The Pennsylvania State University

The Graduate School

Department of Kinesiology

THE IN VIVO EXPRESSION OF THE FORCE-LENGTH RELATIONSHIP AND ITS EFFECT ON SUSTAINED ISOMETRIC FORCE

A Thesis in

Kinesiology

by

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Submitted in Partial Fulfilment
of the Requirements
for the Degree of

Doctor of Philosophy

August 2007

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ABSTRACT

A fundamental property of muscle is the relationship between muscle fiber length and the force it produces. In vivo this relationship is expressed when isometric muscle actions are produced. In this study two aspects of the force-length properties of muscle will be examined. Firstly the source of expressed section of the force-length curve in vivo will be examined, and secondly the fluctuations in force during isometric muscle actions will be examined.

A generalized model of a mono-articular muscle-tendon complex was used to examine the effect of various model parameters on the section of the force-length relationship operated over for a 90 degree joint range of motion. Key architectural properties of muscle were identified and then were systematically varied in the model to examine their influence on the expressed section of the force-length curve. It was shown that the ratio of tendon resting length to muscle fiber optimum length was important in determining the amount of variability in the expressed section of the force-length curve. The effect of this ratio was modulated by the ratio of muscle fiber optimum length to average moment arm. These results indicate there is scope for inter-individual variation in the expressed section of the force-length curve.

In groups of young (19 to 28 years old) and young-old females (66 to 71 years old) isometric knee extensions were performed at 25%, 50%, 75% and 100% of maximum effort. The fluctuations in the moment records were quantified using standard statistical techniques (e.g. standard deviation and coefficient of variation) and methods from statistical physics (e.g., signal complexity, and signal fractal properties). There was no difference between age groups or effort levels in the coefficient of variation. The young females demonstrated more complexity in the knee joint moment signal at all effort levels. There was also different fractal like scaling behavior over shorter and longer timescales,

suggesting that two or more different processes may be responsible for the fluctuations in the joint moment during isometric contractions. Young-old females generally demonstrated scaling characteristics that indicated more slowly repeating processes. To investigate to what extent these differences were influenced by strength levels a similar group of young and young-old females participated in a ten week program of strength training. Strength training produced a small decrease in the coefficient of variation but not in the standard deviation of the moment record in both the young and the older age groups. The complexity of the joint moment record and the fractal like scaling remained unchanged due to training, this suggests that these measures reflect a training resistant factor that deteriorates with age, a possible candidate is the calcium kinetics at the level of the sarcoplasmic reticulum.

In the final experiment a single muscle was examined, which was the first dorsal interosseus. By using this muscle the length and potentially the expressed section of the force-length curve could be manipulated. Subjects produced isometric contractions at long, medium and short muscle lengths and at 5%, 10%, 25%, 50%, 75% and 100% of maximum in three finger positions corresponding to short, medium, and long muscle lengths. The fractal like properties of the signal indicated that two or more different processes may be responsible for the fluctuations in the force produced during isometric contractions. The magnitude of the coefficient of variation was greatest at short muscle lengths, and the fractal like properties were also altered at these lengths; there was no indication of any influence of expressed section. Different motor unit firing characteristics required to achieve full activation at short muscle lengths may explain these results. The differences in the results for this muscle compared with the quadriceps muscle may be due to differences in the relative contributions of motor unit recruitment and rate coding to force gradation in these muscles.

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ACKNOWLEDGEMENTS

I would like to thank the people who kindly donated their time as my subjects. I also need to thank Nori, Nick, Joe, and Jim for their technical assistance. My committee were all generous with their time and constructive in their comments and I really enjoyed working with all of them.

My parents, my sister Emma, and her new family supported me throughout and this work, such as it is, is dedicated to them.

John was the best advisor ever and we had GREAT talks.

CHAPTER 1

INTRODUCTION

1.1 ISOMETRIC FORCE AS A MODEL FOR STUDY

The word ‘isometric’ comes from the Greek, ‘isometria’, meaning ‘equality of measure’. Isometric exercise has been used as an experimental model in biomechanics over centuries of study, and was mentioned by the ‘grandfather of biomechanics’ Giovanni Alphonso Borelli in ‘*De Motu Animalium’* published in 1680.

What exactly is meant by an ‘isometric’ muscle contraction depends on the scale at which the contraction is considered. For example, at the level of the sarcomere an isometric contraction is generally considered to be one where the sarcomere length does not change, whereas at the level of the muscle fiber, it would be considered that the muscle fiber length is held constant. However, the length of individual sarcomeres is likely to change along the muscle fiber (Gordon et al., 1966). At the whole body level in vivo an isometric contraction (sometimes called a static contraction in this context) would be one where the joints crossed by the muscle(s) of interest are held at a constant joint angle. In fact, as force is developed during such a contraction the muscle length changes during activation as the activated muscle produces a force that extends the tendons in series with it. This extension means that the muscle fiber shortens until there is no slack in the muscle-tendon unit. However, it is generally assumed that after a few seconds the muscle and tendon reach an equilibrium and the muscle length remains constant, albeit at a shorter length than when the muscle is at rest. Of course there is no guarantee that even though muscle-tendon complex length remains constant there are not subtle reciprocating changes in muscle fiber and

tendon length while the contraction is sustained. Despite these concerns about changes in the length of the muscle, isometric muscular contractions are used in a wide variety of situations.

Isometric muscle force can provide information about the strength of a muscle, and this capacity is an important determinant of successful motor performance, though the degree of muscle activation and the velocity of the contraction must also be considered when investigating dynamic movements. For example, isometric knee extension strength is considered an important predictor of capacity to perform activities of daily living such as standing up from a seated position (Hughes et al., 1996).

1.2 BACKGROUND AND PURPOSE

The maximum force that a muscle can produce in a given joint configuration is dictated by the force-length and force-velocity relationships, and the parallel and series elastic components of the muscle-tendon complex. The first part of this work identifies what variability may exist for the force-length relationship for different muscles in the lower limb. A muscle model is used to investigate possible sources of this variability.

When the isometric force output of a muscle during a sustained contraction at a given muscle length is measured it is found that the force is not constant, but rather fluctuates (Lippold et al., 1957). Variability in the isometric force produced by a muscle is important since it influences the performance outcome of motor tasks (Enoka et al., 2003; Hamilton et al., 2004). For example, the ability to accurately produce a force can affect the ability to hold or manipulate objects and maintain a desired limb trajectory, and this in turn will influence an individual's ability to perform activities of daily living, and potentially their susceptibility to injury as a result of accidents.

The second part of this work looks at whether these fluctuations in force are affected by the force-length relationship, that is, whether measures associated with the fluctuations in force change with muscle length. Various measures associated with the fluctuations in force will be established and used to quantify the magnitude and time dependent structure of the fluctuations in the resultant joint moment measured at the knee during isometric knee extensions. This experimental model is used since it is known that both young and old adults are able to activate the quadriceps muscle group that is responsible for knee extension to a very high degree (Suter et al., 1996). The effects of effort level, age, and training status on these measures will be quantified. These studies will establish that there are consistent and significant differences in certain measures associated with the structure of the force fluctuations for different age groups and force levels even when there is little or no difference in the magnitude of the fluctuations. The effect of strength training on these measures will be assessed.

Since the quadriceps is a muscle group composed of four muscles that may be operating over different sections of the force-length curve the quadriceps muscle is not a good model to investigate whether muscle length affects the fluctuations in force. Instead, isometric contractions of the first dorsal interosseus will be used to assess whether the force-length relationship affects the magnitude or time dependent structure of the force fluctuations. An advantage of using both the quadriceps and the first dorsal interosseus to investigate the fluctuations in force is that the two muscles rely to different extents on motor unit recruitment and rate coding to produce different levels of muscle activation (Roos et al., 1999; Kukulka & Clamann, 1981). It will therefore possible to gain insight into the effects of these two activation strategies on steadiness.

1.3 SPECIFIC AIMS

The specific aims of this work are as follows.

1. Assess the variability in the expressed section of the force-length curve in different muscles and identify potential factors that may explain the differences in this variability with respect to the parameters typically used in a muscle model.
2. Quantify the differences between young and young-old groups of females in the magnitude and time dependent structure of the fluctuations in the knee resultant joint moment during maximal and sub-maximal contractions.
3. Assess the effect of strength training in young and young-old females on the fluctuations in the resultant joint moment produced at the knee.
4. Assess the influence of muscle length on the fluctuations in force produced by the first dorsal interosseus.

1.4 OVERVIEW OF STUDIES

In the first study (Chapter 3) a muscle model is used to investigate the effect of the different anatomical parameters on the expression of the force-length relationship in different bi-articular muscles of the leg. This work leads to predictions about which muscles are most likely to demonstrate inter-subject variability in the expressed section of the force-length relationship. This study addresses specific aim number one.

In the second study (Chapter 4) the steadiness of isometric knee extension contractions is examined at different effort levels for young and young-old female adults. The magnitude and time dependent structure of the fluctuations in force are quantified. In this study various algorithms from the field of non-linear

dynamics are used to quantify the fluctuations in force. This work establishes that there are differences in the time dependent structure of the force-fluctuations at different effort levels, and for different age groups. This study addresses specific aims two and three.

In the third study (Chapter 5) the effect of strength training on the steadiness of isometric knee extension contractions is examined for different force levels in young and young-old female adults. This work establishes that some measures associated with the fluctuations in force change with strength training, but others appear to be fixed as a function of effort level and age. This work addresses specific aim four.

In the fourth study (Chapter 6) the effect of the force-length curve on the steadiness of isometric contractions at different force levels will be studied for a finger muscle, the first dorsal interosseus. This work addresses specific aim 5. It has been suggested that motor unit firing rates change with muscle length (e.g. Linden et al., 1991), if this is the case then this may influence the steadiness of isometric contractions at different muscle lengths. The first dorsal interosseus is appropriate for this analysis since it is the only muscle that produces forefinger abduction.

1.5 OVERVIEW OF THESIS

This thesis is presented in seven chapters. Chapter 2 reviews the relevant literature concerning the force-length relationship, what work has been done to establish its expression in vivo, and the work that has been done to quantify the fluctuations in the force or moment produced by a muscle or group of muscles. The four studies are contained in chapters 3 through 6, and a general discussion of the findings from these four studies is presented in chapter 7.

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CHAPTER 2

LITERATURE REVIEW

2.1 INTRODUCTION

This chapter reviews the relevant literature on the force-length relationship, and on the fluctuations in force that occur during an isometric contraction. The basis of the force-length curve at the sarcomere level, and then the expression of the force-length curve in vivo will be considered. The various ways of quantifying the magnitude and temporal structure of the fluctuations in force during an isometric contraction are described, and finally the changes in the magnitude of the force or torque fluctuations in response to certain factors and what this suggests about the potential source of the force fluctuations will be reviewed.

2.2 THE FORCE-LENGTH RELATIONSHIP

The earliest work on the variation in the maximum force generated by a muscle with the length of the muscle was described over a hundred years. Technical improvements in the preparation of isolated fibres later allowed experimenters to determine the relationship at the level of the sarcomere, which may be considered the functional unit of muscle. The general shape of the force-length curve was determined by Ramsey and Street (1940), and the ascending region of the curve was determined to have an exponential relationship. However, Gordon, Huxley and Julian later showed that a whole fiber preparation does not have uniform striation spacing along its length, meaning that sarcomeres at the ends of the fiber had more overlap than those in the middle and were thus still able to produce force (Gordon et al., 1966a). When they reinvestigated the

force-length relationship in their classic study (Gordon et al., 1966b) using a procedure that ensured uniform sarcomeres lengths, they elucidated the familiar curve that is now widely reported today (figure **2.1**).

