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an approach to the "peripheral" mechanisms of lateralization

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The Mechanical and Physiological Properties of the First Dorsal Interosseous Muscle

An approach to the "Peripheral" Mechanisms of lateralization

PhD Thesis by

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Preface

This PhD thesis is based on four original papers. The four studies contain new methods of subject examination, data collection and data analysis techniques. Thedevelopment of the methodologies and presentation of the data collected was presented at numerous conferences through posters, oral presentations and mini papers .A detailed description and discussion on the methods and techniques used to analyse and present the data are contained within the relevant publications listed (1-IV). The prototype manual viscoelastometer and the automated viscoelastometer trialled in studies two and three is undergoing patent. Both devices are used primarily in research with future potential for wider clinical application.

Original papers

I .Gutnik, B. Yielder, P., Some mechanical muscle properties as indicators of the peripheral characteristics of manual asymmetry. -Submitted to *Biophysics* (under review and translation)

II .Yielder P, Gutnik B, Kobrin V, Leaver J, Guo W (2007) Viscoelastic properties of a skin-and-muscle compartment in the right and the left hands. -*Biophysics* **52,** 220-226 DOI: 10.1134/S0006350907020133

III. Gutnik, B. Yielder, P., Murphy, B., Kobrin, V. Reliability of an automated viscoelastometer and comparison of the viscoelasticity of the skin muscle compartment of the left and right hands - Submitted to *Biophysics* (under review and translation)

IV.Yielder, P. Gutnik, B. Kobrin, V. Hudson, G. (2009) A possible anatomical and biomechanical explanation of the 10% rule used in the clinical assessment of prehensile hand movements and handed dominance. *The Journal of Electromyography and Kinesiology"*,**19**, e472 to 480. DOI:10.1016/j.jelekin.

Published Conference Proceedings:

1). Yielder, P., Gutnik, B., Miller, J. (2003). Peripheral factors influence the latency period of simple sensory motor reaction time. International Conference of Motor Control (Motor control and learning over the life span). University of Caen, Basse Normandie, France, 20-23 August. Pg. 172.

2).Yielder, P., Gutnik B. (2003). Abnormal features of the first dorsal interosseous muscle in vivo (Force torque muscle contraction and stiffness). 21st Australasian Winter conference of Brain Research. Queenstown, 30 August – 3 September. Pg 23.

3).Yielder, P., Gutnik, B. (2003). Anatomical features of the first dorsal interosseous muscle – structural morphology and MRI reconstruction. 21st Australasian Winter conference of Brain Research. Queenstown, 30 August – 3 September. Pg 23.

4).Yielder, P., Gutnik, B., Hudson, G., Smith, G., Kobrin, V. (2003). Anatomical features of the first interosseous muscle in vivo (Preliminary report). In Proceedings of Australasian Society for Human Biology Conference. Auckland, 7-10 December Population Migration and Diversity Abs. HOMO - Journal of Comparative Human Biology 55 (2004) pg 170.

5).Gutnik, B., Yielder, P., Nash, D., Hinkson, E, Lewis, C., Skirius, I. (2003). How elastic is the first interosseous muscle? In proceedings of Australasian Society for Human Biology Conference. Auckland, 7-10 December. Population-Migration and Diversity Abs. HOMO – Journal of Comparative Human Biology. 55 (2004) pg 154.

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10). Yielder P. Gutnik B. Hudson G. (2005) Peripheral muscular factors in the assessment of hand dominance. In proceedings of Movement Analysis 2005 – Building Bridges Auckland University. Pg.119-122.

11).Gutnik, B., Yielder P. Leaver J. Kobrin V. (2005) .The viscoelastic behaviour of the distal hand muscles in the lateral aspect. (FDI) In proceedings of Movement Analysis 2005 – Building Bridges – Auckland University Pg.115 – 118

12).Gutnik, B., Yielder, P., Leaver, J., Henneberg, M. (2005). Behaviour of distal human muscle under tensile stress"in vitro" – Approach to manual asymmetry. In Proceedings of Russian State Classical Academy – Movement and Clinical symposium "Current Problems in Modern Medicine" (M. Maimonides). p.33

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English summary

The study of cerebral lateralisation was pioneered by Paul Broca in 1860. This work formalised neural concepts of the principle that one hemisphere functionally dominates the other. Subsequent work has been strongly influenced by the concept of cortical asymmetry with cortical differences projected upon paired anatomical structures in the periphery. Studies in this area are often concerned with the functional anatomy and lateralized behavior of the distal hand muscles. The field has remained heavily influenced by the postulate that one side of the body dominates the other during motor behaviour. This focus on the centrally mediated contribution has meant that the contribution of peripheral influences to left-right asymmetry has not been adequately investigated.

This thesis features the left and right first dorsal interossei (FDI) muscles as test muscles for the study of the contribution of peripheral factors to left-right asymmetry. The FDI are intrinsic hand muscles which play a fundamental role in hand grip. The principal aim of the thesis was to design and perform a sequence of studies to quantify some of the mechanical and physiological properties of the first dorsal interosseous muscle (FDI) and also to discriminate the contributions made by some "peripheral" factors that influence human bimanual asymmetry. The overall hypothesis assumed that there would be differences between the right and left hands, specifically in parameters of stiffness and viscoelasticity, and in the production of muscle forces related to the peripheral geometry of the muscle to bone attachment angles of the first dorsal interossous muscle.

Study I was a post-mortem study which set out to identify and quantify some of the residual viscoelastic properties of muscle present in the dennervated state, in order to

differentiate the contribution of the inherent molecular properties of the muscle from overlying neurally mediated muscle tone. Biomechanical indices (yield points, the level of strain, viscoelastic energy, Young's modulus) did not demonstrate a significant difference between dominant and non-dominant hands. Study II aimed to develop a model inclusive of a mathematical approach to discriminate the relative viscoelastic contributions of skin, muscle and connective tissues using a new device purpose designed to quantify muscle visco - elasticity and stiffness in vivo. **This study reported "new data"** concerning the stiffness of the FDI in vivo from a sequence of compression movements in the dorsal- palmar direction but found no difference between the hands. Study III trialed an improved automated version of the manual device used in Study II and investigated it's inter-trial reliability in a comparative study of the tonal viscoelastic properties of the skin-muscle compartment of the left and right first dorsal interossei (FDI) muscles of the hands. The device was found to be highly reliable and again no significant right left differences were found in visco-elasticity and stiffness. Study IV utilized a novel MRI modelling approach to investigate peripheral differences in the intrinsic muscle force related to the geometry of the muscle attachment angle. The study also set out to determine whether the 10% rule (which states that in 10% of cases, the non-dominant hand will be stronger than the dominant) might be partially explained by muscle attachment angle. There was a significantly greater muscle volume for the right FDI muscle as compared to the left as measured from the reconstructed MRI slice data. Those participants who produced greater force with their non-dominant hand were found to have a greater angle of attachment. This study concluded that the 10% rule may be anatomically and biomechanically explained.

This work demonstrates that the classical model of manual asymmetry in motor performance could be enriched by reformulation and inclusion of the complexity of the peripheral muscle-osseous relationship.

Dansk sammenfatning

Resumé: De mekaniske og fysiologiske egenskaber af m. interosseus dorsalis I. En tilgang til de”perifere mekanismer for lateralisation”

I 1860 banede Paul Broca vejen for studiet af cerebral lateralisering. Dette arbejde formaliserede neurale koncepter om princippet, at én hemisfære funktionelt dominerer den anden. Konceptet om kortikal asymmetri har haft stærk indflydelse på det efterfølgende arbejde, hvor kortikale forskelle er blevet anvendt på parrede anatomiske strukturer i periferien. Studier på området beskæftiger sig ofte med de distale håndmusklers funktionelle anatomi og lateraliserede adfærd. Området er til stadighed under stærk indflydelse af postulatet om, at den ene side af kroppen dominerer den anden under motorisk adfærd. Dette fokus på det centralt formidlede bidrag har betydet, at bidraget fra perifere påvirkninger til venstre-højre-asymmetri ikke er blevet undersøgt i tilstrækkelig grad.

Denne afhandling bruger den venstre og højre første dorsale interossei-muskel (FDI) som testmuskler til studiet af bidraget fra perifere faktorer til venstre-højre-asymmetri. FDI er indre håndmuskler, som spiller en fundamental rolle i håndens gribefunktion. Det var afhandlingens vigtigste mål at skabe og udføre et studieforløb med det formål at kvantificere nogle af den første dorsale interossei-muskels (FDI) mekaniske og fysiologiske egenskaber og samtidig at skelne bidragene fra nogle "perifere" faktorer, der har indflydelse på den menneskelige bimanuelle asymmetri. Den overordnede hypotese var, at der ville være forskel på den højre og venstre hånd, navnlig hvad angik parametre som stivhed og viskoelasticitet samt i produktionen af muskelstyrke i forbindelse med den perifere geometri af den første dorsale interossei-muskels fastgørelsesvinkler til knoglen.

