. The discharge properties of motor units of human hand muscles have been described extensively (Sica *et al.*, 1974; Thomas *et al.*, 1986*a*; De Luca *et al.*, 1996; Carpentier *et al.*, 2001). Generally these muscles have relatively large numbers of motor units with low innervation ratios (Sica *et al.*, 1974). Hand muscles such as the thenar group and dorsal interossei rely heavily on rate coding, with individual motor units displaying relatively high discharge rates (Sica *et al.*, 1974; De Luca *et al.*, 1982; Thomas *et al.*, 1986*b*; Zijdewind, 2002; Moritz *et al.*, 2005) allowing the precise control force of production that is essential for manual dexterity.

The discharge behaviour of the hand muscles are in stark contrast to those of AH that were shown to have low peak discharge rates and low rate coding ranges. Abductor hallucis is known to have a low number of motor units relative to its size (Johns & Fuglevand, 2011) and thus has a high innervation ratio, suggests this muscle relies heavily on recruitment to generate force, utilising the high number of muscle fibres innervated by each motor unit to rapidly increase force production. This arrangement of fatigue resistant motor units that utilise a recruitment strategy for force production is similar to other muscles of the lower limb such as the soleus that also play important roles in postural support and locomotion (Oya *et al.*, 2009). An apparent trade-off for this adaptation is the lack of ability to finely grade force, which is indicated by the difficulty experienced by the participants in accurately performing the ramp contractions. However, as the human foot is primarily a load bearing structure, the toes are rarely used for grasping of objects. Thus the requirement for force precision is likely outweighed by the benefit of being able to produce high forces which can be sustained for prolonged periods as is required to provide active support for the LA during standing, walking and running.

Caution should be taken, however, when inferring that the neurophysiological properties of AH represent those of the entire group of plantar intrinsic foot muscles, including FDB or QP. However, given that results from Chapter two, four and five have shown high degrees of similarity in function and activation patterns of AH, FDB and QP it is likely that these muscles would posses

similar discharge characteristics to AH that are suited to their function in providing active support for the LA.

6.1.2 Mechanical function of the plantar intrinsic foot muscles and implications for postural control and locomotion.

This thesis provides detailed insight to the role of the plantar intrinsic foot muscles in contributing to LA biomechanics, highlighting that AH, FDB and QP are recruited in response to loading of the foot and the resulting deformation of the LA. Novel evidence is provided to show that these muscles have the capacity to generate sufficient force to produce angular displacement of the calcaneus (extension, inversion and abduction) and metatarsals (flexion and adduction), countering and reversing compression of the LA that occurs when the foot is encumbered with load. These findings have a number of implications for our knowledge of how the central nervous system (CNS) regulates the activation of these muscles, altering the biomechanical characteristics of the foot in order to maintain upright balance and improve efficiency during locomotion.

Postural control

The "top heavy" architecture of the human body, where the majority of the body's mass is located a considerable distance above our base of support, provides a significant challenge to maintain upright posture (Winter, 1995). Accordingly the CNS must possess the capacity to constantly adapt in a reactive and pro-active manner in order to maintain balance (Winter, 1995; Gatev et al., 1999; Tokuno et al., 2007; Loram et al., 2011). It is well established that the ankle plantar flexors are recruited in response to, or in anticipation of forward sway during upright stance, with their action slowing and subsequently countering anterior displacement of the body centre of mass (COM) preventing forward falling (Winter, 1995; Tokuno et al., 2008; Loram et al., 2011). Data presented in Chapter two provides novel evidence that the intrinsic foot muscles display highly correlated inter-muscular activation patterns in response to medio-lateral displacement of the COP in single leg stance, with activation increasing with medial shifts in the COP. These findings suggest that similarly to the posterior leg muscles, that are recruited in response to antero-posterior shifts in sway, a central control mechanism may also be responsible for the highly synchronised recruitment of AH, FDB and QP, in response to, or in anticipation of medio-lateral sway. The relevance of this discovery in the context of postural control is highlighted further when considered in the context of the mechanical function of these muscles described in Chapter four. Activation of AH, FDB and QP substantially alters foot biomechanics (described above) under loads equivalent to those

encountered during single and double leg support. Thus despite the fact that these muscles are relatively small (Kura *et al.*, 1997; Ledoux *et al.*, 2001; Tosovic *et al.*, 2012) these muscles may have the capacity to produce sufficient force to contribute meaningful alterations in postural alignment.