The force-length relationship of skeletal muscle is explained by the cross-bridge theory. Within a sarcomere there are inter digitating thick (myosin) and thin (actin) filaments and the cross bridge theory states that force production occurs as a result of myosin cross-bridges attaching to actin binding sites (Huxley & Simmons, 1971). Certain assumptions are inherent within this theory:

1. The cross bridges are uniformly distributed along the myosin filaments, and the cross bridge attachment sites are uniformly distributed along the actin filaments.
2. The probability of attachment depends only on the proximity of a cross bridge to an available attachment site, and not to any prior history of attachment.
3. Each cross bridge, when attached, exerts the same force.

Thus the amount of tension developed depends on the number of cross bridges attached, and this in turn depends on the level of muscle activation and the degree of overlap of the actin and myosin filaments. For fully activated muscle this gives rise to a generic force-length relationship, shown in figure 2.1. The force-length relationship has three regions: the ascending region (points 3 to 4 in the figure), the plateau region (points 2 to 3) and the descending region (points 1 to 2).

It should be noted that despite the substantial evidence to support many of the predictions of the theories and the wide acceptance of the theories, not all researchers believe that the mechanisms of muscle contraction have been established irrefutably. For example, Podolsky and Schoenberg (1983) review

evidence that suggests that filament lengths, particularly in the myosin filament, may alter at short sarcomere lengths. There is also some evidence that the neck of the myosin heads may be slightly elastic (Huxley & Simmons, 1971).

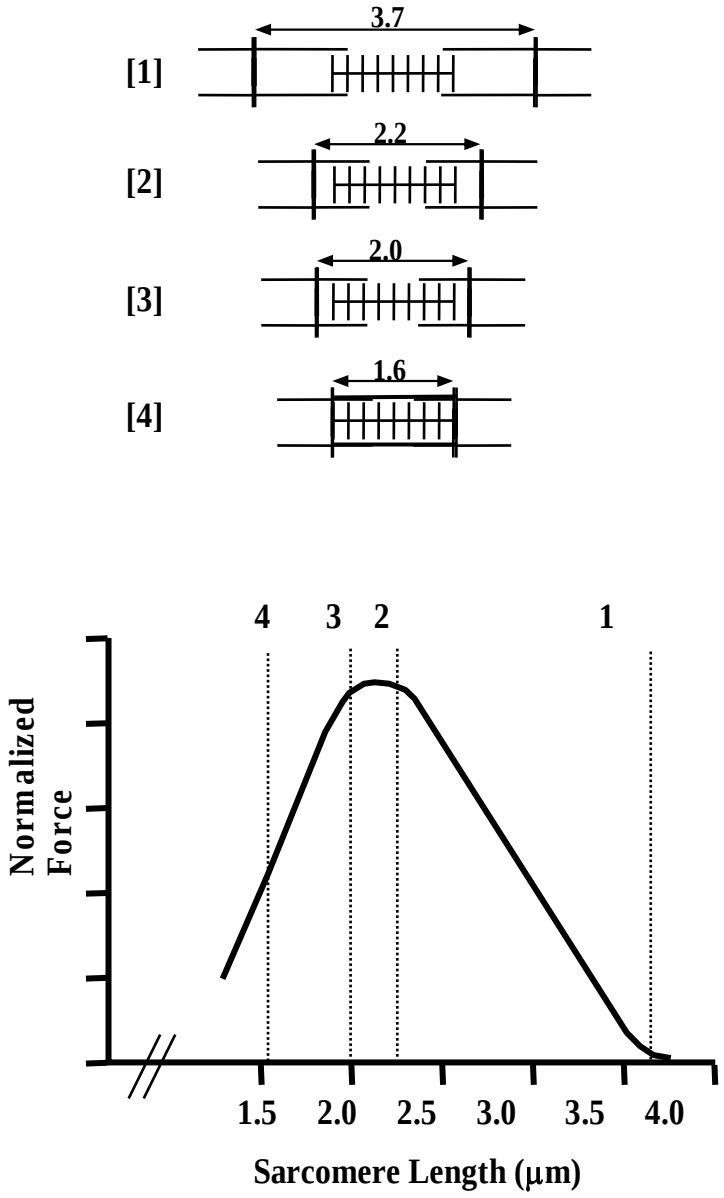

Figure **2.1**: The isometric force-length properties of the sarcomere of frog skeletal muscle, with examples of sarcomere overlap (based on data presented in Gordon et al., 1966b).

2.2.1 THE PLATEAU REGION

The plateau region of the force-length relationship corresponds with the lengths at which optimal overlap of the actin (0.95 µm in length in frog striated muscle) and myosin (1.6 µm) filaments occur (around 2.0 – 2.2 µm given a Z line width of 0.1 µm). Since the mid-zone (0.2 µm) of the myosin filament does not contain cross bridges optimal overlap occurs over a small range of lengths (all measurements are taken from Gordon et al., 1966b). Shortening or lengthening of the sarcomere beyond this small range results in a decreased production of force (Gordon et al., 1966b). Human striated muscle has a slightly longer actin filament length of around 1.27 µm (Walker & Schrodt, 1974) which leads to an optimum sarcomere length for force production of 2.6 – 2.8 µm.

2.2.2 THE ASCENDING LIMB

The ascending limb (sarcomere lengths up to 2.0 µm) corresponds to the decreased force production which results from cross bridge interference due to thin filament overlap as the sarcomere length shortens. At very short sarcomere lengths the force is considerably reduced as the myosin filaments abut the Z line. The Z line is the structure that delimits the sarcomere and is the perpendicular connector between the parallel thin filaments. In certain studies, some of the decrease in force production may be attributable to reduced calcium release from the sarcoplasmic reticulum (Rudel & Taylor, 1971), though this does not alter the general shape of the force length relationship at short muscle lengths.

2.2.3 THE DESCENDING LIMB

The descending limb of the force-length curve (from 2.2 to 3.6 µm) corresponds to the decreased overlap that occurs with increasing sarcomere length. A study

by Edman and Reggiani (1987) found that the upper and lower portions of the descending limb were slightly curved giving the descending limb a symmetrical sigmoid appearance, which they suggested was due to small non-uniformities in sarcomere length. These non-uniformities would have the effect of allowing some force production at the greatest mean sarcomere lengths.

2.3 FLUCTUATIONS IN THE FORCE PRODUCED DURING ISOMETRIC CONTRACTIONS

When an individual performs an isometric contraction the force or torque output fluctuates (Enoka et al., 2003). Changes in the nature of this variability seem to occur with aging (Tracy et al., 2004; Vaillancourt & Newell, 2003), training status (Keen et al., 1994), the intensity of contraction (Sosnoff et al., 2005), and the muscle or joint under consideration (Hamilton et al., 2004).

Typically, the analysis of force variability has proceeded from a viewpoint that fluctuations in the force or acceleration profile will adversely affect the completion of motor tasks (e.g. Christou et al., 2003) since they will make the trajectory of the intended movement unpredictable. Hamilton et al. (2004) proposed that a fundamental motor control strategy should involve minimizing the influence of any such variability. Some researchers have measured force steadiness in order to track recovery following nerve impingement (e.g. Bandholm et al., 2006). Researchers working from this viewpoint have typically measured the magnitude of the force fluctuations using measures such as the standard deviation of the force record, or the coefficient of variation (see section 2.3.1). However, algorithms drawn from the fields of statistical mechanics and non-linear dynamics have increasingly been applied to biological time-series over the past decade. Studies analyzing the time-dependent structure of have shown that a wealth of information is present in these physiological signals that cannot be detected by simple statistical measures. These studies have shown that these algorithms

can differentiate between old and young joint kinematics during walking (Kurz & Stergiou, 2003), healthy and pathological heart beats (Lake et al., 2002), and maximal isometric plantar flexion moments in young and old men (Challis, 2006). Two of the measures that will be used in chapters 4, 5, and 6 will be described in Section 2.3.2: Sample Entropy and the Detrended Fluctuation Analysis. Instead of quantifying the magnitude of the variability, these measures quantify the variability in terms of the predictability of the variability.

2.3.1 QUANTIFYING FLUCTUATIONS USING SIMPLE STATISTICAL MEASURES

If it is often assumed that these fluctuations are normally distributed around a fixed value, or mean force then the standard deviation (SD) of the force gives information about the dispersion or size of the fluctuations. The coefficient of variation (CV) is a dimensionless ratio that standardizes the standard deviation in terms of the mean, so that the fluctuations can be compared for different force levels and conditions. Expressing the magnitude of the fluctuations in terms of the CV can be useful in order to demonstrate whether the magnitude of the fluctuations scales in a simple way with force or effort level (e.g. Tracy & Enoka, 2002; Hamilton et al., 2004). These two measures are the most common way of quantifying the force fluctuations during isometric contractions and are the measure of choice in the vast majority of studies carried out on fluctuating force or moment records, for example Hamilton et al., (2004), Sosnoff et al., (2005), Keen et al., (1994). The Root Mean Square Error (RMSE) has been used in a small number of studies (e.g. Vaillancourt & Newell, 2003). However, a problem with the use of these simple statistical measures is that they are really only appropriate when applied to normally distributed populations. One of the properties of the fluctuating force record that has been revealed by the use of Sample Entropy and the Detrended Fluctuation Analysis is that the fluctuations in

force are not normally distributed (e.g. Vaillancourt & Newell, 2002), so the utility of the SD, CV and RMSE is difficult to judge.

2.3.2 QUANTIFYING FLUCTUATIONS IN THE FREQUENCY AND TIME DOMAINS

As the force output is sampled at equally spaced time intervals the collection of force values forms a discrete time parameter series to which signal processing or time series analysis techniques may be applied. The structure of the force signal has been analyzed in the frequency domain using spectral analysis (Vaillancourt & Newell, 2003), and in the time domain using Approximate Entropy to quantify signal regularity (ApEn) (Sosnoff et al., 2005) and a Detrended Fluctuation Analysis to determine the presence or otherwise of long or short term correlations (Vaillancourt & Newell, 2003). The following sections will outline the theoretical basis of these measures.

2.3.3 QUANTIFYING THE FRACTAL SCALING INDEX USING A DETRENDED FLUCTUATION ANALYSIS

Self-similar processes have the property that they are composed of units, sub-units and sub-sub-units over multiple levels that statistically resemble the structure of the whole object. The fractal scaling index gives information about the range of timescales over which characteristic behavior is repeated. For a one dimensional times series, this means that when the x and y axes are expanded by similar factors, similar fluctuations are seen for many expansions of the two axes. Self-similarity has been measured in many different situations, for example self-similarity has been shown to exist in the fluctuations in the stock market (Mandelbrot & Van Ness, 1963), the finishing times of a marathon race (Alvarez-Ramirez & Rodriguez, 2006), and in the repeating branching pattern of the lungs (Peng et al., 2000).

A problem with physiological processes is that they are bounded, that is they can adopt y values only within certain ranges, and this means that the y axis expansion will not scale in the same way as the x axis expansion. For example, blood pressure measurements cannot take on any value, instead in vivo blood pressure measurements are restricted to a certain range outside of which the individual may be considered dead. Integration of a physiological time series maps the bounded process to an unbounded self-similar process (Peng et al., 1995) allowing the computation of the self-similarity or scaling parameter α.