Studie I var et obduktionsstudie, som havde til formål at identificere og kvantificere nogle af de tilbageværende viskoelastiske muskelegenskaber i den denerverede tilstand med henblik på at differentiere bidraget fra de medfødte molekylære muskelegenskaber fra den overliggende neuralt medierede muskeltonus. Biomekaniske indikatorer (strækgrænser, grad af overbelastning, viskoelastisk energi, Youngs mål) påviste ikke en signifikant forskel mellem dominante og ikke-dominante hænder. Studie II tilstræbte at udvikle en model, inklusive en matematisk metode, til at skelne de relative viskoelastiske bidrag fra hud, muskel og bindevæv ved hjælp af en nyt apparat, som var udviklet til at kvantificere muskelviskoelasticitet og stivhed in vivo. Studiet resulterede i "nye data" om FDI's stivhed in vivo fra en række klemmebevægelser i dorsal-palmar-retningen, men påviste ingen forskel mellem hænderne. Under studie III afprøvede man en forbedret, automatiseret udgave af det manuelle apparat, som blev anvendt under studie II, og undersøgte dets pålidelighed i et komparativt studie af de tonusviskoelastiske egenskaber ved hudmuskelrummet på den venstre og højre første dorsale interossei-muskel (FDI) i hænderne. Det blev konstateret, at apparatet var særdeles pålideligt, og igen blev der ikke påvist nogen signifikante højre-venstre-forskelle i viskoelasticitet og stivhed. Under studie IV blev der anvendt en ny MRI-modelleringstilgang for at undersøge perifere forskelle i den indre muskelstyrke i forhold til geometrien af muskelfastgørelsesvinklen. Studiet forsøgte også at fastlægge, hvorvidt 10 %-reglen (som siger, at den ikke-dominante hånd vil være stærkere end den dominante i 10 % af tilfældene) delvist kan forklares med muskelfastgørelsesvinklen. Der var en betydeligt større muskelvolumen for den højre FDI-muskel sammenlignet med den venstre i målingerne fra de rekonstruerede MRI-data. De deltagere, som producerede større styrke med deres ikke-dominante hånd, viste sig at have en større fastgørelsesvinkel. Dette studie konkluderede, at 10 %-reglen muligvis har en anatomisk og biomekanisk forklaring.

Dette arbejde viser, at den klassiske model for manuel asymmetri i motorisk præstationsevne kan beriges ved omformulering og inklusion af kompleksiteten ved det perifere muskel-ossøse forhold.

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Glossary of General Abbreviations

AIR	Australian Institute of Radiography
ANOVA	Statistical method for the analysis of variance.
AutoCAD 2004	Automated computer aided draughting (Software package)
CCC	Concentric contraction
CMC	Carpo - metacarpal
CT	Computed Tomography
DICOM	Digital CD viewer
2D	Two dimensional
3D	Three dimensional
ECC	Eccentric contraction
EMG	Electromyograph
FDI	First dorsal Interosseous muscle
FOV	Field of view
fMRI	Functional magnetic resonance imaging
Gd-DTPA	Gadolinium chelate – exogenous contrast agent
PCSA	Physiological cross sectional area of the muscle
MCP	Metacarpophalangeal
MPRAGE	Magnetisation prepared gradient echo (acquisition sequence)
MRA	Magnetic Resonance Angiography
MRI	Magnetic resonance imaging
MTB	Muscle Tendon Bone Unit (Whole muscle analysis)
MVC	Maximal voluntary contraction.

NMR	Nuclear magnetic resonance
NZIMRT	New Zealand Institute of Medical Radiation Technology
RF	Radio frequency Pulse
ROI	Region of interest
T1	Inversion time
T2	Decay time
TE	Transverse excitation
TR	Transverse relaxation
UNITEC	Institute of Technology in Auckland New Zealand

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Introduction

This PhD thesis features the bi lateral first dorsal interossei (FDI) muscles and is principally concerned with the problem of the peripheral influence and contribution that these muscles and their associated osseous and connective tissues make to bimanual actions and bimanual performance asymmetry. Early work in the study of cerebral lateralization pioneered by Paul Broca (1861) introduced the principle of cortical asymmetry and established the hypothesis that one hemisphere functionally dominates the other. Subsequent work in neuroscience has been strongly influenced by this classical approach. Over the last 50 years some research in the field of bimanual actions has offered a different orientation than the classical emphasis on cortical dominance favouring an approach that emphasizes complimentary hemispheric specialization (Hecean and De Ajuriaga 1964) (Guiard 1987) (Hecean and De Ajuriaga 1964; Hellige 1993). In this sequence of research, the principle of lateral specialisation_was modified to assert the complimentary actions of both hands in bimanual performance and the adaptive advantage of complementariness in human manual specialisation.

This trend reflects the neurophysiologic realization that a theory assigning connectivity and complimentary motor and cognitive functions to the two halves of the brain would possess better explanatory capability than one assuming that one hemisphere is more important or sophisticated than the other. However, despite anatomical and functional evidence that a complimentary relationship exists between the bi-hemispheric and the bilateral manual (motor) systems, a conceptual translation from *lateral dominance* to *lateral specialization* and complimentary bilateral bimanual function has not really taken place in the study of manual skills. Even though frequency of the use of the term *lateral* *dominance* has declined in the contemporary literature, the field remains heavily influenced by the postulate that one side dominates the other in the various expressions of motor behavior.

Central and Peripheral Dichotomy

Many of the problems considered current in the study of movement coordination were recognized during the first half of the 20thcentury by the Russian neurophysiologist and movement scientist Nikolai Bernstein. His assertion that the central nervous system's (CNS) hierarchy of control mechanisms for posture and movement is organized hand-in-hand with distributed and parallel processing, which is also subject to evolutionary pressures, challenged the view held in McGraw's and Gesell's time (O'Boyle 2006) of a hierarchical system within the body whereby commands for movement were issued by the brain. Bernstein's view was that motor development was not primarily dependent on brain maturation, but was also heavily influenced by adaptations to constraints of the body (changes in the growing infant's body mass and proportions) and responses to exogenous conditions (gravity, surface, specific tasks to be performed). He posited that performance of any kind of movement results from an infinite variety of possible combinations, or degrees of freedom, involving neuromuscular, skeletal and connective tissue elements emphasizing the complexity of the interrelationship between movement co-ordination and localization (Bernstein 1967). His mathematically derived movement equations complimented his descriptive functional analogues that defined two essential movement patterns, namely the chain cycle (peripheral associations) and the comb cycle (top down associations). The chain cycle contains the mutual interdependence between the position and the moment involved in the movement and is purely mechanical. So this type of approach implies that the motor system may be considered as self-organizing, with body elements coordinated, or assembled, in response to specific tasks reactive to exogenous and peripheral influences that are not directly under the control of the brain. His comb cycle assimilates the chain cycle as a foundation principle of movement expression, emphasing a similar interdependence between the position and the degree of excitation ***(E).*** This connection is physiologically based on reflexes but is related to the activity of the central nervous system. The traditional view accepted and retained by physiologists and clinicians is biased towards the comb, top-down domain of Bernstein's second cycle (Annett 1998; Dassonville et al. 1998; Amunts et al. 2000; Gazzaniga 2000; Sainburg and Kalakanis 2000). Within this scheme, a central impulse always produces a movement and the peripheral components are under dominant control of central impulses. The executor in the cortical motor area (M1 - Brodmann Area 4) performs, therefore, like a distributor with push button controls. However, Bernstein's view is that this approach ignores the state of the periphery which can produce completely different effects because of the interplay of external forces and variations in internal conditions. Since its original inception in Russia, and eventual dissemination in the West, Bernstein's approach has become influential within the numerous sub-disciplines of the study of human movement and motor behaviour. It also rather uniquely presents a historical foundation and precursor to current theories and ideas involving neural and musculoskeletal plasticity. A recent expression of Bernstein's thought, continuing the discussion on the central vs. peripheral dichotomy and the theme of adaptive plasticity referring to the hand hemisphere system is discussed by Carson (Carson 1993), in the guise of a behavioral approach adopting dynamic systems theory.

Possible Peripheral Factors

Bernstein's approach contains an implicit challenge to consider peripheral influences as fundamental components in the study of movement patterns and particularly in those involving inter-limb coordination and lateralisation. Rather paradoxically peripheral influences in general, and those involving lateralization and the phenomenon of handedness in particular, are poorly specified and are rather inadequately represented in the literature. However, over the last decade the study of the peripheral contribution
In the context of surgical joint reconstruction and limb function has featured sophisticated modelling work involving the transmission of forces both inside and between adjacent skeletal muscles and connective tissue elements. This approach has demonstrated that morphologically defined muscles are not exclusively independent actuators but are capable of mechanical interactions via their connective tissue structures (Huijing 1998; Meijer et al. 2007). The term myofascial force transmission is now commonly used to indicate force transmission via pathways other than myo tendinous routes (Rijkelijkhuizen et al. 2007), hence myofascial force transmission between muscles fibres and fascial connective tissues is influenced by the arrangement of the intramuscular stroma of adjacent muscles and the intramuscular connective tissues.   To execute movement, momentary forces need to be exerted at various locations within the musculoskeletal subsystem and in order to exert force onto the skeleton, active or passive force generated within the sarcomeres of muscle fibres has to be transmitted across the sarcolemma and the various connective tissues involved (Huijing et al. 2007). When combined with the biomechanical features and the geometric arrangement of the tissues,

these contributing factors co-determine how much force is exerted, both actively and passively, in a given state or instance of movement.