The synchronised manner in which these muscles respond to medio-lateral shifts in the COP highlights the functional role of the plantar intrinsic foot muscles during upright stance. Weakness of these muscles may impair the capacity of the CNS to control medio-lateral motion during periods of single leg support in standing and during gait, possibly leading to larger medio-lateral displacements of the COM and as such, poorer balance control. While this hypothesis has not been addressed within the current thesis, it provides some explanation for why weakness in these muscles may lead to poor balance and an increased risk of falls (Menz *et al.*, 2005; Mickle *et al.*, 2009). The contribution of these muscles to standing balance requires further investigation. This may be achieved by the use of research techniques that temporarily block the function of these muscles in healthy participants, or in clinical populations with conditions such as diabetic polyneuropathy and Charcot Marie Tooth disease, where function of these muscles is compromised due to neurological impairment (Menz *et al.*, 2004; Lencioni *et al.*, 2014).

Locomotion

Potentially the most important finding of this thesis relates to the discovery of a mechanism by which the plantar intrinsic foot muscles actively modify the stiffness of the foot in response to the forces encountered during locomotion. It is widely acknowledged that human legs function as springs during locomotion, with the CNS actively altering the mechanical characteristics (stiffness) of the lower limb allowing the body to constantly adapt in response to variation in loading and environmental demands (Farley *et al.*, 1998; Ferris *et al.*, 1998). Chapter five provides evidence to suggest that the stiffness of the foot may also be actively adjusted during locomotion, contrary to the previous belief that the spring-like behaviour of the foot was passive in nature (Hicks, 1954; Ker *et al.*, 1987). Based on the results from Chapters four and five, it is apparent that the relative contribution of the passive and active components to foot stiffness regulation may vary depending on the demands of the task. For example, at lower gait velocities, the magnitude of the vertical ground reaction force is relatively low and contact time is prolonged. Thus, the passive structures of the arch can provide sufficient stiffness to allow ankle plantar flexion torques to be transferred via the foot to the ground during propulsion, with only minor contributions needed from the intrinsic foot muscles. However, at higher gait velocities when torques transmitted between the body and

ground are substantially higher and the time in which these torques need to be transmitted is greatly reduced, the capacity of the intrinsic foot muscles to actively stiffen the foot may be a considerable advantage.

The energetic benefits of the spring like behaviour of human lower limbs has been described extensively (Alexander, 1984; Lichtwark & Wilson, 2007; Roberts & Konow, 2013). The potential for the intrinsic foot muscles to actively contribute to this mechanism during locomotion is a new insight that further highlights the importance of the LA as a structure that facilitates habitual upright bipedalism. The key finding of Chapter five was that the MTU's of AH, FDB and QP undergo a cyclical process of gradual active lengthening and subsequent rapid recoil during stance, alongside LA compression and recoil that occurs in response to the ground reaction forces during the stance phase. This novel finding reveals that not only do these muscles regulate the stiffness of the LA, as described in Chapter four, but they also have the capacity to absorb and generate mechanical power during locomotion, acting in conjunction with the plantar aponeurosis. During the loading phase of stance, active lengthening of the intrinsic foot muscles will serve to stiffen the arch, resisting excessive LA compression and allowing mechanical energy to be absorbed with the MTU. During mid to late stance, active recoil of the MTU will allow mechanical power to be returned and possibly even generated, aiding forward progression. Additionally, activation of the intrinsic foot muscles may also serve to optimise energy storage and return within the MTU itself, by stiffening the contractile component of the MTU and potentially allowing greater utlilisation of elastic energy within the tendinous connective tissues. The AH, FDB and QP MTUs are comprised of relatively short fibres (AH~*23mm, FDB ~23mm, QP~25mm)* and long tendons (Kura *et al.*, 1997; Ledoux *et al.*, 2001; Tosovic *et al.*, 2012), thus similar to other muscles of the lower limb, these muscles are well suited to storing mechanical energy within the long elastic component of the MTU during early stance and returning it via tendon recoil, providing mechanical power for propulsion (Alexander, 1984). This hypothesis has not been investigated within this thesis and thus remains speculation. Therefore, further research exploring the potential for elastic energy utilisation within the intrinsic foot muscles and how this may influence the economy of locomotion is warranted (discussed in detail below).

Another potential benefit of the intrinsic foot muscles actively stiffening the foot in response to higher loading forces is the reduction in plantar aponeurosis strain that occurs, due to reduced arch compression. Repeated excessive strain in the plantar aponeurosis is considered a contributing factor in common musculoskeletal injuries of the foot, such as plantar fasciitis (Wearing *et al.*, 2006). The potentially protective effect provided by the intrinsic foot muscles may have

implications for how conditions such as plantar fasciitis are managed in a clinical environment. Further research should now be conducted to determine if differences in activation patterns and force generating capacity of these muscles are apparent between people with various foot structures (eg. low and high arched feet) and also in people with clinical conditions such as plantar fasciitis. This research may also investigate the impact of strengthening programs for these muscles on foot function and foot pain, in clinical populations.