The Detrended Fluctuation Analysis (DFA) is used to calculate the scaling parameter. In this algorithm, the time series is first integrated and then the vertical characteristic scale of the integrated time series is measured. The integrated time series is divided into boxes of length n and a least-squares line is fitted, representing the trend in each box. The y coordinate of the straight line segment of length n in the kth box is denoted by $y_n(k)$, and the integrated time series is detrended by subtracting the local trend in each box. For a given box size, n, the characteristic size of fluctuation for the integrated and detrended time series is given by Equation **2.1**.

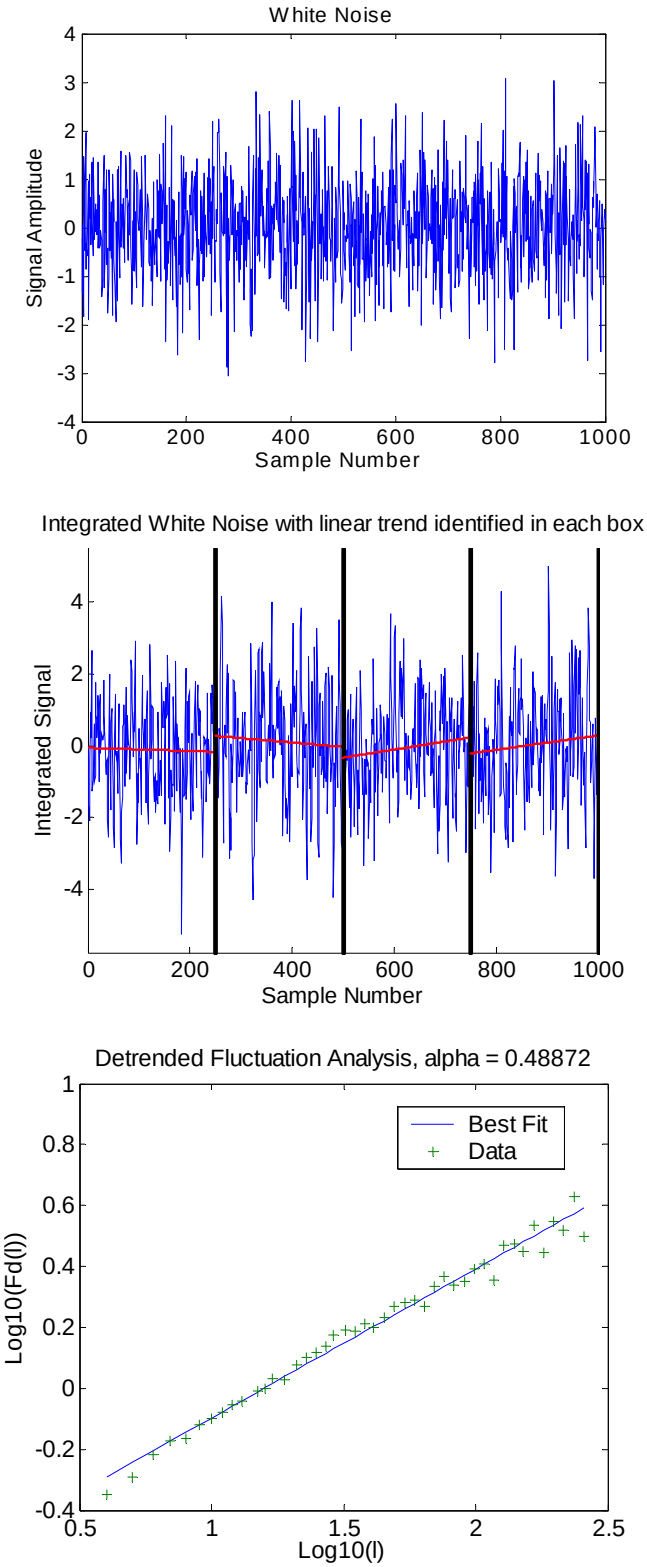

Figure **2.2**: Demonstration of the DFA procedure: a) white noise, b) integrated white noise with a linear trend identified, c) the slope of the log-log plot is the scaling parameter, α.

$$F(n) = \sqrt{\frac{1}{N}\sum_{k=1}^{N}\left[y(k) - y_n(k)\right]^2} \qquad [\mathbf{2.1}]$$

An example of this process for 12 data points and a box size of 6 data points is shown in Table **2-1**. This computation is then repeated over all time scales or box sizes to provide a relationship between box size and F(n). The slope of the log-log plot of n and F(n) determines the scaling parameter α. The procedure is illustrated in Figure **2.2**.

When α=0.5 then this indicates that the time series is completely random in the same way that white noise is completely random. For a random white noise process every value will be completely independent of the values of previous observations. When $\alpha \neq 0.5$, each observation is not completely independent and is correlated to a greater or lesser extent with the values that previous observations took on. When $0<\alpha<0.5$ power law anti-correlations are present and when $0.5<\alpha<1$ power law correlations are present. When $\alpha>1$, correlations exist but they cease to be of a power law form. Brown noise is indicated by α=1.5. Brown noise represents a random walk process and can be obtained by integrating white noise. Whereas for white noise the value of the next element of the time series is completely independent of the past values, for brown noise only the increment is independent of the past. Brown noise is therefore completely predictable, whereas white noise is completely unpredictable. Time series with α=1 therefore represent a mid-point between the complete predictability of brown noise and the complete unpredictability of white noise (Press, 1978).

Table **2-1**: Illustration of the DFA procedure for two boxes of size six data points.

Original Data	Integrated Data Less Grand Mean	Local Trend	Column 2 Less Column 3	RMSE for Box
1st box of size 6 data points				
2.88	-2.318	-1.3333-0.012x	-0.973	1.647
2.54	-4.976	-1.3333-0.012x	-1.301	
7.32	-2.854	-1.3333-0.012x	3.491	
3.50	-4.552	-1.3333-0.012x	-0.317	
4.04	-5.71	-1.3333-0.012x	0.235	
2.66	-8.248	-1.3333-0.012x	-1.133	
2nd box of size 6 data points				
10.17	-3.276	1.485-0.0317x	3.519	2.355
4.10	-4.374	1.485-0.0317x	-2.520	
5.08	-4.492	1.485-0.0317x	-1.508	
3.97	-5.72	1.485-0.0317x	-2.586	
8.70	-2.218	1.485-0.0317x	2.176	
7.41	-.006	1.485-0.0317x	0.917	

Note 1: In the next step in the procedure the Root Mean Square Error (RMSE) would be averaged over all boxes of the same size. The box size and averaged RMSE then become one data point on the log-log DFA plot.

2.3.4 QUANTIFYING SIGNAL ENTROPY

The use of entropy as a measure of the complexity or regularity of biological signals has provided insight into physiological changes associated with aging

and disease (Pincus & Goldberger, 1994). The concept of entropy originates from thermodynamics and the availability or convertibility of energy. However, the entropy of biological signals is more easily related to the concept of entropy from information theory. In information theory a highly predictable, simple or regular signal has low entropy because little information is conveyed. For example, the signal 'HHHHH' would have low entropy in comparison to the signal 'HELLO' since there is less predictability, and more information conveyed, in the letters of the second signal.

When quantifying the entropy of biological signals the aim is usually to describe the regularity of the signal. If a data set is simple, predictable, highly ordered, or highly regular, the entropy will approach zero. High entropy values reflect data sets that are complex, unpredictable, or irregular. A problem with the calculation of formal entropy theoretically requires perfectly noiseless data sets of infinite length, whereas biological time series are noisy and of finite length. Approximate Entropy (ApEn) is an algorithm developed by Pincus (1991) to address these problems. The ApEn algorithm has a tolerance or range that is designed to account for the first problem of anticipated noise within the data. This tolerance is the parameter r which is set by measuring the noise in the data arising, for example, from the measurement system. Although the second problem of a data set of finite length cannot be completely solved, Pincus recognized that for data sets of similar lengths an imperfect estimate of entropy could be used to rank sets of times series and that this ranking could still provide useful information about the relative complexity of physiological processes (Pincus et al., 1991).

ApEn quantifies the negative natural logarithm of the conditional probability that a template is repeated during the time series. Figure **2.3** shows a template of length m=2 points. Matching templates that remain arbitrarily similar (i.e. within the tolerance, r) are then counted, the number of matches to the ith template of

length m is designated B_i. Then the number of these matches that remain similar for the m+1th point is counted, this number for the ith template is designated A_i. The conditional probability that the template including the m+1th data point matches given that the template of length m is then calculated for each template match. The negative logarithm of the conditional probability is calculated for all templates and the results averaged (Equation. **2.2**). If the data is highly ordered then templates are similar for m points are likely to also be similar for m+1 points. For such data sets the conditional probability will therefore be close to 1, and the negative log and therefore the entropy will be close to zero (Richman et al., 2004). This will reflect low complexity and high predictability.

$$ApEn(m,r,N) = \frac{1}{N-m}\sum_{i=1}^{N-m} log\frac{A_i}{B_i} \qquad [\mathbf{2.2}]$$

Where:

N is the number of data points in the time series,

m is the length of the template,

A_i is the number of matches of the ith template of length m+1 data points, and

B_i is the number of matches of the ith template of length m data points.

One of the problems with ApEn is that it relies on the matching of templates in the data series. To avoid the occurrence of $ln(0)$ a template is allowed to match itself. Therefore each template occurs at least once. However, this introduces bias that has been shown to lead to inconsistent results from data series of similar lengths (Richman & Moorman, 2000). A more recent algorithm, Sample Entropy (SampEn) was developed to correct this bias by taking the logarithm after averaging (Equation **2.3**). This method avoids the introduction of self-matching SampEn has been shown to preserve relative consistency more often than ApEn, and to be more robust to outliers (Richman & Moorman, 2000).

$$SampEn(m,r,N) = -log\left(\frac{\sum_{i=1}^{N-m} A_i}{\sum_{i=1}^{N-m} B_i}\right) = -log\left(\frac{A}{B}\right) \quad [\mathbf{2.3}]$$

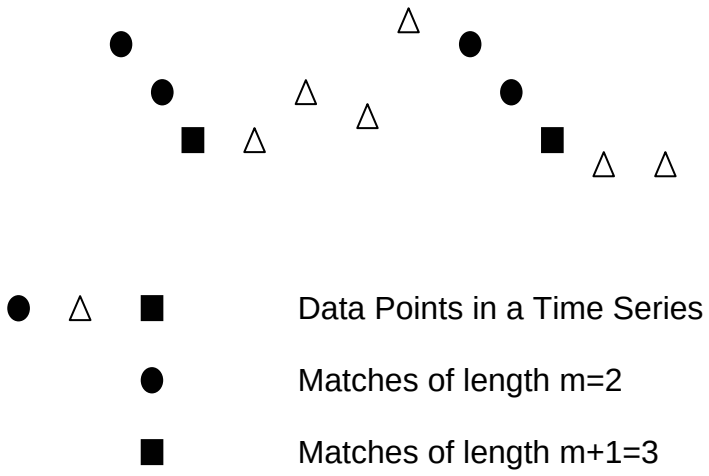

Figure **2.3**: A data series showing a template of length m=2 and its match. The same data points are included in a template of length m+1=3 and its match.

The SampEn algorithm has been used to identify differences between congestive heart failure patients and normal individuals in the inter-beat intervals taken from electrocardiogram (ECG) records (Govindan et al., 2007), and to identify incidences of neonatal sepsis from the ECG records of newborn babies (Lake et al., 2002).