This complex morphological arrangement and interplay of tissues also determines, to some extent, the viscoelastic properties of muscle (Huijing 1992) and the mechanical strength of the intramuscular connective tissue compartment during the development and ageing of living skeletal muscle (Carmeli et al. 2003). These visco-elastic properties are dynamic within living muscle and preserved to some extent within the molecular structure as protein residues in post mortem muscle. There are some studies that that have approached the question of the periphery using morphological and compositional techniques to disclose patterns of lateralization. Walters et al. (1998) identified higher bone mineral density in the ulna of the dominant forearm and this was reported as a possible index of dominance. The compositional argument being preceded by Mortensson and Thonell (1991) to explain why in trauma to the upper extremities, fracture incidence is twice as common on the left as on the right side.

There are also studies indicating that the architectonics of muscle conformity may contribute to the general influence of peripheral factors that dictate handedness, (Jozsa et al. 1981; Fugl-Meyer et al. 1982; Tanaka et al. 1984; Gutnik et al. 2004) The architectonic theme related to reactive muscle plasticity and the involvement of peripheral connective tissues is reported by Adam et al (1998) who observed that preferential use of selected muscles is known to initiate changes to physiological characteristics and mechanical responses. The author attributed these changes to alterations in fibre type and internal composition with associated neural adaptation and changes to the contractile mechanics of the sarcomere, and hence the visco-elastic behaviour of the muscle.

Viscoelasticity and Stiffness

Movement is generally considered to be a consequence of the forces applied to the skeleton by muscles, involving the activity of cross bridges within the sarcomeres and also the elasticity of tendons. Tendons are the medium by which the force generated within an activated muscle is transmitted to the skeleton with modification to the original force produced by interaction with the material properties of the tendon and modulation by the neural pathway involving the Golgi tendon reflex circuitry (Kubo et al. 2000; Fukuanaga et al. 2001). When muscles tendons and ligaments are stretched, the essential molecular composition and tissue structures resist the stretch and exert an elastic force upon the skeleton. For tendons, the stretch can be caused by either a passive increase in the joint angle or an active shortening of the muscle fibres. For ligaments, the stretch occurs when some mechanical action (perturbation) causes a distraction of the articulating surfaces. This stress strain relationship is quite complex and with regard to the performance of muscles often leads to a consideration of the *relative stiffness* of the movement system. So why is it considered important to develop techniques to quantify stretch, elasticity and stiffness? In clinical work understanding of the stress-strain properties of the musculoskeletal system in vivo during the static state and also during normal movements is an essential foundation for understanding the mechanism of muscle trauma when mechanical stress is the leading factor (Roy and Edgerton 1992). Viscoelasticity and musculoskeletal stiffness are likely to be modified by the age, nutrition and the physical activity level of the individual. Stiffness is also subject to variation in the magnitude of the mechanical properties of different categories of the same material with suprisingly little or no standard reference data reported (Watkins 1999).

Hooks Law and Young's Modulus - methods for discriminating viscosity and elasticity

The principle of the method used to quantify viscoelasticity and stiffness adopted in studies II and III is based on Robert Hook's original work involving the stress strain properties of balanced timepiece springs (Watkins 1999). His work contributed a method used to quantify the elasticity and force-influenced behaviour of stretched tissues. When the magnitude of the stretch is relatively small, the elastic force can be represented by the properties of an ideal spring as defined by Hook's Law where $Fe = - kx$ (Fe = elastic force; k =spring stiffness; x = elongation). However, to distinguish between small and large stretches, the force length relationship of tendons and ligaments are usually divided into an elastic region and a plastic region (Enoka 2002). In the elastic region, the tissue behaves like a spring; however when the stretch parameters extend into the plastic region, the structure of the tissue is altered and the slope of the force length relations changes. These dynamic changes to the elastic behaviour of the tissue are usually regarded as 'stiffness". These changes are specific to tissue type and among structural subtypes of the same tissue. In most materials, all or part of the stress strain curve within the elastic range is linear, conforming to Hook's Law. Hence the linear profile of the stress strain curve is referred to as the Hookean region with the gradient profile of the curve quantified as the modulus of elasticity (E) being defined as the ratio of stress ***(ợ)*** to strain (ϵ) or "Young's modulus of elasticity" a constant in the mathematical equation named after Thomas Young who extended the original work of Hook (Watkins 1999). Young's work adopted defined the stiffness of a material being the resistance of the material to deformation, referred to as the stress per unit strain producing a modulus that evolved as a standard measure of stiffness for comparing different materials with the modulus indicating the amount of stress needed to produce 100% strain. Strain represents the change in length of the tissue relative to its initial length, therefore the stress strain characteristics are representative of the intrinsic force capacity and extensibility of tendons, ligaments and elastic connective tissues.

Muscle Tone and Viscoelasticity

Clinical deliberations on the normal expression of elasticity and stiffness in skeletal muscle and connective tissues invariably lead to a consideration of the significance of muscle tone. Muscle tone is a state of continuous partial contraction of a muscle dependent on the integrity of a monosynaptic reflex arc. Minimal healthy muscle tone contraction level is approximately five twitches per second, based upon the summation of the twitches of many fibres excited asynchronously at low frequencies. Up to five per second (or 5 s^{-1}) generates a total force that does not fluctuate (Schmidt et al. 1985; Cohen and Wood 2005). This is neurally mediated muscle tone, or the more commonly encountered characteristic state of partial contraction commonly referred to as *normal muscle tone.* It is partly maintained by continuous excitation of motor impulses with the primary goal of maintaining body posture. Normal muscle tone is abolished if any part of the essential reflex arc is destroyed (Schmidt et al. 1985; Guyton and Hall 2005). If this occurs, the muscle becomes atonic and atrophies rapidly. Samsom et al (1998) distinguish two tonal states, active tone and passive tone. The active state of muscle tone is perhaps the simpler of the two to identify, as when a muscle extends and develops tension under stretch and is then restored to its original length when the tension is released (Cooke 1986). In this state, the muscle clearly expresses a range of tonal responses throughout the movement.

The passive tonal state is somewhat harder to identify however, as even when apparently functionally inactive, a skeletal muscle possesses variable elasticity and is capable of expressing subtle variations in “passive tone”. When adopted clinically, the term is most often used to describe muscular resistance to stretch. This is often expressed as the amount of contraction in a resting muscle seemingly related to concepts of passive and normal muscle tone. Arguably, a more precise definition would include the idea of a static balanced isometric contraction between agonist and antagonist (internal forces within the muscle) for the purpose of maintaining joint integrity and posture.

Nevertheless, despite variance in the use of the terminology, clinical models that seek to quantify muscle tone may be of use when evaluating patients with conditions that subjectively exhibit increased or decreased tone in skeletal muscle. It follows that it is important to measure tone in individuals without impairment or disability to serve as a comparison. Investigation of the stiffness and tonicity of the skeletal muscle system are also important when assessing levels of adaptation and training (Gosselin et al. 1998; Almeida-Silveira et al. 2000; Rosager et al. 2002; Bojsen-Moller et al. 2003; Magnusson et al. 2003; Magnusson and Kjaer 2003) as these states may be altered in a number of CNS pathologies. Rather surprisingly, there is no fully validated method used to measure the level of muscle tone or in its extreme state “spasticity”, although there are numerous sources that express muscle tone and visco-elasticity for clinical purposes using the

Ashworth five-point scale (Bohannon and Smith 1987; Sloan et al. 1992; Haas et al. 1996; Gregson et al. 2000).

Viscoelasticity has been shown in various studies to exert marked influences on human motor behaviour and is a general term adopted to describe the function of a composite, biological material containing a combination of stiff and elastic fibres embedded in a gel medium that predispose the tissue to its unique behaviour. Inherent viscoelasticity is therefore a significant contributor to subjective states of muscle elasticity and stiffness. Both of these states are difficult to quantify, nevertheless they are often reported as a criterion and index of effectiveness and efficiency of muscle adaptation (Magnusson et al. 2001) during contraction and movement and also an expression of the level of flexibility in the different kinematic chains (Voigt et al. 1995; Watkins 1999).

Handedness and the 10% Rule

For the last 350 years it is possible to identify a line of research that is concerned with the study of cortical lateralization, and the phenomenon of dominance within the motor system that projects onto the periphery. It is well known that most people are right handed, and that in the majority of these cases the left cerebral cortex is apparently dominant and that this dominance extends through the descending pathways of the motor system involving the distal, and rather less frequently the proximal portions of the limbs (Annett 1998; Dassonville et al. 1998; Amunts et al. 2000). This apparent a priori emphasis on cortical lateralization during motor execution implies a genetic predisposition to express an architectonic and functional asymmetry with much of the literature on bimanual charatecteristics still concerned with uncovering the precise mechanisms of handed dominance (Elliott and Chua 1996) and how these are conditioned by cortical lateralization. The behaviorist approach asserts that handedness is the clearest example of behavioral lateralization in humans (Corballis 1981; Springer and Deutsch 1981; Bragina and Dobrochotova 1984; Kolb and Whishaw 1995; Annett 1998; Annett 1998; Corballis 2003) and it is generally agreed that the majority of people show a pronounced asymmetry between the hands in motor performance, usually favoring the right hand (Coren and Porac 1977; Annett et al. 1979; Todor and Smiley 1985; Roy and Edgerton 1992; Elliott and Chua 1996).