The recent increase in the application of multi-segment foot modelling approaches to provide detailed insight to lower limb biomechanical function (Leardini *et al.*, 2007; Caravaggi *et al.*, 2009; 2010) has emphasised that the human foot is considerably more flexible than previously thought (Winter, 1983; Thorpe *et al.*, 2007; Zelik & Kuo, 2010). Chapter five of this thesis reports that up 20 degrees of motion occurs about the mid-foot during running and that the muscles within the arch have the capacity to absorb and generate mechanical power about this functional joint. This new knowledge suggests that the assumption of the foot as a rigid segment for the purposes of inverse dynamic calculations may lead to inaccuracies in interpretation of ankle joint kinematics and kinetics. For example, traditional modelling techniques model the foot as a rigid segment spanning from the calcaneus to the distal ends of the metatarsals, with any rotation of the shank about the foot considered to be rotation of the ankle (Winter, 1983; DeVita *et al.*, 2008; Zelik & Kuo, 2010). However, in light of the findings from this thesis and other studies employing multi-segment foot models (Leardini *et al.*, 2007; Caravaggi *et al.*, 2009) it is likely that motion of the shank over the foot will be a combination of angular rotation about the ankle (shank – calcaneus) and mid-foot (calcaneus – metatarsals). Modelling ankle joint motion as rotation of the articulation between the rear-foot (calcaneus) relative to the shank may provide a more accurate reflection of the ankle joint motion and thus improve the accuracy of inverse dynamic calculations. Likewise, the mid-foot should also be included as an additional joint in inverse dynamic solutions. The lack of studies modelling the ankle and mid-foot as separate joints during locomotion may be in part due to the technical difficulty of performing inverse dynamic calculations across the mid-foot. Thus future research should investigate the influence of including a joint at the mid-foot on ankle joint kinematics and kinetics.

Another known limitation of using three-dimensional motion capture is the use of skin-mounted markers to determine changes in body segment motion. Soft tissue motion can possible influence the accuracy of data collected during tasks such as locomotion. While there is minimal soft tissue located between the skin mounted markers and the bones of the foot, this technique may

underestimate some of the motion of the mid-foot (Lundgren *et al.*, 2008; Nester *et al.*, 2014) and therefore may also impact on our modelling of MTU lengths. Future research may benefit from incorporating emerging imaging techniques such as x-ray reconstruction of moving morphology, that combine the use of dual plane fluoroscopy and CT imaging to create highly accurate in-vivo animations of bone motion (Brainerd *et al.*, 2010). This type of technology is yet to be employed to study motion of bones within the human foot. However, its previously successful application in small (Brainerd *et al.*, 2010) and large (Baier & Gatesy, 2013) animals indicate that this type of technique could increase the accuracy of modelling foot bone motion and hence MTU lengths.

6.3 Directions for future research

This thesis proposes a novel biomechanical model of foot function that provides greater explanation for the highly adaptable nature of the human foot. This new model includes both active and passive components functioning in parallel to control the stiffness of the LA, with the intrinsic foot muscles actively modifying arch stiffness during tasks that require high forces to be transmitted between the foot and the ground, while the plantar aponeurosis provides primary structural support for the LA during tasks when forces are low, such as standing and slow walking (Hicks, 1954; Ker *et al.*, 1987). This new insight has substantial implications for research in lower limb biomechanics. Further research is now warranted to improve our understanding of this mechanism. A number of areas for future research questions and proposed directions of research are outlined below;

6.3.1 How important are the plantar intrinsic foot muscles in foot stiffness regulation during locomotion?

The 'foot spring' mechanism has previously been considered a largely passive process involving the plantar aponeurosis and ligamentous structures (Ker *et al.*, 1987; Alexander, 1991) and it has been estimated that these mechanism allows storage and return of approximately 17% of the metabolic energy required for a single gait cycle (Ker *et al.*, 1987). However, given the evidence provided within this thesis that the plantar intrinsic foot muscles are capable of adjusting foot stiffness and that these muscles activate in proportion to the forces experienced by the foot, it is likely that these muscles may augment the contribution of the passive ligament structures in control of foot stiffness. This action would serve to provide "on demand" adjustments in foot stiffness, tuning the foot in response to the forces or deformation encountered. This is a potentially important mechanism that may enhance efficiency and versatility of the leg during locomotion. However, while this thesis highlights the existence of this mechanism, at present we have little understanding of the magnitude of contribution from the intrinsic foot muscles to foot stiffness regulation, as well as the subsequent