2.4 EFFECTS OF CONTRACTION INTENSITY, MUSCLE SIZE, AGE, AND TRAINING STATUS ON FORCE OR MOMENT FLUCTUATIONS

The effect of several factors, including the intensity or effort level of the contraction, the size or strength of the muscle or muscle group producing the force, and the age and training history of the individual, on the magnitude of the force or moment fluctuations have been quantified. Some studies have also quantified the effect of age on the time-dependent structure of the force or moment fluctuations. Studies examining these factors will be reviewed in the following sub-sections.

2.4.1 CONTRACTION INTENSITY

Keen et al. (1994) and Tracy and Enoka (2002) found that for the first dorsal interosseus and the quadriceps muscles respectively the SD of the force increased with increasing force level. However, when normalized to the mean force level as the coefficient of variation a parabolic relationship was seen such that the smallest CV values occur at intermediate force levels and higher CV values are seen at very low (2.5% of maximum voluntary contraction force or MVC) and high (above 50% MVC) levels of force. For example, for the first dorsal interosseus, over a 20 second isometric abduction contraction, the mean CV for 10 subjects at 2.5% of MVC was 5.6%, at 20% of MVC was 2.0% and at 50% was 3.5% (Keen et al., 1994). For an 8 second isometric knee extension contraction using the quadriceps the mean CV ranged between 2 and 3%, with the largest values seen at 2% and 50% of MVC (Tracy & Enoka, 2002).

2.4.2 MUSCLE SIZE

Hamilton et al. (2004) measured the coefficient of variation in the isometric torque produced around different joints in the upper limb. Moving in a distal to proximal direction from the finger, to the wrist, to the elbow, the size of the muscle groups acting across the joints increases, and the size of the maximum torque that these muscle groups can produce also increases. For example, the first dorsal interosseus has around 120 motor units, whereas the Biceps brachii have around 440 motor units and can produce around 10 times as much torque. The authors claimed that, since the SD and the CV decreased as the maximum voluntary torque increased, they had shown that stronger muscles are more accurate than weaker muscles. Some subjects did decrease from a CV of 4% to a CV of 1% as the joint torque increased from 1 to 20 Nm at different joints, however several subjects demonstrated a flat relationship between CV and joint torque such that the CV was around 1.5% for all joints and joint torques.

2.4.3 AGE

Keen et al. (1994) and Tracy and Enoka (2002) found that for the first dorsal interosseus and the quadriceps muscles respectively the CV was greater for older adults aged 59-74 years compared to younger adults aged 18-27 at low forces only, that is at force levels of 2.5%, 5% and 10% of MVC. These differences disappeared for contraction intensities of 20% of MVC and above. The largest difference in the CV of force was measured by Galganski et al. (1993) at 5% of MVC force for the first dorsal interosseus. The mean coefficient of variation for the old group was 11%, whereas for the young group it was around 6%. However the differences in CV seen with aging are more typically of the order of 1 or 2%, if differences are evident at all. These differences at low force levels disappeared following 12 weeks of finger abduction strength training (Keen et al., 1994).

2.4.4 TRAINING STATUS

Strength training is not generally associated with a reduction in the CV for isometric contractions in either the first dorsal interosseus (Keen et al., 1994), or the quadriceps muscle (Tracy et al., 2004). An exception to this general finding is that older adults do show a decrease in the CV at low force levels (less than 20% of MVC) following strength training of the first dorsal interosseus (Keen et al., 1994), and this seems to reverse age-related differences in the CV at these force levels. However, this effect does not seem to rely on increases in strength alone since Keen et al. (1994) did not find differences in the reduction in CV at low force levels between groups that strength trained with high and low loads. Furthermore, it has been shown that decreases in the CV for low intensity contractions (i.e. at a low percentage of MVC) of the finger muscles have been shown following practice of a skilled hand movement even when there is no increase in strength (Ranganathan et al., 2001). This means that it is likely that some form of neural adaptation rather than increased strength is responsible for the training effect seen in older adults at low force levels.

2.5 POTENTIAL SOURCES OF THE FLUCTUATIONS IN FORCE

Potential characteristics that could influence the force fluctuations are: number of motor units, the force associated with individual motor units, discharge rate variability, non-uniform activation of the agonist muscle, alternating activity of agonist and antagonist muscles, and common input (or correlation in the input) to the motor neuron pool. There may be more than one underlying cause of the variability, and it may be that the relative importance of the causal factors is different for different subject populations, muscles, and contractions (Enoka et al., 2003).

The effect of the number of motor units and the force associated with individual motor units has been examined using strength comparisons (e.g. Ranganathan et al., 2001), comparisons of young and older adults (e.g. Vaillancourt & Newell, 2003), and using simulations (e.g. Taylor et al., 2002). Stronger muscle groups with more motor units have been associated with reductions in the coefficient of variation for force (Hamilton et al., 2004). However, it has been shown that a reduction in the magnitude of the force fluctuations during a sub maximal pinch grip occurs with training even when there is no increase in strength (Ranganathan et al., 2001). Ageing is associated with a process of de-nervation of fast muscle fibres followed by a re-nervation by slow motor unit nerves (Gardner, 1940). This process results in fewer motor units with a larger number of muscle fibres per motor unit. It might seem reasonable that this process may be responsible for some of the differences seen between young and old adults, however such differences are not always consistently seen in muscles that might have been expected to have undergone this process (Enoka et al., 2003).

Older adults do show an increase in the magnitude of force fluctuations as quantified by RMSE (Vaillancourt & Newell, 2003). However, simulations of a pool of motor units with a range of recruitment thresholds, discharge rates, innervation ratios, conduction velocity, motor unit territory, and twitch characteristics showed that variations in twitch force and motor unit numbers had a minimal effect on the magnitude of the force fluctuations (Taylor et al., 2002). The initial condition for the motor unit pool was 120 motor units with an exponential distribution of motor unit forces ranging from 1 to 100 arbitrary units (au) (a 100-fold range). When the pool was changed to comprise 90 motor units with twitch forces ranging over a 30-fold range, or 90 motor units with a 140-fold range of twitch forces there was no difference in the CV for force. In this simulation study changing the discharge rate of the motor neurons did affect the CV for force such that CV increased with discharge rate. However, Semmler et al. (2000) found larger force fluctuations in older adults compared with younger

adults at the same percentage of maximum voluntary contraction (MVC) levels despite similar discharge rates.

It has been suggested that the increased fluctuations associated with ageing are associated with variability in the discharge rate rather than differences in the average discharge rate per se (Moritz et al., 2005). It may also be the case that different processes are more influential in different muscles and different individuals since the relative importance of recruitment and firing rate modulation in the gradation of force differs between muscles (Milner-Brown et al., 1973).

There is some evidence that preferential recruitment of some motor units occurs depending on the task performed (Denny-Brown, 1949). For example, there are some alterations in the rank recruitment order for a small number of motor units in the first dorsal interosseus depending on whether a flexion, abduction or pinch movement was performed (Thomas et al., 1986). Yet despite a replication of this finding, it has been determined that older adults show activity in the same areas of the muscle during an isometric contraction as younger adults exhibiting a lower SD in the fluctuations (Laidlaw et al., 2002). Since both younger and older adults show activation in the same parts of the muscle, that is, both age groups show non-uniform activation, this suggests that non-uniform activation may not be associated with differences in age-related differences in force fluctuations. The same study also demonstrated that there was no relationship between patterns of activation in the antagonist muscle and the SD of the fluctuations.

Synchronization of motor unit firing is associated with an increase in force fluctuations in motor unit firing in simulated motor neuron pools (Yao et al., 2000). This is because if several motor units innervating different motor units fire at the same point in time, then several motor units will increase and decrease in tension at the same time. However, the increased force fluctuations observed

with age are not associated with an increase in motor unit synchronization measured via intramuscular electrodes (Semmler et al., 2000).

In summary, it seems likely that the contribution of some mechanisms to the magnitude of force fluctuations may vary in different muscles and populations. However, the number of motor units and the twitch force associated with each motor unit seems to affect the magnitude of force fluctuations very little. Synchronization and variability in the discharge rates seem to be more strongly associated with changes in the force fluctuations, but these factors may not explain all of the age-related differences in the magnitude of fluctuations in force or moment quantified using the coefficient of variation.

2.6 SUMMARY

This chapter has reviewed research related to the force-length curve and its expression in vivo, and the work that has been done in quantifying the fluctuations in force or torque produced by a muscle. The next chapters will describe the studies performed to identify factors affecting the expression of the force-length relationship, and to quantify how the fluctuations in force vary with muscle length.

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CHAPTER 3

THE EXPRESSION OF THE FORCE-LENGTH RELATIONSHIP IN VIVO: A SIMULATION STUDY

3.1 ABSTRACT

The relationship between the length of a muscle and the force it can produce is one of the most important characteristics of human skeletal muscle. A generalised model of a mono-articular muscle-tendon complex was used to examine the effect of various muscle architecture parameters on the section of the force-length relationship operated over for a 90 degree joint range of motion. The parameters investigated were: the ratio of tendon resting length to muscle fibre optimum length (L_{TR} / Lf_{OPT}), the ratio of muscle fibre optimum length to average moment arm (Lf_{OPT} / r), the normalised tendon strain at maximum isometric force (c), the muscle fibre pennation angle (θ_{PENN}), and the joint angle at which the optimum muscle fibre length occurred (θ_{REF}). Each parameter was varied systematically through a realistic range of values as reported in the literature for various muscles. It was shown that L_{TR} / Lf_{OPT} was important in determining the amount of variability in the section of the force-length relationship that a muscle operated over. The effect of this ratio was modulated by Lf_{OPT} / r. The muscle operated over only one limb at intermediate values of these two ratios, whether this was the ascending or descending limb was determined by the relative values of c, θ_{PENN}, θ_{REF}, and L_{TR} / Lf_{OPT}. The potential for inter-individual variability in these parameters for a given muscle is discussed.

3.2 INTRODUCTION

The force-length relationship of muscle is a fundamental mechanical property of muscle. It is an important component of most biomechanical models of movement since it determines the maximum isometric force that can be produced at a given joint configuration. The force-length relationship has been shown to consist of three regions at the sarcomere level (Gordon et al., 1966): the ascending limb, the plateau, and the descending limb. However, in vivo different skeletal muscles may operate over all or only some of these regions of the force-length curve, i.e. over physiological joint ranges of motion only part of the force-length relationship may be expressed. The section of the force-length relationship that a muscle operates over given the physiological range of motion of the joints crossed by the muscle will be referred to as the expressed section. Previous work has shown that there is a great deal of variability in the expressed section for the rectus femoris (Herzog & ter Keurs, 1988; Winter, 2004) and the hamstrings (Savelberg & Meijer, 2003). There is apparently not much variability in the expressed section of the gastrocnemius (Herzog et al., 1991; Winter, 2004). The reason for the different amount of variability in the expressed section in different muscles has not been investigated. The section of the force-length relationship that a muscle operates over must affect the pattern of force production across the range of motion. The changing muscle force with muscle length must present a substantial challenge to the successful control and co-ordination of movement. It is therefore of considerable interest to investigate what determines which section of the force-length relationship is expressed in vivo, and to understand why some muscles show more variability in this property than others.