Much research on manual asymmetries is therefore concerned with two major aspects of handedness, notably preference and comparative performance asymmetry. Given the emergent interest in the study of peripheral factors it is rather surprising that there has been very limited investigation of these factors related to handedness and the contribution they make to bi manual co-ordination and individual muscle function.(Jozsa et al. 1981; Fugl-Meyer et al. 1982; Tanaka et al. 1984; Gutnik and Hyland 1997; Gutnik et al. 2005). This may be partly explained by the anatomical arrangement and functional complexity of the hand. Napier (Napier 1956), attempted to classify the function of the hand as a whole unit based on prehension mechanisms. Prehension movement involves grasping or taking hold of an object that is usually categorized as precision grip or power grip. These highly skilled movements represent the remarkable synthetic integration of the human hands adaptive capability to grasp or wrap around an object (Carmeli et al. 2003). In the developmentally accomplished form, these movements they are are unique to humans, although similar primitive patterns are observed in other primate species. There are therefore numerous clinical techniques that adopt anthropometric variables and study force measures to assess hand dexterity and preference, principally to provide indicators of underlying pathology.

One of these techniques featured in study IV is the 10% rule that is often invoked in the dynamometric approach to determine lateralization of hand function. The rule states that in 10% of cases, the non-dominant hand will be stronger than the dominant hand and is generally applied in situations where the non-dominant hand produces less force that the dominant hand (Provins et al. 1982; Mathiowetz et al. 1984; Mathiowetz et al. 1985; Gutnik 1990; Bohannon 1997; Bohannon 1997; Hanten et al. 1999; Incel et al. 2002). However the basis of the 10% rule is rather uncritically and unconvincingly explained in these studies. Study IV presents the possibility that the 10% variance may be partly explained by the complex role of peripheral factors and the individual arrangement of the anatomical components of the various muscles and osseous segments involved in the compartmental biomechanics.

The First Dorsal Interosseous Muscle (FDI)

The dorsal interossei muscles are located within the dorsal muscular compartment of the human hand developing from the fusion of the primitive dorsal abductors and short flexor muscles of the fingers (Lewis 1965). They are usually classified as *bipennate* muscles, referring to muscles that possess a central tendon or myo-fascial partition that seperates the muscle tissue. The first dorsal interosseous muscle (FDI) is the largest of the four dorsal interossei. It is also classically named the Abductor Indicis, inhabiting the dorsal inter - digital space between the thumb and index finger. The FDI is considered the most important because of the role it performs during execution of prehensile movements. Both academic and surgical literature agree that the FDI performs a stabilizing influence upon the muscles of the thenar compartment during pinch and grip movements of the thumb and index finger (Bilbo and Stern 1986; Riodan 1995). Bilbo also observes that a significant difference exists in the performance of these movements between the dominant and non dominant hands (Bilbo and Stern 1986). Anatomical accounts of the FDI muscle usually describe two heads or bellies. The largest is the radial head arising from the proximal half of the ulnar border of the 1st metacarpal bone. The smaller ulnar head arises from the proximal 2/3 of the radial border of the second metacarpal bone. The radial head, is the larger of the two, contributing about 65%-70% of the entire muscle mass (Bilbo and Stern 1986). The literature contains ambiguities and inconsistencies in the descriptive classification and it is clear to the critically informed reader that descriptions of the attachment and insertion sites have been oversimplified even though a number of morphological variations are identified by cadaver dissection surgical intervention and imaging studies (Naouri and Kuhlman 1984; Masquelet et al. 1986; Van Sint and Rooze 1992; Fuglevand et al. 1993; Smith et al. 1996; Difelice et al. 1998). However, there is consensus that the attachments of the FDI muscle are not single pointed or projected upon precise osseous targets and that they may constellate as singular or multiple loci with the potential for considerable variability between individual subjects (Bilbo and Stern 1986). In this thesis, Study IV is partly concerned with the geometric arrangement of these attachment sites and the action of the deep radial head of the muscle as rather paradoxically the role and significance of this deep head, the larger of the two bellies, especially on thumb action has not been well studied. The importance of the attachment angle of this head of FDI and its contribution to force production during an arc of horizontal movement has not been previously investigated, which is rather surprising as the radial head of the muscle is often involved in reconstruction surgery following trauma.

Commentary on the Deep Radial Head of the FDI

There are only a small number of intramuscular electromyographic (EMG) studies that have investigated the importance of the deep radial head of the FDI to thumb movement, in particular those movements involved in precision grip. When the insertion of the FDI onto the base of the proximal phalanx of the 2nd digit is held fixed, the primary action is exerted by the deep head of the FDI which attaches to the ulnar border of the first metacarpal. This portion of FDI is also positioned to contribute substantially to the force produced during tasks where the hands are held stationary in a pronated posture and the thumbs are used to guide an object such as when using a lathe or guiding a piece of timber through a sawbench. In this situation, the primary axis of movement is occurring at the point of attachment of the FDI on the ulnar border of the first metacarpal**.**

Studies based on fine wire EMG recordings during a number of thumb movements, demonstrate that the FDI is an essential muscle for the execution of precision grip which is movement of the thumb, to bring it towards the index finger (second digit), as occurs during a precision grip and handling (Long et al. 1970). They describe precision grip as requiring that compression be maintained between the thumb and index finger and that specific arch-like thumb positions are held rigidly. In a study using fine wire EMG in the hands of 115 subjects, Long et al (1970) studied the EMG activity of both intrinsic and extrinsic hand muscles during a variety of functional tasks involving precision grip and power grip and manipulation of hand tools. He demonstrated that during clockwise turning of a knob involving precision grip, the FDI acts strongly on the first metacarpal joint of the thumb, and is quiet during the return phase. Likewise, during counter-clockwise rotation, the FDI is quiet during the handling phase and active during the return phase of the movement. More recently, Johanson et al. (2001) recorded the activity of a number of intrinsic hand muscles, including the FDI, with fine wire EMG during a variety of pinch tasks in both a stable and unstable conditions. FDI contributed a significant amount of force to all the pinch tasks involving force application with thumb. An earlier study by Johansen et al. (1996) clearly showed that FDI acts as a phasic muscle during thumb closing in all hand positions. EMG studies have further confirmed the role that the FDI plays in the grip on the most commonly used modern tool, the computer mouse (Agarabi et al. 2004). For some individuals, the amplitude of EMG activation from the FDI was greater than the extrinsic hand muscles located in the forearm, when subjects gripped the mouse, in an isometric hold with the force exerted in the direction of drawing the thumb in towards the hand. The FDI has also been adopted as target muscle in studies using transcranial magnetic stimulation (TMS) as it has a strong cortical drive and is easily accessible via surface EMG and easily excited using TMS. Interestingly, there are no hemispheric differences in suppression of intracortical inhibition (ICI) during a graded isometric contraction of FDI (Zoghi and Nordstrom 2007), indicating that an *a priori* difference in ICI between the two hemispheres may not be the central mechanism by which lateral preferences are manifested. This lends support to the notion that preferential use may lead to peripheral changes that influence hand function, and makes the contribution of peripheral factors in FDI asymmetry worthy of further study.

Aims of the thesis and the four studies

The principal aim of the thesis was to design and perform a sequence of studies to quantify some of the mechanical and physiological properties of the first dorsal interosseous muscle (FDI) and also to discriminate the contributions made by some "peripheral" factors that influence human bimanual asymmetry. The initial hypothesis assumed that there would be differences between the right and left hands, specifically in parameters of stiffness and viscoelasticity, and in the production of muscle forces related to the peripheral geometry of the muscle to bone attachment angles of the first dorsal interossous muscle. Studies I-IV are reported in the following chapters prefaced by a commentary on general methodological considerations pertinent to the design of each of the four studies. A more detailed account of the development of these methods with a full summary and report of the findings can be found in the published articles and those submitted for publication. as listed in the preface on pages 3/4 of this thesis.

General Methodological Considerations:

Ethics

All subjects who participated in the three in vivo studies in New Zealand gave their informed consent. None had any history of neurological or muscular disorders. All studies were conducted in accordance with the Declaration of Helsinki and were approved by the ethics committees of the academic and clinical institutes involved.

Ethical permisssion for the Cadaver study was granted by Adelaide University South Australia and perfomed at the Department of Anatomy in the School of Medicine.

Subject groupings

Study I involved 13 cadaver subjects (9 males and 4 females). Known correlates of behavioural and morphological asymmetry, utilized by Kulaksiz & Gozil (2002), Plato, Wood and Norris (1980) and Stoklosa (1992) were used to determine handedness from a group of 40 cadavers. Only those cadavers where there was a clear difference (>10%) size increase of the bi-epicondylar and bi-styloid circumferenceson the right side were designated as probable expressors of right handed ness in life and included in the study.