mechanical and energetic benefits this might have for tasks like walking and running. Future studies attempting to isolate the contribution of these muscles to maintenance of foot spring function during locomotion are necessary in order to quantify the relative importance of these muscles to the overall function of the foot during locomotion and may also elucidate the mechanical and or metabolic cost of their activation. This may be achieved by employing research techniques that remove the contribution of the active components (eg. peripheral nerve blocks) and examining the effect this has on the mechanical function of the foot and the net metabolic cost of locomotion.

6.3.2 Do the plantar intrinsic foot muscles utilise their relatively long tendons to store and return elastic energy during locomotion?

The final study of this thesis has shown that the plantar intrinsic foot muscles undergo active lengthening and shortening during each foot contact, absorbing mechanical power during early stance, and generating mechanical power in late stance – essentially acting as both a break and motor. While this function is known to occur in any muscle of the lower limb that undergoes both lengthening and shortening during the stance phase of gait (Alexander, 1991), there is an accumulating amount of evidence to support the idea that this function is achieved primarily through the spring-like action of the elastic tendinous tissues (Lichtwark, 2005; Lichtwark & Wilson, 2006). The use of ultrasound imaging to examine the length changes of both the medial gastrocnemius muscle fascicles and Achilles tendon has clearly shown that during stretch-shorten activities like hopping, walking or running, the Achilles tendon and the gastrocnemius aponeurosis undergo the majority of the stretch and shortening of the MTU (Lichtwark, 2005; Lichtwark & Wilson, 2006). Using this data and models of muscle-tendon interaction and energetics, it has been reported that the compliance of the Achilles tendon is such that it minimises the required lengthening and shortening of the muscle fibres, which acts to reduce both the magnitude of activation of the muscle and as such the energy required to perform the action (Lichtwark & Wilson, 2007). The architecture of the intrinsic foot muscles is similar to the gastrocnemius and Achilles tendon, with short fibres and relatively long tendons (Kura *et al.*, 1997; Ledoux *et al.*, 2001; Tosovic *et al.*, 2012) and they also undergo cyclic lengthening and shortening contractions in response to load during each stride cycle. The arrangement of relatively short muscle fibres in series with long elastic tendons may enable these muscles to remain largely isometric during the MTU lengthening and shortening phases that occur during every foot contact, with the majority of lengthening and shortening occurring within the elastic tendons. This mechanism would serve to reduce the net mechanical work performed by the contractile element, optimising force output and enhancing movement efficiency. Further studies utilising a combination of ultrasound,

electromyography and three dimensional motion analysis are required in order to investigate this hypothesis.

6.3.3 What are the central and peripheral mechanisms regulating intrinsic foot muscle activation?

The experiments contained within this thesis have consistently found that activation of the plantar intrinsic foot muscles increase in response to increased loading forces. It is now of benefit to develop a greater depth of understanding pertaining to the sensory mechanisms that regulate the activation of these muscles. As with other locomotor muscles (Lacquaniti et al., 2012), it is likely that central pattern generators play an important role in governing the activation of the plantar intrinsic foot muscles. However the involuntary activation of these muscles during tasks such as the foot loading experiments performed in Chapter four, suggests these muscles are highly susceptible to afferent feedback and it is highly likely that a combination of various sensory afferents contribute to the regulation of intrinsic foot muscle activation during standing and gait, including the joint mechanoreceptors, muscles spindles and golgi tendon organs. One area of particular interest is the role that sensory cutaneous receptors of the foot sole play in the recruitment and activation of the plantar intrinsic foot muscles, with suggestions that these receptors play an important function in providing afferent feedback for postural control (Lowrey et al., 2010; 2013; Mouchnino & Blouin, 2013; Lowrey et al., 2014). The slowly adapting type one (SAI) and type two (SAII) receptors are particularly sensitive to pressure and skin stretch, respectively (Macefield, 2005; Lowrey et al., 2013; Bent & Lowrey, 2013). These sensory cutaneous receptors are known to trigger activation in muscles of the lower (Lowrey et al., 2010; Mouchnino & Blouin, 2013) and upper (Bent & Lowrey, 2013) limbs in response to pressure and stretch during postural activities. Given the close proximity between the plantar intrinsic foot muscles and the sensory cutaneous receptors on the sole of the foot, it is likely that these sensory organs play a role in regulation of intrinsic foot muscle activation. This direction of research may have substantial implications for the development of textured insoles that stimulate the cutaneous receptors on the sole of the foot, possibly improving balance control in groups that are prone to falls, including people suffering from Parkinson's disease (Hiorth et al., 2014) and the elderly (Mickle et al., 2009).