There are several possible sources of the reported variation in the expressed section of the force-length relationship. These are: anatomical differences, for example in the distance of muscle insertion points from joint centres relative to

segment length; differences in mechanical properties such as tendon compliance; and differences in muscle architectural features, such as pennation angle. These musculo-skeletal features are reflected in the parameters usually included in muscle models, for example the muscle pennation angle is included in many muscle models (e.g. Otten, 1988). In a previous study gastrocnemius muscles operating over different sections of the force-length curve were modelled in order to assess the ability of an in vivo testing method to accurately reconstruct different sections of the force-length relationship (Winter, 2004). In formulating models for muscles operating over different sections of the force-length relationship it was found that certain model parameters affected the expressed section of the force-length relationship more than others.

The purpose of this study is to undertake a more systematic examination of the effect of such parameters on the expression of the force-length curve in vivo using a muscle model. The model is initially formulated as a generalised mono-articular muscle-tendon complex and then each parameter is systematically varied in turn over ranges that reflect the range of parameter values found in several mono-articular muscles. It was hypothesised that varying the ratio of resting tendon length to the muscle fibre optimum length (L_{TR} / Lf_{OPT}) would have the greatest influence on the section of the force-length relationship that was expressed.

3.3 METHODS

This section will describe the components of the muscle model, and the model parameters that were manipulated. Finally, the simulation procedure will be described.

3.3.1 MODEL DESCRIPTION

The muscle model comprises a contractile component that models the behaviour of the muscle fibres, and a series elastic component (Figure **3.1**). The force produced by the muscle model (F_M) is described by Equation **3.1**.

$$F_M = q.F_{MAX}.F_L(L_F).F_V(V_F) \qquad [\mathbf{3.1}]$$

where,

q - current active state of muscle model,

F_{MAX} - maximum isometric force possible by the muscle model,

$F_L(L_F)$ - fraction of the normalized force-length curve that the model can produce at its current fibre length (L_F),

and $F_V(V_F)$ is the fraction of normalized force-velocity curve that the model can produce at its current fibre velocity (V_F).

The current active state of the model (q) represents the recruitment as well as the firing rate, or rate coding, of the α-motor neurons. The value of q can range from 0 to 1. In the simulations only maximal isometric conditions were examined so the muscle fibres were assumed to have a velocity of zero, making $q = 1$ and $F_V(V_F) = 1$. The value of F_{MAX} was always set to be 100 arbitrary units of force.

The normalised force-length properties of the muscle were represented by Equation **3.2**.

$$F_L(L_F) = 1 - \left(\frac{(L_F - L_{F,OPT})}{w.L_{F,OPT}} \right)^2 \qquad [\mathbf{3.2}]$$

where:

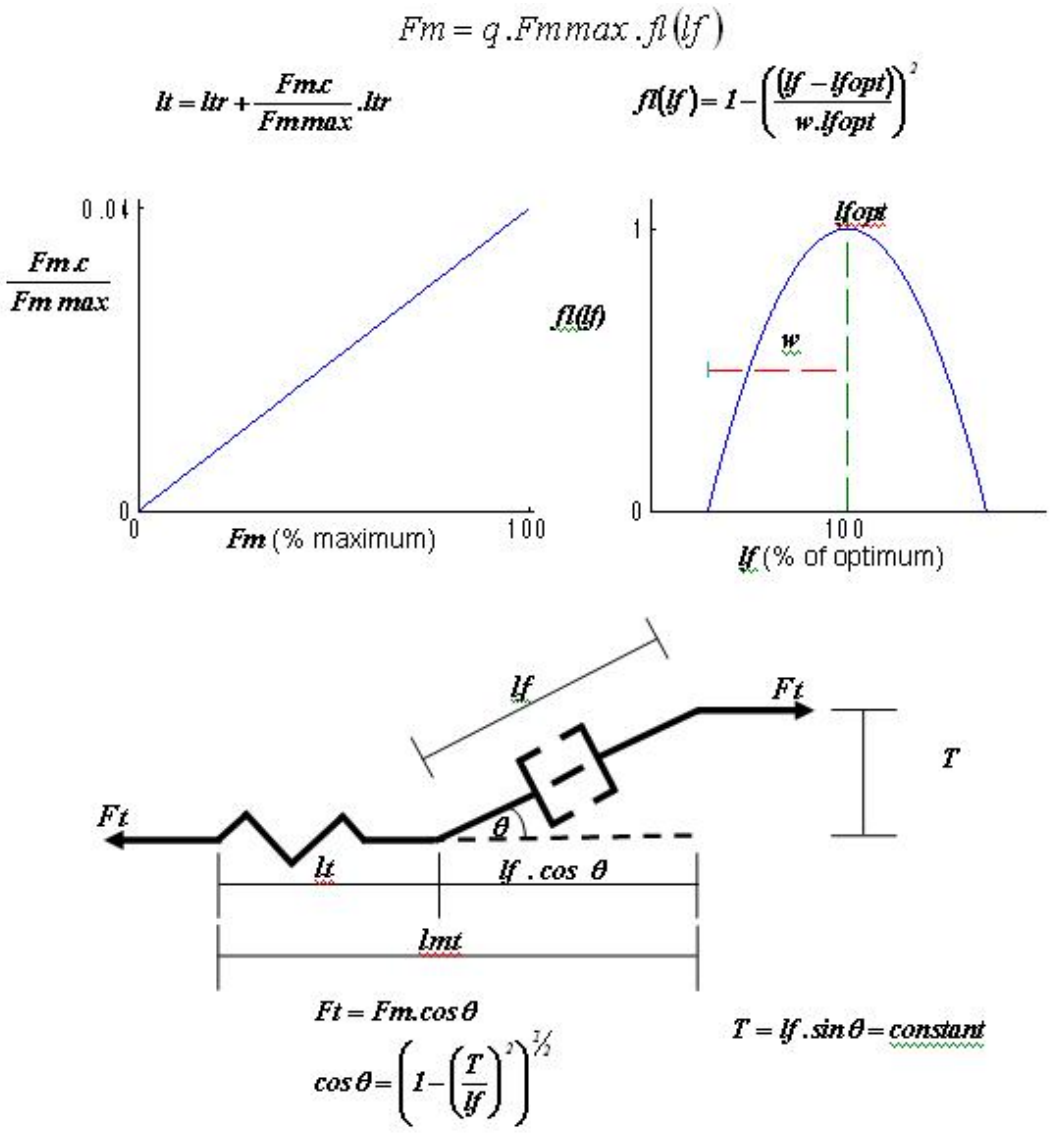

Figure **3.1**: The essential elements of the muscle model, including the series elastic component and the force-length properties. Where ***Fm*** – force produced by the muscle fibres, ***q*** - current active state of muscle ($0 \leq q \leq 1$), ***Fmmax*** - maximum isometric force possible by muscle, ***fl(lf)*** - fraction of maximum isometric force muscle can produce at current length (***lf***), ***lt*** - the current length of the tendon, ***ltr*** - the resting length of the tendon, ***c*** - extension of tendon at fmmax expressed as fraction of tendon resting length, ***lfopt*** - optimum length of muscle fibre, ***w*** - parameter indicating width of force-length curve, ***T*** – thickness of muscle, ***lmt*** – length of muscle-tendon complex, $\theta_{\pi\varepsilon\nu\nu}$ – pennation angle, and ***Ft*** is the force in the tendon.

$L_{F,OPT}$ is the optimum length of the muscle fibres, and

$\boldsymbol{w}$ is a parameter specifying the width of the force-length relationship (Figure 3.1).

The muscle fibre optimum length is the length at which optimal overlap of actin and myosin occurs and therefore maximum muscle force can be produced. The value for w for single fibres in vitro has been reported as 0.56 (Gordon et al., 1966).

In series with the contractile component is an elastic component. Although this component reflects the behaviour of any elastic structure in series with the contractile component, the series elastic component mainly reflects the behaviour of the tendon. The model of this element assumes that the tendon has a linear stress-strain curve (Figure 3.1). The force-extension curve of this element is represented by Equation **3.3**.

$$L_T = L_{TR} + \frac{F_M . c}{F_{max}} . L_{TR} \qquad [\mathbf{3.3}]$$

where:

L_T is the current length of the tendon,

L_{TR} is the resting or slack length of the tendon, and

$\boldsymbol{c}$ is the extension of tendon under maximum isometric force as a fraction of tendon resting length.

The length of muscle-tendon complex (L_{MT}) is the length from origin to insertion. For a paralleled fibred muscle it is equal to the length of the muscle fibres plus the length of the tendon (Equation **3.4**).

$$L_{MT} = L_F + L_T \qquad [\mathbf{3.4}]$$

The muscle fibres can be pennate (Figure **3.1**). In a planar model of pennate muscle it is assumed that the area of the muscle fibres remains constant, this is equivalent to the constant volume assumption for actual muscle (Otten, 1988). Given that the thickness (T) of the muscles must remain constant, the pennation angle (θ_{PENN}) can be computed from Equation **3.5**.

$$cos(\theta_{PENN}) = \sqrt{1-(T/L_F)^2} \qquad [\mathbf{3.5}]$$

where:

θ_{PENN} is the muscle fibre pennation angle.

If the muscle is pennate then the force in the direction of the tendon is not equal to the force in the muscle fibres (Figure 3.1), instead the correction given in Equation **3.6** has to be applied.

$$F_T = F_M \, cos(\theta_{PENN}) \qquad [\mathbf{3.6}]$$

where:

F_T is the force in the direction of the tendon.

The length of the muscle-tendon complex can then be computed from Equation **3.7**.

$$L_{MT} = L_F \, cos(\theta_{PENN}) + L_T \qquad [\mathbf{3.7}]$$

For input into the model it was necessary to know the length of the muscle-tendon complex (L_{MT}). In many muscle models (e.g. Out et al., 1996) the length of the muscle-tendon complex is computed from the joint angle according to an experimentally determined relationship (e.g. Grieve et al., 1978). The muscle moment arm is then computed by taking the derivative of this muscle-tendon complex length-joint angle relationship according to the method proposed by An et al. (1983). However, in order to examine the effect of the ratio Lf_{OPT} / r on the expressed section of the force-length relationship the value of *r* had to be specified in advance, and the change in the length of the muscle-tendon complex was therefore obtained by integration of the moment arm-joint angle relationship. This ratio is important since it determines the length change that the muscle must go through in order to move through the joint range of motion.

The reference length of the muscle-tendon complex (L_{MTR}) was specified according to Equation **3.8**.

$$L_{MTR} = Lf_{OPT} + L_{TR} \qquad [\mathbf{3.8}]$$

The value of the reference length of the muscle-tendon complex was always set to be 50 arbitrary units long. The lengths Lf_{OPT} and L_{TR} were set according to the desired value for the ratio L_{TR} / Lf_{OPT}. The angle at which this reference muscle-tendon complex length occurs (θ_{REF}) was specified, this parameter specifies the angle at which the reference length occurs and is therefore important in determining the range of lengths used for a certain joint range of motion. The moment arm length at this reference angle (r_{REF}) was computed according to the desired value for Lf_{OPT} / r. The moment arm-joint angle relationship could be constant, increasing, or decreasing according to Equation **3.9**. The range of motion for the joint was always 0 to 90 degrees.

$$r = r_{REF} + r_{SLOPE}(\theta_{JOINT} - \theta_{REF}) \quad \textbf{[3.9]}$$

where:

r_{SLOPE} is the slope of the moment arm-joint angle relationship, and

θ_{JOINT} is the current joint angle.

For a constant moment arm r_{SLOPE} was set to zero.