Study II involved a group of 25 young male subjects. Study III involved a group of 22 young male subjects. Both groups of subjects were selected because of their strong positive assessment of right handedness.

Study IV (Part A) involved an initial group of 25 young male subjects selected for their strong positive assessment of right handedness. Those participants from part A, with laterality indices greater than 85% for right handed dominance were invited to participate in Part B.

Study IV (Part B) Nine out of eleven of those invited agreed to participate in Part B, the MRI calculated-force study.

The standard position of the hand used in studies II III IV

The sequence of the three in vivo studies involved a baseline anatomical position of the hand with the palmar surface of the hand in contact with the base plates of the respective data collection devices. In this position the longitudinal axis of the FDI muscle is aligned parallel to the longitudinal axis of the hand. The angle between the axis of the thumb and the segments of the index finger was close to 90 degrees as in previous kinematic research reporting force production from the FDI muscle (Tanaka et al. 1984; Lieber 2002). In this position the dorsal surface of the hand confronts the observer and the (FDI) muscle is accessible to palpation and surface analysis. It is possible to assign topographical landmarks and also locate the radial artery pulse; the likely site of origin of the interfascicular partition between the radial and ulnar heads of the (FDI) muscle.

Assessment of Handedness and the Edinburgh handedness Inventory.

The design of all four studies required a preliminary assessment of participant handedness to initiate the overall aim and study theme of the contribution of peripheral factors upon bimanual asymmetry**.** There are numerous approaches used to assess handedness usually requiring some form of assessment based on comparative observation of a task related to bimanual performance or assessment of the difference of magnitude of maximum isometric force produced by each hand (Brand and Hollister

1999). Preeminent in the conventional assessment of handedness is the work of Annett (1967) and Oldfield (1971) who developed questionnaires using the traditional approach based upon the contextual belief that human skills reside in the special capabilities of the so called dominant hand. In the three *in vivo* studies, preliminary assessment of handedness was established using the commonly adopted Edinburgh Handedness Inventory (Oldfield 1971). The inventory allows the calculation of a laterality quotient, where +100 represents complete right hand dominance, and – 100 represents complete left hand dominance. Strong right handedness is deemed to be a laterality quotient of + 85 or above on the scale of the Edinburgh Handedness Inventory (Oldfield 1971). However as Guiard (1987) points out, questionnaires on hand preference systematically include questions relating to bimanual actions - in other words, actions when both hands contribute to the action. Significantly in Annett's questionnaire (1967), five of the eight items refer to bimanual acts and in the popular "Edinburgh Handedness Inventory" (Oldfield 1971) eleven of the twenty items presented relate to bi manual acts. In the more recent 75 item questionnaire of Provins and Milner et al. (1982) the task inventory demonstrates a similar paucity of unimanual tasks relevant to the study of manual preference.

Study I Principles and general description of the method used to assess viscoelasticity in Cadaver Muscle

This post-mortem study set out to identify and quantify some of the residual viscoelastic properties of muscle present in the dennervated state, as in the *in vivo* state it is difficult to differentiate the contribution of the inherent molecular properties of the muscle from overlying neurally mediated muscle tone. It was initially hypothesized that there would be significant differences in the post mortem viscoelastic properties of the dominant and non-dominant FDI muscles possibly reflecting the adaptations to the neural drive during life. The sample of 13 preserved cadavers included nine males (65 to 96 years old) and four females (63 to 90 years old) and is a typical number of cadavers used for anatomical research (Smith et al. 2003). All cadavers were preserved with an ethanol glycol mixture containing less than 1% formaldehyde. Both FDI muscles were removed from the cadaver hands and subjected to stretching using a force length technique previously applied to preserved tissue and the testing of post-mortem specimens (Yahia et al. 1993; Sokolis et al. 2002; Barker et al. 2004). The muscle was suspended in the stretching device in the baseline position and measured (Figure 1). The corresponding force, produced by the tensile stress of the stretched muscle during each step of the incremental movement, was measured and recorded by a force meter scaled in corresponding kilograms of weight (kg) with 0.05 kG graduations on the scale. Units of kg were converted to Newtons (1 kg corresponding to 9.81 N) for further calculations. On completion of the straining process indicated by the tearing of muscle fibres, the muscle was detached from the device and its length measured once again along the initial longitudinal axis. Calculations of the stress-strain characteristics and total viscoelasticity of each sample of muscle tissue were perfomed using an adapted mathematical technique similar to the approach used by Linder-Ganz and Gefen (2004) with an extension to the model to indicate regions of elastic and plastic behaviour.

Figure 1: Stretch device with cadaver muscle in situ

Study II Principles and general description of the method used to Assess Viscoelasticity in living Muscle

Study II was designed to measure stiffness of the relaxed muscle in the vertical direction using a force dial (stress strain) elastometer (Gutnik et al. 2003; Yielder et al. 2003; Gutnik et al. 2004). The principle of the vertical approach is that under direct compression, muscle as well as other elastic soft tissues will be deformed. This level of deformation will be associated with a resistance to the original deformation, and this difference can be measured and expressed in units of force, calculated using a tension stiffness plot. This method has been used previously to discriminate changes in the mechanical behaviour of the contractile and elastic elements of muscles and tendons (Granzier and Wang 1993) and other biological tissues (Stidham et al. 1997; Uchiyama et al. 1998). This differs to Morgan's approach (Morgan 1977; Cook and McDonagh 1996) where the stiffness of the muscle was measured in the active state, during a short period of eccentric muscular contraction. The manual device specifically designed for this study was named a force dial visco-elastometer as demonstrated in Figure 2. The device incorporated a monitoring stylus with a diameter of 3.5 mm, providing a monitoring sensitivity of 0.001 N connected to a signal encoder and signal amplifier interfaced to a computer incorporating the design software to calculate the tension stiffness plot.

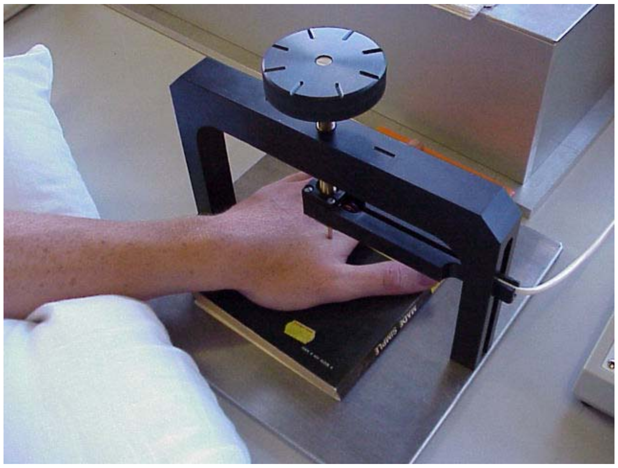

Figure 2: Manual Force Dial viscoelastometer

All participants were asked to sit in a completely relaxed sitting posture with the arm partially flexed at the elbow and the forearm extended. The hand being examined was placed under the stylus of the elastometer in the standard position. The stylus was positioned on the dorsal skin surface over the FDI muscle compartment in contact with a predetermined skin location. The participant was blindfolded when initial light touch sensation from the stylus was confirmed and was then asked to achieve a state of relaxed awareness and to try to maintain this state throughout the trial. For six participants, the stylus was applied to four to six locations with Ag-AgCl surface EMG electrodes in place over the belly of the FDI, to confirm that there was no EMG activity during the viscoelastometer application. The EMG was sampled at 1000 Hz and bandpass filtered between 10 and 500 Hz using a two channel PowerLab system (ADI instruments). EMG could not be monitored during the main experiment because the recording electrodes would have obscured some of the application sites. The overall strain and sampling range of compression of the cutaneous-muscular structure was regulated by the subject and terminated when a subjective sensation of pressure discomfort was reported.

Study III The Automated Elastometer

The automated device featured in study III contained several improvements over the original manual elastometer. A review of the performance of the manually controlled force applicator indicated that is was subject to operator inconsistencies, specifically the speed of application which relied on the operator of the device being able to maintain a consistent rate of force application, across subjects and for both hands. The design of the automated viscoelastometer incorporates a monitoring stylus of 3.5 mm diameter, providing a sensitivity of $1x10^{-3}$ N. The improved device applied a graduated compression to muscle and viscoelastic tissues with progressive deformation using a calibrated precison motor drive. The level of deformation is therefore precisely controlled and associated with resistance to the original deformation measured and expressed as units of force (Figure 3). The rate of deflection was held constant at 0.43 mm/s as it was determined in preliminary experiments to be the fastest rate that avoided painful sensation and which did not elicit stretch reflexes and involve central mechanisms in the reaction. The data processing chain involved a signal amplifier, computer and purpose designed interpretative software.

Figure 3: Photograph of automated viscoelastometer

Study IV a) Principles and general description of the method used to assess the push force using the dynamometer

In study IV, the isometric model of force assessment was adopted principally because isometric testing of skeletal muscle under laboratory conditions in vivo is a common assessment tool (Wilson 2000) and because isometric strength tests are considered to possess high test-retest reliability (Viitasalo et al. 1980; Bemben et al. 1991). This approach is used to quantify muscle strength because the force developed in an isometric concentric contraction will not decrease as a function of the speed of the shortening of a muscle (i.e., force-velocity relationship rule) (Herzog 1998), therefore maximal force production occurs during isometric muscular work.