Future studies may also investigate the role of the central nervous system (CNS) in modulating the responsiveness of the spinal pathways that facilitate recruitment of the plantar intrinsic foot muscles. Responsiveness of the Ia-afferent pathway is known to be modulated in response to postural sway location and velocity in other muscles of the lower limb via pre-synaptic inhibition (Gatev et al., 1999; Tokuno et al., 2007; 2008; 2009). Thus it is possible that similar processes may also contribute to the regulation of plantar intrinsic foot muscle activation during postural tasks.

Knowledge gained from studies investigating the central and peripheral mechanisms regulating intrinsic foot muscle function may provide valuable insight to the importance of these muscles in balance control.

6.3.4 Can the function of the plantar intrinsic foot muscles be enhanced in order to improve efficiency of locomotion, increase performance and reduce the risk of injury and/or falls?

Given that this thesis has shown the capacity for the intrinsic foot muscles to provide active adjustments in LA stiffness, it is now of interest to determine if it is possible to influence the function of these muscles, in order to increase their capacity to contribute to the "foot spring" mechanism. This may involve studies that aim to improve neural activation and force producing capacity of the intrinsic foot muscles, in order to determine if these changes lead to an improvement in the foot stiffness regulation during locomotion. This may be particularly pertinent in individuals who display increased compliance in the LA, where increased strength of these muscles may allow more effective LA stiffness regulation, reducing load on the plantar aponeurosis. Changes in intrinsic foot muscle morphology (PCSA) and activity have been reported (Jung *et al.*, 2011*b*; 2011*a*) after specific 'short-foot' training exercises, providing some preliminary evidence that this is possible, however it is unknown whether these changes in muscle morphology relate to enhanced foot stiffness regulation. Longitudinal training studies evaluating changes in muscles strength and volume, as well as any resulting alterations in LA biomechanics may help to address these questions. Results from these studies may have implications for the use of strength training programs as part of rehabilitation from lower limb musculoskeletal injury.

It is also of interest to investigate if augmented stimulation of sensory cutaneous afferents on the plantar aspect of the foot can influence intrinsic foot muscle activation, thus providing an additional opportunity to modify the function of these muscles, enhancing postural control. As mentioned above, the SAI and SAII receptors on the sole of the human foot are thought to provide valuable information that enhances postural control during standing (Macefield, 2005; Lowrey *et al.*, 2013; Mouchnino & Blouin, 2013; Bent & Lowrey, 2013). Selective stimulation of these sensory afferents may increase the activation of the plantar intrinsic foot muscles during stance and gait. Ritchie and colleagues (Ritchie *et al.*, 2011) recently examined the effect of textured insoles that were designed with the aim to stimulate sensory receptors on discrete regions of the sole of the foot. They reported that foot motion was considerably altered when wearing the "stimulating" insoles, however these changes could not be attributed to any alteration in leg muscle activation. It is possible that the reported alterations in foot motion may have been due to activation of the intrinsic foot muscles,

which are located in close proximity to the cutaneous receptors on the plantar aspect of the foot and are now known to have substantial influence on foot biomechanics. Knowledge gained from these investigations may have implications for footwear design, specifically the incorporation of cutaneous stimulation within the insoles of footwear as an approach to improve balance control in the elderly, as weakness and dysfunction of these muscles is known to contribute to falls risk in this population (Menz *et al.*, 2005; Mickle *et al.*, 2009; Spink *et al.*, 2011).

6.4 Conclusion

This thesis has explored the hypothesis that the plantar intrinsic foot muscles play an important function in stabilising the longitudinal arch during postural and locomotion tasks. Results from this group of studies provide unique evidence that these muscles have the capacity to actively stiffen the longitudinal arch, augmenting the contributions of the passive ligamentous structures. Activation of these muscles is regulated in response to loading forces that are encountered during postural and locomotion tasks, allowing additional mechanical power to be absorbed and generated within the LA. These novel findings contribute substantially to our knowledge of functional anatomy of the plantar intrinsic foot muscles and control of longitudinal arch biomechanics. Information from thesis may now be integrated into applied research for health (musculoskeletal injury and rehabilitation), athletic performance and the development of lower limb prostheses.

6.5 References

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