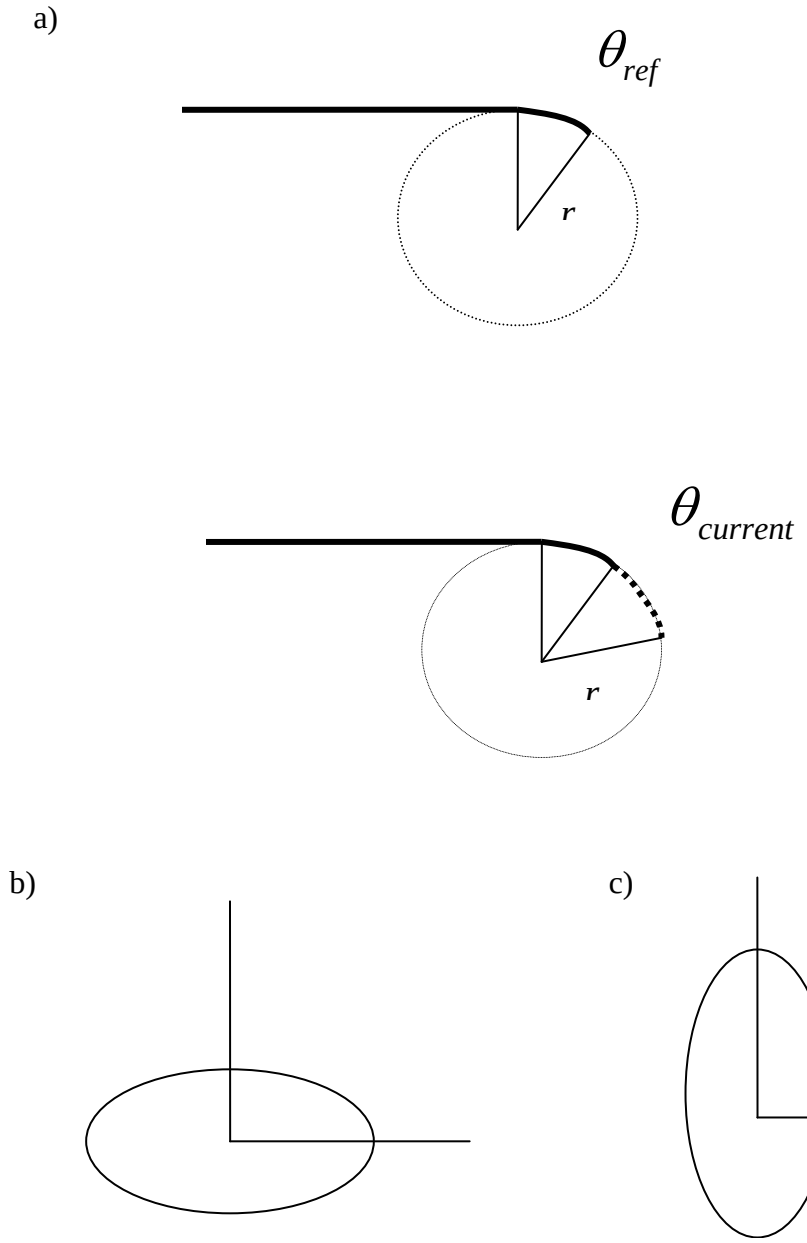

Figure **3.2**: The reference length of the muscle-tendon complex length was specified for a given joint angle (θ_{REF}): a) for a constant moment arm the change in the muscle-tendon complex length (dotted line) was $r\,(\theta_{JOINT} - \theta_{REF})$, b) and c) show alternative moment arm geometries that could be modelled by specifying a positive value for r_{SLOPE} (b) or a negative value for r_{SLOPE} (c).

The length of the muscle-tendon complex at the current joint angle was then computed by integrating the moment arm-joint angle relationship and adding the reference muscle-tendon complex length (Equation **3.10** and Figure **3.2**).

$$L_{MT} = L_{MTR} + r_{REF}(\theta_{JOINT} - \theta_{REF}) + \frac{1}{2} r_{SLOPE}(\theta_{JOINT} - \theta_{REF})^2 \qquad [\mathbf{3.10}]$$

For a given joint angle the moment arm of the muscle was computed and muscle-tendon lengths were computed. Given these muscle-tendon lengths the maximum isometric force the muscle could produce was computed. The length of the fibres was determined by an iterative procedure. First fibre length was estimated by subtracting resting tendon length from the muscle-tendon length at a given set of joint angles. This value was used to estimate muscle isometric force. The tendon stretch under this force was then computed, and therefore a new muscle fibre length was computed, and a new isometric force computed. This sequence was continued until a consistent value for maximum isometric force was produced, which was achieved in 20 iterations. This procedure was repeated for a joint range of motion from 0 to 90 degrees.

3.3.2 MODEL PARAMETERS

The model parameters under investigation are: the muscle fibre pennation angle (θ_{PENN}), the compliance of the tendon (c), the ratio of the muscle fibre length to the size of the moment arm (Lf_{OPT} / r), the joint position at which the reference muscle-tendon complex length occurs (θ_{REF}), and the ratio of resting tendon length to fibre optimum length (L_{TR} / Lf_{OPT}). The model is formulated initially as a generalised mono-articular muscle-tendon complex and then each parameter is systematically varied in turn over ranges that reflect the range of parameter values found in a variety of mono-articular muscles. Five mono-articular muscles were chosen to reflect a variety of anatomical and architectural features. The

muscles are: the soleus (SOL), vastus lateralis (VL), the short head of the biceps femoris (SHBF), the brachialis (BR), and the extensor carpi radialis brevis (ECRB). Although the ECRB arises partly from the lateral epicondyle of the humerus it will treated as a mono-articular muscle here since it is only a weak elbow flexor (Ettema et al., 1998; Riek et al., 2000). Table **3-1** shows the source of the values used for each muscle for the θ_{PENN}, Lf_{OPT} / r, c, and L_{TR} / Lf_{OPT} parameters. The intention is referring to these parameter values is to ensure that the range of values investigated with the model covers the range of parameter values typically found in vivo.

The maximum normalised tendon strain is specified by c, it is expressed as a percentage here. The values for c were directly specified for SOL by Magnusson et al. (2001) and for ECRB by Loren and Lieber (1995). For the VL and SHBF the value for c was computed by taking the values for the tendon and muscle cross sectional areas from Pierrynowski and Morrison (1985) and Wickiewicz et al. (1983) and then using the relationship given in Equation **3.11**.

$$c = \frac{PCSA \times ST}{TCSA \times E} \qquad [\mathbf{3.11}]$$

Where:
$PCSA$ is the physiological cross sectional area of muscle
ST is the specific tension of muscle (0.3MPa taken from Close, 1972)
$TCSA$ is the tendon cross sectional area, and
E is the Young's Modulus of muscle (1,500MPa taken from Alexander, 2002).

No information on either c or the tendon cross sectional area could be found for Brachialis.

Table **3-1**: Model parameter values for the soleus, vastus, short head of the biceps femoris, brachialis and flexor carpi ulnaris.

Parameter	Muscle	Value	Source
θ_{PENN} (degrees)	SOL	9-35	Morse et al. (2005)
	VL	7-33	Kawakami et al. (2006)
	SH BF	0 23-25	Alexander and Vernon (1975) Wickiewicz et al. (1983)
	BR	6.5-12.9	Herbert and Gandevia (1995)
	ECRB	5-13	Lieber et al. (1990)
c (%)	SOL	4.4-5.6	Magnusson et al. (2001)
	VL	1%	Wickiewicz et al. (1983) & Pierrynowski & Morrison (1985)
	SH BF	1-2%	Wickiewicz et al. (1983) & Pierrynowski & Morrison (1985)
	ECRB	1.99	Loren & Lieber (1995)
L_{TR} / Lf_{OPT}	SOL	11.25	Hoy et al. (1990)
	VL	2.68	Hoy et al. (1990)
	SH BF	0.52	Hoy et al (1990)
	BR	3.0 5.87	Winters and Stark (1988) Garner and Pandy (2003)
	ECRB	2.89	Loren et al. (1996)
Lf_{OPT} / r	SOL	0.5 1.5	Maganaris et al. (2006)
	VL	1.5-2.4	Maganaris et al. (2006)
	SH BF	4.39	Hoy et al. (1990)
	BR	1.6-7.56	Ettema et al. (1998) & Garner & Pandy (2003)
	ECRB	3.62	Loren et al. (1996)

Note: The muscles are: the soleus (SOL), vastus lateralis (VL), the short head of the biceps femoris (SHBF), the brachialis (BR), and the extensor carpi radialis brevis (ECRB).

The joint angle at which the reference muscle-tendon complex length occurs is the parameter θ_{REF}. The reference muscle tendon length is equal to the resting tendon length plus the optimum fibre length. The parameter θ_{REF} was varied in order to shift the optimum length to different points in the joint range of motion.

The joint angle at which the optimum length occurs is difficult to determine in vivo since more than one muscle crosses each joint, and for this reason the θ_{REF} parameter was varied through the whole range of motion (0 to 90 degrees). When the muscle is activated at the reference position the muscle fibres will exert force and stretch the tendon. Under full activation the muscle fibres will therefore shorten slightly due to tendon stretch. This means that the angle at which the optimum muscle fibre length occurs under full activation will be slightly greater (closer to 90 degrees) than whatever angle has been set as the reference angle if a compliant tendon is specified in the model, nevertheless, the two angles will be close.

3.3.3 SIMULATION PROCEDURE

It was not feasible to examine all possible parameter set combinations, but based on the data presented in Table 3.1 a representative range was selected. The ratio Lf_{OPT} / r was varied from 0.5 to 5 with the value of Lf_{OPT} set to 12.5 arbitrary units (au) and the value of L_{TR} set to 37.5 au giving an intermediate value of three for L_{TR} / Lf_{OPT}. The value of c was set to an intermediate value of four percent, and θ_{REF} and θ_{PENN} were set to 45 and zero degrees respectively. The value of θ_{REF} was varied from zero to 90 degrees in 15 degree intervals with Lf_{OPT} / r set to two, L_{TR} / Lf_{OPT} set to three, c set to four percent and θ_{PENN} set to zero. The effect of tendon compliance was investigated by varying c (the tendon extension as a percentage at maximum isometric force) between 0 and 8% for different values of Lf_{OPT} / r, L_{TR} / Lf_{OPT}, and θ_{REF}, with θ_{PENN} set to zero degrees. Finally the value of θ_{PENN} was varied between zero and 45 degrees with Lf_{OPT} / r and L_{TR} / Lf_{OPT} set to three. A 90 degree range of motion was used since it is a typical range of motion for many joints (Pheasant, 1986).