In Study IV part A, subjects were asked to push the button of a purpose designed electronic dynamometer as powerfully as possible. Headphones were placed on the subject who was asked to react to a sound tone (1000 Hz) by isometrically pushing the button as strongly as possible without regard to the time of development of the force. The signal interval between stimuli was 10 seconds in order to avoid fatigue.

The hand was positioned in the standard position with the palmar surface of the distal phalanx of the thumb adjacent to the centre of the push button. The angle between the axis of the thumb and the axis of the segments of the index finger was close to 90 degrees (Figure 4) where the deep radial head of FDI was in a position to provide a large contribution to isometric force production

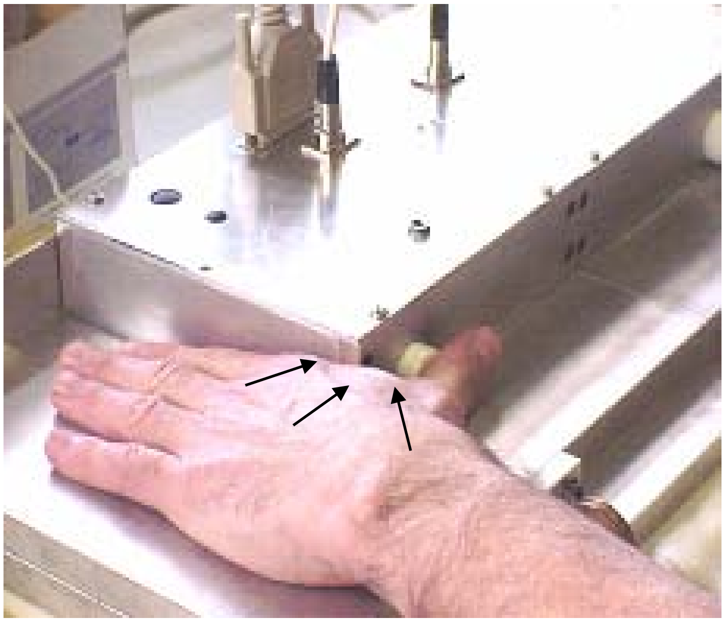

Figure 4: Measuring the Force of FDI with the electronic push force dynamometer. Arrows are pointing to the FDI muscle belly, under tension.

Study IVb) Method used to assess the Calculated force of the FDI

Magnetic resonance imaging (MRI) was introduced into the clinical repertoire of diagnostic imaging in 1981and has emerged as the modality of choice for the demonstration of many organ systems and is well suited to demonstrate components of the musculoskeletal system. Study IV, part B features structural MRI, combined with a purpose designed modelling technique, to examine the basis of the 10% rule previously discussed. The design of this approach is a response to difficulties encountered by in vivo muscle researchers when attempting to isolate individual moments of force and specifying functional characteristics attributable to an individual muscle when the muscle is functioning within its synergistic group (Herzog 2000). In order to overcome some of these difficulties, various modelling techniques involving clinical imaging modalities notably MRI, CT and Ultrasound have been developed (Maganaris and Baltzapoulos 2000). In this study a conventional clinical magnetic resonance imaging technique was adopted to aquire data for further processing and analysis. In study IVb, two image acquisition sequences per hand were performed with the hand positioned in the standard position previously described. MRI data were acquired using a 3-D Turbo FLASH expanded MPRAGE (Magnetisation Prepared Rapid Gradient Echo) acquisition sequence (Siemens Corp) designed for the precison imaging of musculosketal structures (Stark and Bradley 1999; Bernstein et al. 2004) using the following sequence specifications (MPR 12.*R ***(T1)*** 300ms: TR. 9.7ms: TE.4ms: FOV 175x200: 1.5mm -2 mm slice- thickness using a high resolution 12 cm diameter surface coil. The data was acquired using a no gap technique and spatially assigned using a 256 X 256 matrix with a four minute acquisition time per sequence. The modelling technique developed for study IVb was based on a contouring approach combined with a mathematical and biomechanical model that uses surface extraction as the first step in establishing a geometric hierarchy within the data. Applied to format images it establishes spatially accurate tissue relationships, profiling point sources, faces and margins within the data and is well suited to the examination of individual tissues and relationships between defined tissue data sets (Maganaris and Baltzapoulos 2000). This situation prevails as long as the viewing port is standardised and the user does not change viewing parameters. A theoretical necessity with this approach is the requirement to integrate 2D and 3D slice reconstruction techniques when using 2D sections to reconstruct and visualize 3D solid bodies (Sirakov et al. 2004). This modeling design adopted a two stage geometrical approach (Boissonnat and Geuger 1993) (Moody and Lozanoff 1997). The initial data set was configured in 3D within the MRI system and transported into AutoCAD 2004 (Fowler et al. 2001). The final muscle contour – line of action was based on the 3D summation of consecutive 2D extracted muscles slices. The osseous centroids were 3D volumetric calculations performed by the AUTOCAD software representing individual subject and group standardised anatomical locii in a spatially standardized viewing port (Rusinek et al. 1989). Further in order to ensure that the observed differences reported were not due to differences in gross muscle size, muscle volume for both the right and left FDI muscles was calculated from the reconstructed muscle slice data. The method involved a grid system superimposed on the scaled image of each muscle slice with the area of each slice recorded. Each slice area was multiplied by the slice thickness and the slice volumes added to obtain overall muscle volume.

Discussion of the Four Studies

Study I. Some mechanical muscle properties as possible indicators of the peripheral characteristics of manual asymmetry

As previously introduced this method was designed to quantify residual energy stored in the FDI muscles of cadavers as in the post mortem state the molecular properties of muscle devoid of cortical influence are inherently preserved. The FDI muscles were chosen because in life they have a strong cortical drive emanating from the contralateral hemisphere and are more likely to demonstrate preserved differences in the viscoelastic properties between the dominant and non-dominant hands (Herzog 1999; Gazzaniga 2000; Lieber 2002; Hamill and Knutzen 2003; Linder-Ganz and Gefen 2004). It was hypothesized that there would be significant differences in the post mortem viscoelastic properties of the dominant and non-dominant FDI muscles possibly reflecting the neural adaptations in life and that neurally mediated muscle tone could be considered as a type of system noise that could be eliminated by the use of inert muscle in its final dennervated state. This would accomplish the goal of isolating purely peripheral factors for study, as post mortem muscle is devoid of the influence of alpha motor neurones and the regulatory action of motor units and is not functionally influenced by contractile elements and cross bridges. These muscles do however; possess residual dead proteins from connective tissue, specifically the myofascial membranes (Herzog 1999; Lieber 2002; Hamill and Knutzen 2003; Linder-Ganz and Gefen 2004) with a residue of inherent viscoelastic properties that perform like a type of biological rubber band. Although this type of study has limitations associated with the use of preserved tissue, there is support for the general approach offered by various studies and propositions within the literature. The method adopted to stretch the cadaver FDI muscle cadaver is precedented by studies perfomed on the muscular characteristics of different muscles under applied tensile stress (Titze 1994; Magnusson et al. 2000; Rosager et al. 2002; Khalsa and Ge 2004), inclusive of the related principle that accurate discrimination of viscoelastic characteristics may be used as an index indicating the effectiveness and efficiency of muscle adaptation (Magnusson et al. 2000). Some studies using changes in force and length have produced scales reporting levels of overall "stiffness" (Cook and McDonagh). The force length type study approach has been previously applied to preserved tissue and the testing of post-mortem specimens (Yahia et al. 1993; Sokolis et al. 2002; Barker et al. 2004).

This study compared paired the FDI muscles from 13 cadavers that were subjected to graduated tensile stress. Mass, density, yield point, Young's modulus and two variables of stored energy were recorded. From a total set of 117 variables of nine selected indices from 13 cadavers, 45 (38.5%) possessed a greater magnitude on the non dominant side. Overall, the muscle stretch capability, as calculated, corresponds to previously reported values in the literature (Wang et al. 1991). The mathematical model approach is this study is designed to indicate regions of elastic and plastic behaviour. The data demonstrating elastic behaviour were modelled by a linear equation using MS- EXCEL software ($R^2 > 0.98$). A pseudo-Young's Modulus (E), expressed in N/mm, was determined from the linear equation and is representative of the muscle stiffness (Lieber 2002) in the elastic range (Hamill and Knutzen 2003). The pseudo-Young's modulus is the ratio of the induced force to the deflection in contrast to the classical definition of Young's modulus that is the ratio of induced stress to strain.

The individual data reported here demonstrate substantial individual variance in the range of all reported variables, probably attributable to age-related degenerative changes in life (Deschenes 2004). While it is acknowledged that a cadaveric approach has limitations because preserved muscle tissue undergoes significant shrinkage during the fixation process (Yamaguchi et al. 1990) with muscle bundle shrinkage being reported to be as high as 20% (Friederich and Brand 1990) the chemical effects of preservation and the age and gender of the cadavers of these cadavers would be essentially similar between hands and should not impact detrimentally on the results of the paired comparisons. The findings on the peripheral variables of the residual characteristics preserved in these muscles do not provide unequivocal support for right handed dominance. There was only one index, representing the specific energy of the total muscle deformation that was significantly greater on the dominant side. This may indicate that cortical asymmetry is not entirely reflected in the peripheral properties of muscle. This is likely to be related to substantial individual variance in part attributable to environmental adaptations and age related, degenerative changes in life. This approach offers a method for the quantification of residual energy stored within inert tissue and the findings offer qualified support for Bernstein's overall view that a complimentary interplay exists between cortical and peripheral levels. *In vivo*, these potential states of peripheral autonomy and laterality are likely to be cortically conditioned within the overall field of motor control. It is therefore challenging to develop techniques to discriminate and quantify these states in the living subject particularly with regard to the complex musckuloskeletal changes that occur during the aging process notably alterations to the viscoelasticity of connective tissues and stiffening of muscles.

Study II. Viscoelastic properties of a Skin and Muscle Compartment in the right and left Hands

Musculoskeletal stiffness is a complex state said to be influenced by the age, nutrition and physical level of activity of the individual. Chronic effects of ageing and altered physical activity usually occur over time leading to structural changes in the architecture organisation and composition of the various tissues involved (Carmeli et al. 2003). The effects of temperature, strain rate and loading history applied to these tissue may also effect acute changes in the functional architecture with associated changes to collagen cross links in the visco elastic tissues. The stiffness state is generally considered to be difficult to standardise and quantify, hence stiffness values are often variably reported. In study II we have reported and quantified "total stiffness" in the static state as a product of passive, intrinsic and reflex mediated components in healthy young males. The study featured the use of of a unique device that was named a force dial elastometer (Gutnik, 1990). The principle of the method has been previously described. During the compression procedure the stylus mechanism progressively indented the musculocutaneous compartment with the vertical movement and compression increment being applied via a screw applicator operated by one of the researchers. Stiffness was measured on both hands. Each trial contained three data acquisition sequences performed upon each hand and was completed within 60 - 90 seconds. A precise sequence detailing the mathematical model and statistical methods used to process and report the data are included in the text of study II.

Our sequence analysis provided the elastic modulus and the specific energy of deformation for both the total tissue compartment and also the separate cutaneous and muscular compartments. Both individual and group data were analysed. The study demonstrated a broad range of peripheral laterality (cumulative index of right hand preference). In this study no isolateral differences between the elastic modulus and specific energy for either the muscular or cutaneous compartments were identified, initially suggesting a parallel to research that did not demonstrate statistical differences between gross sizes of isolateral structures (Mysorekar and Nandedkar 1986; Alter 1996). The behavioural component of this study specified a controlled state of relaxation, without significant voluntary cortical input to the muscle. In this case the state of potential dominancy of the right FDI muscle in these strongly right handed subjects would be arguably diminished, modifying the classical predisposition of imposed dominancy on the muscle by the motor cortex of the left hemisphere (Kandel et al. 2000) as the state of compressive deformation of the muscle in this study occurred during a diminished state of neuromuscular activation (e.g. muscle relaxation). However, the application of the stylus with the muscle in a passive state seemed to evoke spinal stretch reflexes which were interpreted as a response to the technique of the incremental sequence and the timing during the compression procedure. Studies using electrophysiological measures have revealed significant changes in these passive properties in spastic conditions in the lower limb (Sinkjaer and Magnussen 1994). Some investigators have presented the idea that changes in the intrinsic muscle properties are largely responsible for spastic hypertonia while other other investigators conclude that the major cause of spastic muscle hypertonus is the widely accepted pathological increase in the stretch reflex activity (Ashby et al. 1987; Thilmann et al. 1991). The work on the significance of the stretch reflex and its integrative significance within the central nervous system comes from Sherrington’s original animal studies, however the role of the stretch reflex incident from muscle receptors has remained controversial despite the large number of studies that have been carried out over the years targeting the apparent simplicity and arrangement of the strong monosynaptic connections from primary muscle spindles to α – motorneurons (Liddell and Sherrington 1924; Agarawal and Gottlieb 1985). This continuing controversy is representative of the difficulty encountered when researchers try to discriminate the mechanical consequences of reflex activity from those of the intrinsic properties of the muscle and the joint. Attempts to discriminate these properties have compared the mechanical behaviour of these tissues under normal conditions and in states of induced deafferentation, mainly using surgery, localised anaesthesia; or induced ischaemia (Sinkjaer and Hayashi 1989). Paradoxically, clinically focussed research emphasizes the dynamic profile of stiffness as a product of stretch reflex activity produced during specified joint movement. The dynamic approach is multi-faceted and also attempts to discriminate and quantify stretch reflex and intrinsic contributions to the overall stiffness profile (Kearney et al. 1997), contrasting with the approach adopted in this study that specified an ipsilateral muscle in a passive state. The relevance and use of handedness “questionnaires” with emphasis on the theme of “dominant characteristics” is raised by the results reported in the index of laterality. These results suggest differential modes of preference adopted by the hands within the scale of bimanual movements as opposed to dominance, an interpretation that is broadly in agreement with the theoretical assertion contained in the work of Guiard (1987). It may, however, be pre-emptive to suggest that the current emphasis on “dominance” should be replaced by an approach emphasising preference and complimentary reciprocity when studying human lateralization.

Study III. Reliability of an automated viscoelastometer and comparison of the viscoelasticity of the skin muscle compartment of the left and right hands

Study III features the use of an automated viscoelastometer less dependent on operator control than the previously described manual version featured in study II.

It has been discussed previously that inherent viscoelasticity is considered to be a significant contributor to subjective states of muscle elasticity and stiffness. However both of these states are difficult to quantify, nevertheless they have been reported as a criterion and index of effectiveness and efficiency of muscle adaptation (Magnusson et al. 2001) contraction and movement (Voigt et al. 1995; Watkins 1999) and also an expression of the level of flexibility in the different kinematic chains (Voigt et al. 1995; Watkins 1999).

In Study II, the paired FDI muscles were assessed for viscoelastic asymmetry with difference being observed between the right and left sides. However, the original study used a manually controlled force deformation applicator that was judged to be inconsistent when applying the force increment and also subject to operator inconsistency. There was also concern regarding the possible elicitation of stretch reflexes implying poorly controlled system noise sourced from the neural circuitry.

The automated device contained improved features over the manual prototype. Principally the addition of an adaptable stylus arm that extends the possible use of the device and further development of the technique to sites other than the distal limb muscles and the use of an automatic driver to standardise the compression procedure.

Improvements were also made to the data acquisition and data management components specifically improved calibration specifications to the auto compression motor drive and the internal specifications of the stylus applicator (patent pending). In this study 23 strongly right-handed male participants had three compressions each applied to the left and right first dorsal interosseous muscles of the hands. The average values for energy, specific energy and Young's modulus were calculated using these data for both the right and left hands of the individual subjects. Reliability was calculated using intraclass correlation co-efficients (ICC) and Paired T-tests were used to compare the left and right parameters related to stiffness

In this study, the ICCs for data specifying Total energy, Specific Energy, and Young's modulus indicated a high reliability (range 0.7 to .95) for all parameters confirming a high confidence in the use of the automated version of the device. The findings of the original study with the manual viscoelastometer (Yielder et al. 2007) were confirmed, in that there were no significant differences in viscoelastic properties between the right and left hands. This pattern of neutral assymetry may be explained by considering the homogenous selection criteria of the subject group even though individual differences in the mechanical properties of these tissues have been reported (Barney and LeVeau 1992; Alter 1996). These authors report that the concentration of collagen and elastin proteins (containing spring like qualities) is highly individualised and may be individually lateralised, rather paradoxically, without reference to handedness or hand dominance. We consider that habitual patterns of use as a form of training could induce adaptive changes and modifications in the contractile and elastic protein composition of the muscles involved. In vivo, these potential states of peripheral autonomy are likely to be cortically conditioned within the overall field of motor control, but nonetheless, represent an important consideration in studies of laterality.

Study IV. A possible anatomical and biomechanical explanation of the 10% rule

Study IV features the comparative quantification of forces and patterns of peripheral lateralisation produced by the FDI muscle from two different methods used to calculate the muscle force. The first method is an established technique commonly used to measure force in a dynamic push button task. The second is a new method designed to isolate the momentary force produced by the FDI muscle during an isometric contraction in a specific peripheral moment of the muscle, tendonous and bone relationship. This study was also concerned with the clinical assessment of lateralization of hand function and the hypothesis underlying the 10% rule adopted in the dynamometric approach to determine lateralization of hand function. In this study, a novel MRI based modelling approach was applied to the first dorsal interosseus muscle, to determine the significance of the 10% rule and to ascertain if the 10% may be partially explained by the arrangement of the anatomical components of the FDI and the functional states of connective tissues in the periphery. Initially the force generated by the movement of the thumb segment in the horizontal plane during an isometric pushing was measured from 25 strongly right-handed young males. Nine of these participants then had structural magnetic resonance imaging (sMRI) of the thumb and index osseous compartment. A modelling technique was used to extract the muscle data and quantify the muscle line of action onto to the first metacarpal bone segment in order to quantify the muscle force at the point of momentary rotation and static equilibrium. The technical specifications of the dynanometer data acquisition sequence and the progression of the design of the MRI modelling technique is presented and discussed in detail in Study IV.