3.4 RESULTS

Varying the ratio Lf_{OPT} / r with L_{TR} / Lf_{OPT} held constant affects how much of the force-length relationship is expressed (Figure **3.3**). This was the case regardless of whether the moment arm was held constant over the range of motion or whether the moment arm increased or decreased over the range of motion. Under the model formulation with a constant moment arm the change in the length of the muscle-tendon complex was equal to the length of the moment arm multiplied by the change in joint angle from the reference position in radians. This means that the amount of the force-length relationship used also depends on the joint range of motion relative to the width of the force-length relationship (w). Consequently the proportion of the force-length relationship that is used (p) can be computed using the inverse of the ratio Lf_{OPT} / r, the joint range of motion (ROM) and w using Equation **3.12**.

$$p = \frac{r}{Lf_{OPT}} \cdot \frac{ROM}{2w} \qquad \textbf{[3.12]}$$

For example, with Lf_{OPT} / r equal to 1, ROM equal to 90 degrees or $\pi / 2$ radians and w equal to 0.56 the length change required would be 1.40 times the range of the force-length relationship (Equation **3.13**).

$$p = \frac{12.5}{12.5} \cdot \frac{\pi / 2}{2(0.56)} = 1.40 \qquad \textbf{[3.13]}$$

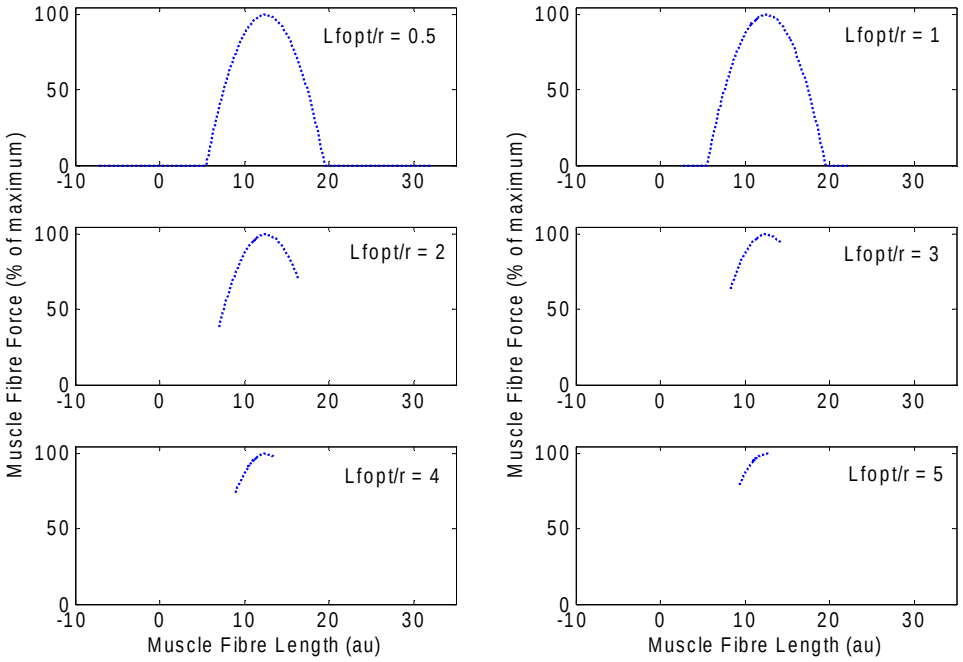

Figure **3.3**: The effect of varying ratio of optimum fibre length to moment arm length (Lf_{OPT} / r) for a moment arm that is constant through the range of motion.

The value of Lf_{OPT} / r at which the whole of the force-length relationship is used when there is a constant moment arm and a 90 degree joint range of motion is around 1.4 for an inextensible tendon and slightly more if a compliant tendon is used (Figure **3.4**). This means that only values of Lf_{OPT} / r above 2 will allow some variability in the expression of the force-length relationship.

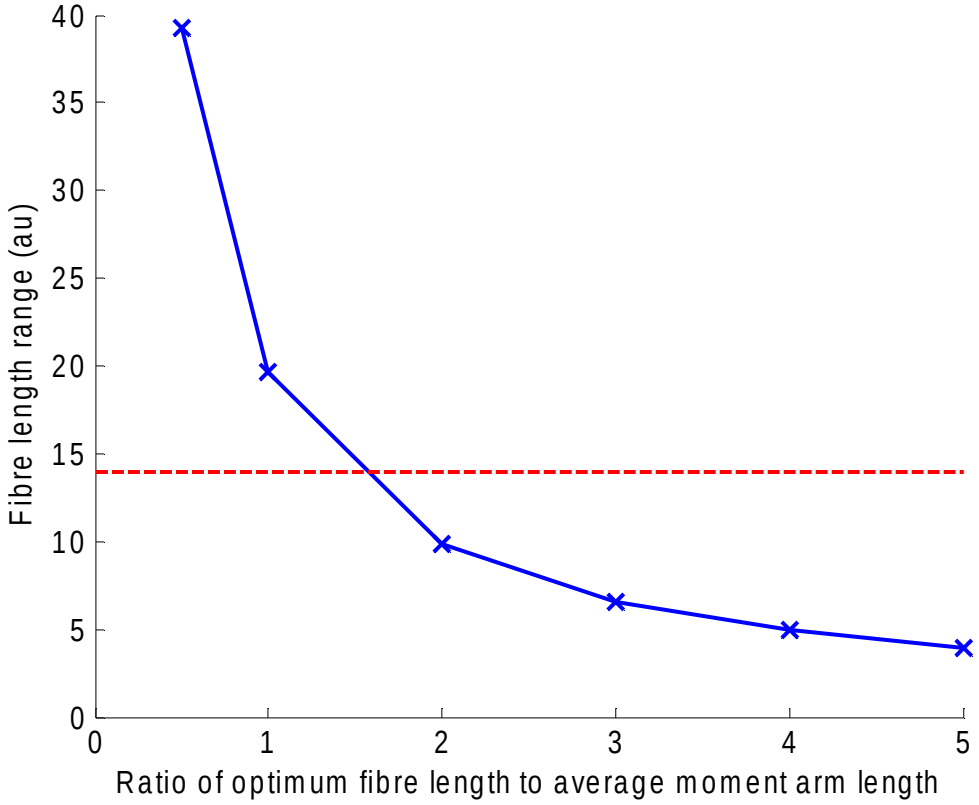

Figure **3.4**: The range of fibre lengths (maximum length less minimum length) required for different values of Lf_{OPT}/r with an Lf_{OPT} value of 12.5 arbitrary units. The dotted line shows the length range of the force-length relationship when an optimum length of 12.5 au, a value of 0.56 is used for w, and a value of 4% for c.

The effect of varying the θ_{REF} throughout the range of motion was to shift the expressed section of the force-length relationship from the descending limb (for θ_{REF} equal to zero degrees), to the plateau (for θ_{REF} equal to 30 to 60 degrees), and then to the ascending limb (for θ_{REF} equal to or greater than 75 degrees) (Figure **3.5**).

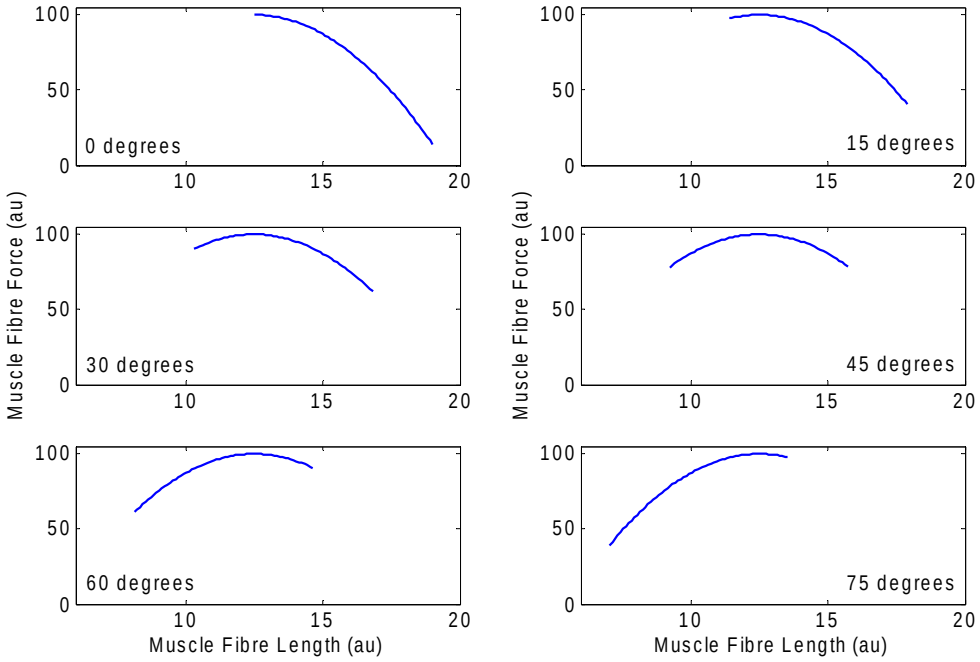

Figure **3.5**: The effect of varying the θ_{REF} parameter throughout the range of motion. The ratios Lf_{OPT} / r and L_{TR} / Lf_{OPT} were set to 3, c and θ_{PENN} were set to zero.

Tendon compliance means that the tendon stretches when the muscle is activated and applies force, resulting in a shorter muscle fibre length at a given joint angle with increasing compliance and so shifting the expressed section to shorter muscle fibre lengths. This means that a muscle, with θ_{REF} set to 45 degrees so that the optimum length occurs in the middle of the range of motion, would operate over the plateau region if the tendon were considered inextensible, but would shift to shorter lengths so that it operates over the ascending limb for values of c close to 8% (Figure **3.6**). Similarly a muscle with θ_{REF} set to 0 degrees would operate over the descending limb for values of c between zero and five percent, but the muscle would be shifted to the plateau region for values of c above 6% (Figure **3.7**). The effect of changing the

parameter c would be smaller for lower values of L_{TR} / Lf_{OPT}, since the tendon would be considerably shorter.

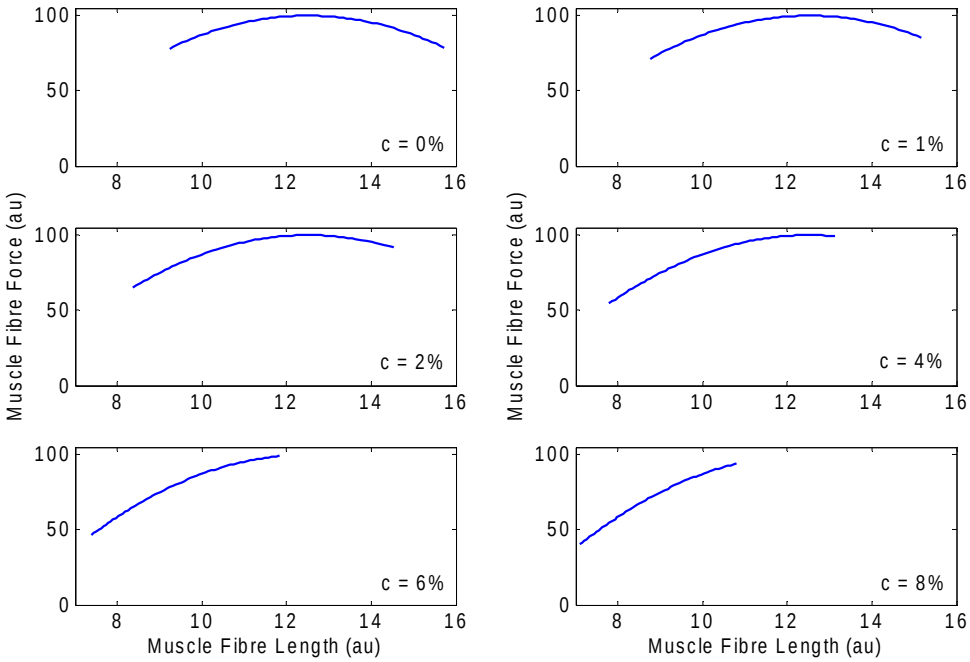

Figure **3.6**: The effect of varying tendon extension at maximum isometric force (c) from 0 to 8% for a muscle with θ_{REF} set to 45 degrees. The ratios Lf_{OPT} / r and L_{TR} / Lf_{OPT} were set to 3, and θ_{PENN} was set to zero.