The main finding from the push force dynometric study was that eight out of 25 subjects exhibited stronger force production from the left hand, while in the MRI modelling study six out of nine subjects possessed significantly greater angles of attachment of the index osseous compartment on the left (non-dominant) hand. These six subjects also generated greater maximal isometric forces from the FDI of the left side.

The results from the "Push Force Study" are broadly similar to reported lateralised force differences in the FDI muscles (Tanaka et al. 1984). There was overall group difference in force production between the left and right hands, a similar trend being reported alongside a critique of methods adopted to assess grip strength (Provins and Cunliffe 1972). These researchers regard the grip strength test as unreliable and in their opinion, parallel work is likely to produce some isolateral differences between left- and right-sided muscles. One of the shortcomings of this approach is that complex grip and pinch movements of the hands involve numerous functional compartments making it difficult to specify and quantify the precise contribution of the muscles and joints that are involved in force production during the various contractile states (Richards et al. 1996; Bohannon 1997).

In the MRI modelled force study, the results support the proposition that relative asymmetry of the maximal isometric forces generated by the FDI muscles is partly attributable to asymmetrical and different projectile angles of attachment of the bulk of the FDI to the 1st metacarpal (osseous) segment with the general conclusion that the greater projected muscle attachment angle is influential upon isometric force production and lateralization at the periphery. The articular relationship between the trapezium and 1st metacarpal bones during the isometric contractile state was also analysed and an instantaneous point of rotation representing the moment of the movement calculated and assigned using the AUTOCAD software. The resolution of the MRI images produced highly detailed anatomical images of the articular anatomy. Visual study of the trapezium and the 1st metacarpal articular interface confirms the involvement of a spherical facet adjacent to the anterior radial tubercle of the trapezium. This facet is probably responsible for the axial rotation of the metacarpal during compartmental movements. This is in accord with the view of Zancolli and Ziadenberg et al. (1987) who report that the saddle shaped facets are concave in the sagital plane (abduction and adduction) and convex in the frontal plane (flexion and extension). The spherical facet is convex in all directions (opposition and reposition). This implies that flexion and extension of the joint occurs along an oblique antero-posterior axis while abduction and adduction occur around a modified oblique coronal axis because of the angle of inclination and orientation of the trapezium.

This complex interrelationship dictates the range of movement performed by the first carpometacarpal joint and was initially reported by (Cooney 1981). In this report, flexion and extension occur in parallel orientation to the palm of the hand. Abduction and adduction are performed perpendicular to the palm and they simply state that the rotational movement occurs without offering a precise description. These descriptions prefigure discussion on the complex interplay of segmental movements of the thumb and index finger and the two main vectors associated with the complex interplay of osseous segments and locus of muscle attachments and insertions within the movement moment.

One of these vectors is associated with the rotary force that is considered to be primarily responsible for the pushing action on the button in Study IV, Part A (Smith et al., 1996; Hall, 1999). This vector is applied perpendicular to the osseous axis of attachment. The other vector represents the so-called “joint reaction force” that exhibits a type of dislocation action projected upon the trapezio- metacarpal joint involving both previously described articular facets on the lateral surface of the trapezium. Terminology to describe the complexity of this movement is lacking in the literature and is not discriminated by the standard texts in movement studies. Hence if the angle of attachment of the FDI is greater on the left hand, then the magnitude of the rotary force is potentially greater and consequently the muscle tension (force) produced is likely to be used more economically and/or with more effect. This would suggest that conventional dynamometric measurements of maximal isometric muscle force, even when derived from a single muscle, are imprecisely adopted when used to predict handedness.This type of study is an example of precision when modern clinical imaging techniques are integrated into the design of whole muscle in vivo study methods (Herzog 2000).

General Conclusions made from the results of the Four Studies

A comprehensive report and analysis of the results is contained within the associated reports and publications arising from each study. This brief section presents the general conclusions that directly relate to the formulated aims in this thesis leading to a short commentary on some of the practical implications and possibilities for future work.

Study I Biomechanical indices (yield points, the level of strain, viscoelastic energy, Young's modulus) in vivo and in post mortum examination have not demonstrated a significant difference between dominant and non-dominant hands. These results support the existence of molecular residues and functional states at the periphery that are not directly cortically influenced and are contributory to lateralised differences

Study II Stiffness of the FDI- this study has reported "new data" concerning the stiffness of the FDI in vivo from a sequence of compression movements in the dorsal-palmar direction. The range of this data for muscle is between (3.26 – 0.35 Newtons per/mm). Also quantified and reported is the specific energy of deformation of the muscle. This ranges between (23.9 - 1.04 Joules/mm).

Study III-this study reported reliability data for an automated version of the viscoelastometer. The automated device showed high inter-trial reliability with intraclass correlation co-efficients ranging from 0.7 to 0.95 for total energy, specific energy and Young's modulus.

Study IV (A) Reactive “push” force from previous studies is not representative of the intrinsic quantum of force generated by the FDI. The calculated force originates from the reciprocal contribution of central and peripheral factors. These parameters are highly individual and specific to individuals.

Study IV (B)

Anatomical Analysis indicates that the angle of attachment of the muscle to the osseous territory is significant when calculating muscle force: 67% of right handed participants produced greater muscle force from the non-dominant hand and this appeared to be related to attachment angle.

Practical Implications

Study I offers a method for the quantification of residual energy stored within inert tissue.While it is acknowledged that a cadaveric approach has limitations because preserved muscle tissue undergoes significant post mortem changes, the findings indicate that cortical asymmetry is not entirely reflected in the peripheral properties of muscle offering qualified support for Bernstein's overall view that a complimentary interplay exists between cortical and peripheral levels

Study II introduced the principle of the method and use of the elastometer with improvements made to the original device trialled and tested in study III.

Study III demonstrated that the automated visco-elastometer was highly reliable and has the capability to contribute to studies involving the assessment of muscle tone and muscle stiffness.

Study IV presents the possibility that the statistical tolerance involving the 10% rule may be anatomically and bio-mechanically explained.specifically because of the size, magnitude and geometry of the attachment arrangement between muscle and bone in combination with the viscoelastic properties of connective tissues.

The general trend that emerges from consideration of the results of the four studies would support the suggestion that the classical model of manual asymmetry in motor performance could be enriched by a reformulation that includes the complexity of the peripheral muscle-osseous relationship and visco-elastic properties. This reformulation could be considered to be complimentary to conventional theory and current practical testing procedures especially in cases when force production from the left hand is recognisably stronger even though grip dynamometry and handedness questionnaires indicate so called right handed dominance.

Possible Future work.

Study I Featured the residual viscoelastic properties of muscle present in the dennervated state post mortem. The conditioning and relative states of these viscoelastic components during various life stages could be studied using the viscoelastometer in transient denervation experiments to differentiate the contribution of active neuromuscular tissue from the passive components in vivo.

Study II and III

Given that muscle is anisotropic, it would be interesting to apply the elastometer at different directions (angles of pennation) relative to the lines of action of the muscle to determine the effects on measured visco-elastic parameters. We also attempted to measure stiffness in relaxed muscle, but as our results demonstrated stretch reflexes were possibly elicited, local anaesthetic nerve block could be used to transiently denervate the muscle so the peripheral factors could be studied independently of innervation (in vivo) It would be possible to utilize the viscoelastometer to characterize alterations in muscle and connective tissue properties that accompany various pathological states.

The possible relationship of cellular asymmetry to the origins of handedness is discussed in a motoneuron morphometric study performed at spinal cord level by (Melsbach et al. 1996) This study compared segmental innervation of the arms and hands with segments that innervated the upper trunk These authors demonstrated a pattern of morphological asymmetry within the spinal cord on a single cell level The viscoelastometry approach could be applied for investigation of spinal segmental reflex asymmetry between the right and left sides, we would be able to assess the amplitude and frequency of the stretch reflexes from the skeletal muscle tissue from both sides of the body and possibly graduate the level of asymmetry on the spinal level.

Study IV

It would be interesting to extend the modelling approach of the MRI study to determine if there are volume differences between the left and right sided muscles and also to perform a volumetric analysis to more accurately describe skin and muscle depth for the Young's modulus calculations in the stiffness study.

With regard to the internal forces that are generated within individual muscles, Comparative analysis of asymmetries in fibre type, blood flow and muscle function between the dominant and non-dominant hand has not previously been investigated for the FDI muscle. However recent work has indicated that functional magnetic resonance imaging (fMRI) has the potential to discriminate the relative proportion of slow twitch oxidative muscle fibres in relation to blood supply and capilliarisation (Liebner, 2002). This type of study could be very well matched to a morphological dissection study that reports the conformity of the muscle bellies, the topography of the so called attachment and insertion sites and also the nerve innervation to the discrete muscle heads and the pattern of arterial perfusion pathways.

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