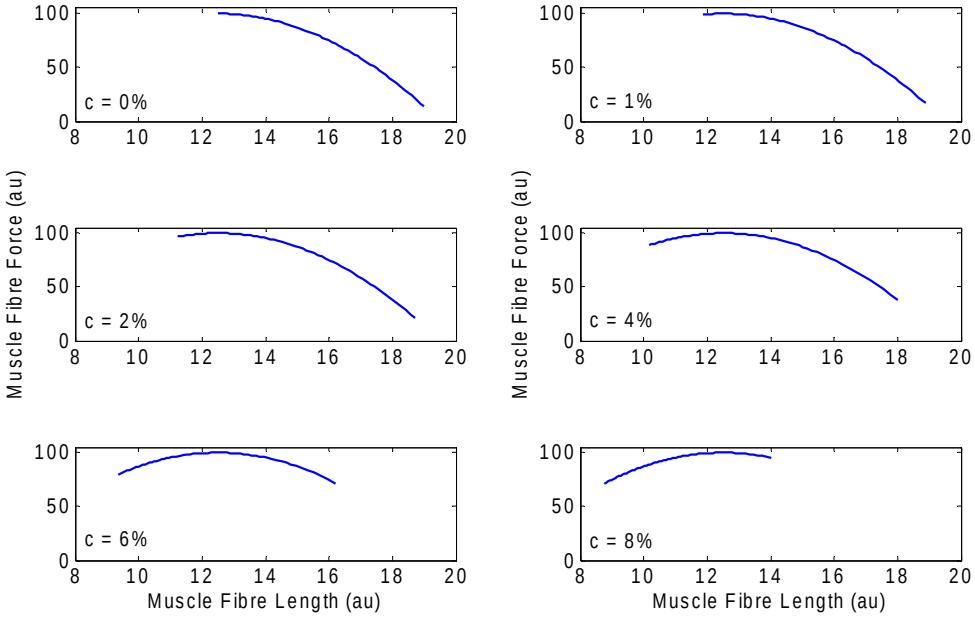

Figure **3.7**: The effect of varying tendon extension at maximum isometric force (c) from 0 to 8% for a muscle with θ_{REF} set to 0 degrees. The ratios Lf_{OPT} / r and L_{TR} / Lf_{OPT} were set to 3, and θ_{PENN} was set to zero.

The effect of varying the value for L_{TR} / Lf_{OPT} depended partly on the size of the moment arm, r (Figure **3.8** and Figure **3.9**). For small moment arms (high ratios of Lf_{OPT} / r) and low ratios of L_{TR} / Lf_{OPT} the muscle always operated over the plateau, regardless of the joint angle at which the optimum length was set. The optimum length had to be set at non-physiological joint angles in order to make the muscle operate over one of the limbs (ascending or descending) of the force-length relationship. For large moment arms (low values of Lf_{OPT} / r) and high values of Lf_{OPT} / r the whole range of the force-length relationship was used.

a)

b)

c)

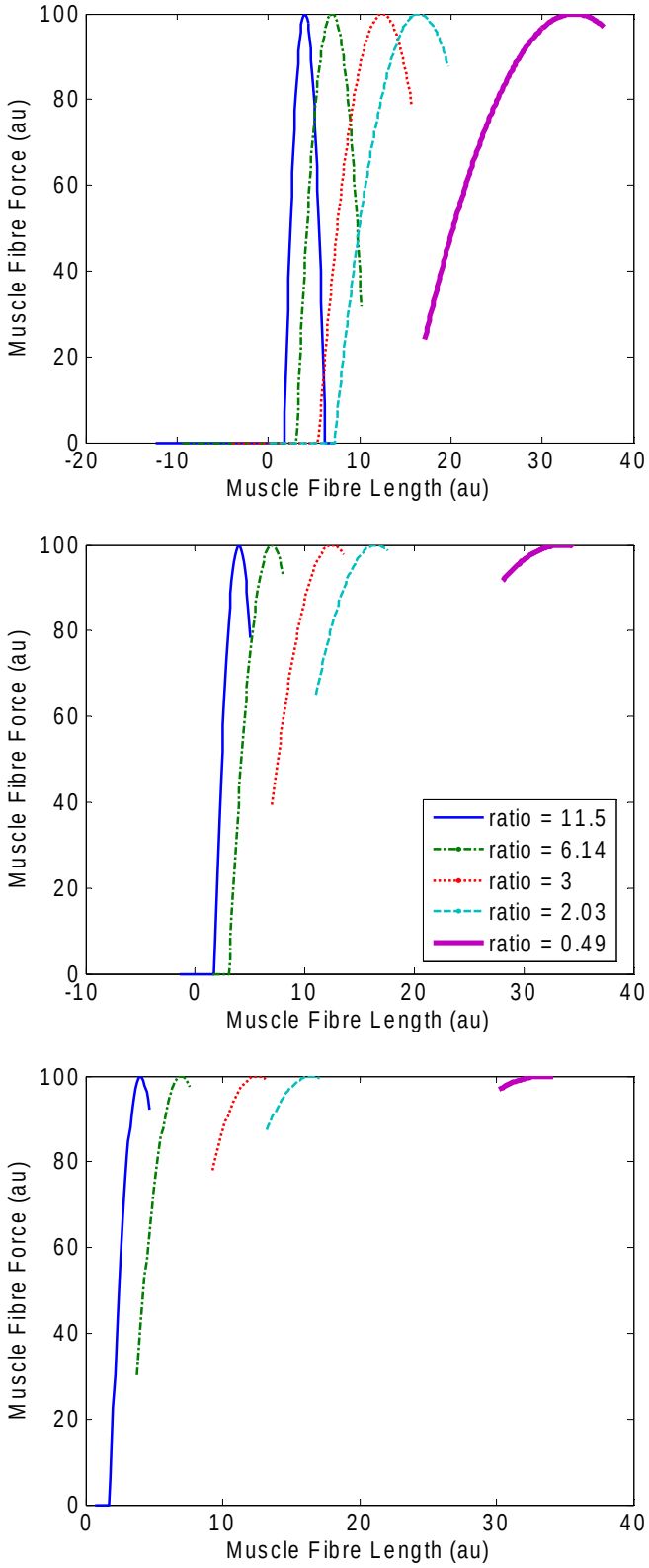

Figure **3.8**: The effect of varying the ratio L_{TR} / Lf_{OPT} with θ_{REF} equal to 75 degrees and Lf_{OPT} / r equal to a) one, b) two, and c) three.

The muscle could only operate over just one limb of the force-length relationship when both ratios were at high values, or when both ratios were at low values, or when both ratios were at intermediate values. Figures 3.8 and 3.9 show the effect of varying the ratios L_{TR} / Lf_{OPT} and Lf_{OPT} / r while c is set to zero. When c was set at values above 1% the expressed section was shifted to shorter lengths.

The effect of varying the pennation angle of the muscle fibres (θ_{PENN}) was to shift the expressed section to longer lengths, i.e. towards the descending limb (Figure **3.10**). This is because the fibre length at a given joint angle is inversely proportional to the cosine of the pennation angle. As the pennation angle increases, the cosine of the angle decreases and the fibre length at the specified joint angle increases. However, the shift in the operating range was not sufficient to change the expressed section from one limb to the other, i.e. from the ascending limb to the descending limb. The maximum force in the direction of the tendon decreased with increasing pennation angle, this would be expected as the force in the direction of the tendon is only the cosine of the pennation angle times the force in the muscle fibres. The cosine of 45 degrees is 0.707, so the force in the direction of the tendon is only around two thirds of that in the muscle fibre with such a high pennation angle. The value specified for θ_{PENN} represents the pennation angle at rest; the pennation angle increases with decreasing muscle length.

a)

b)

c)

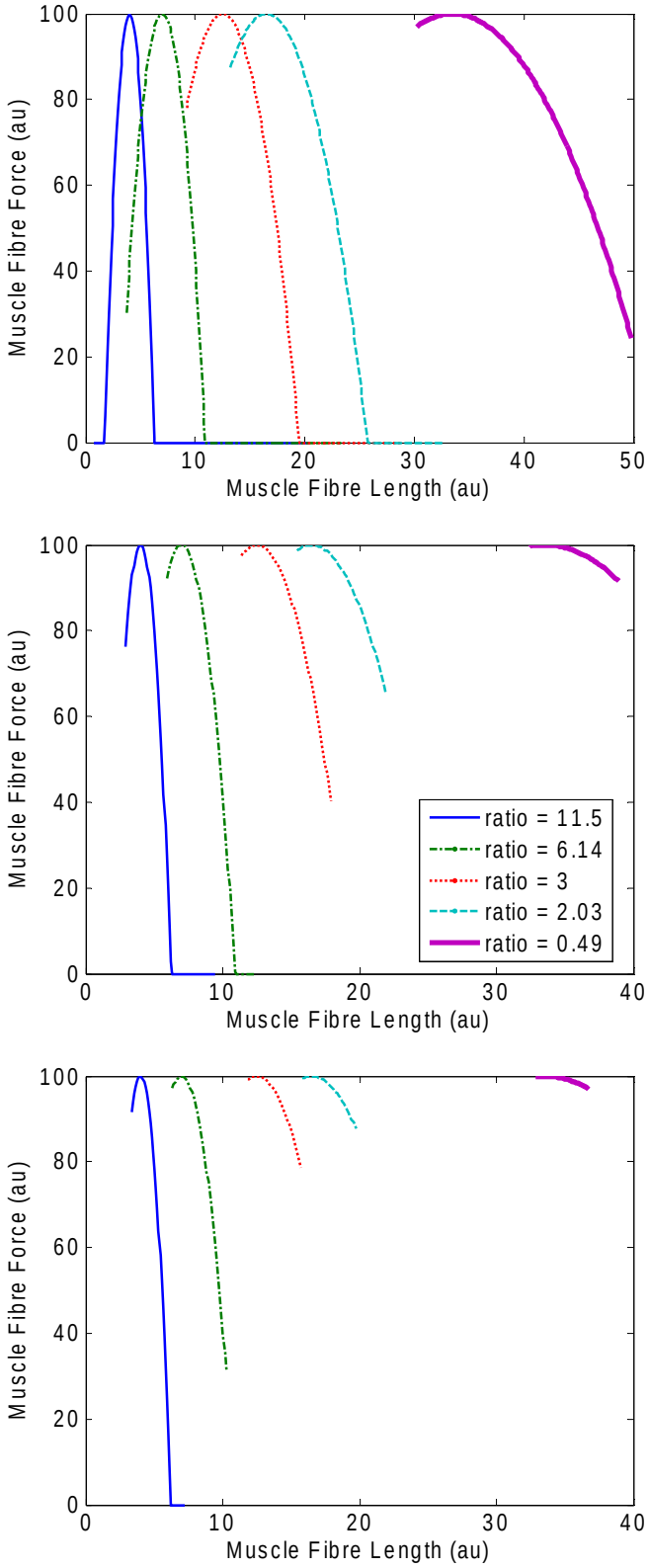

Figure **3.9**: The effect of varying the ratio L_{TR} / Lf_{OPT} with θ_{REF} equal to 15 degrees and Lf_{OPT} / r equal to a) one, b) two, and c) three.

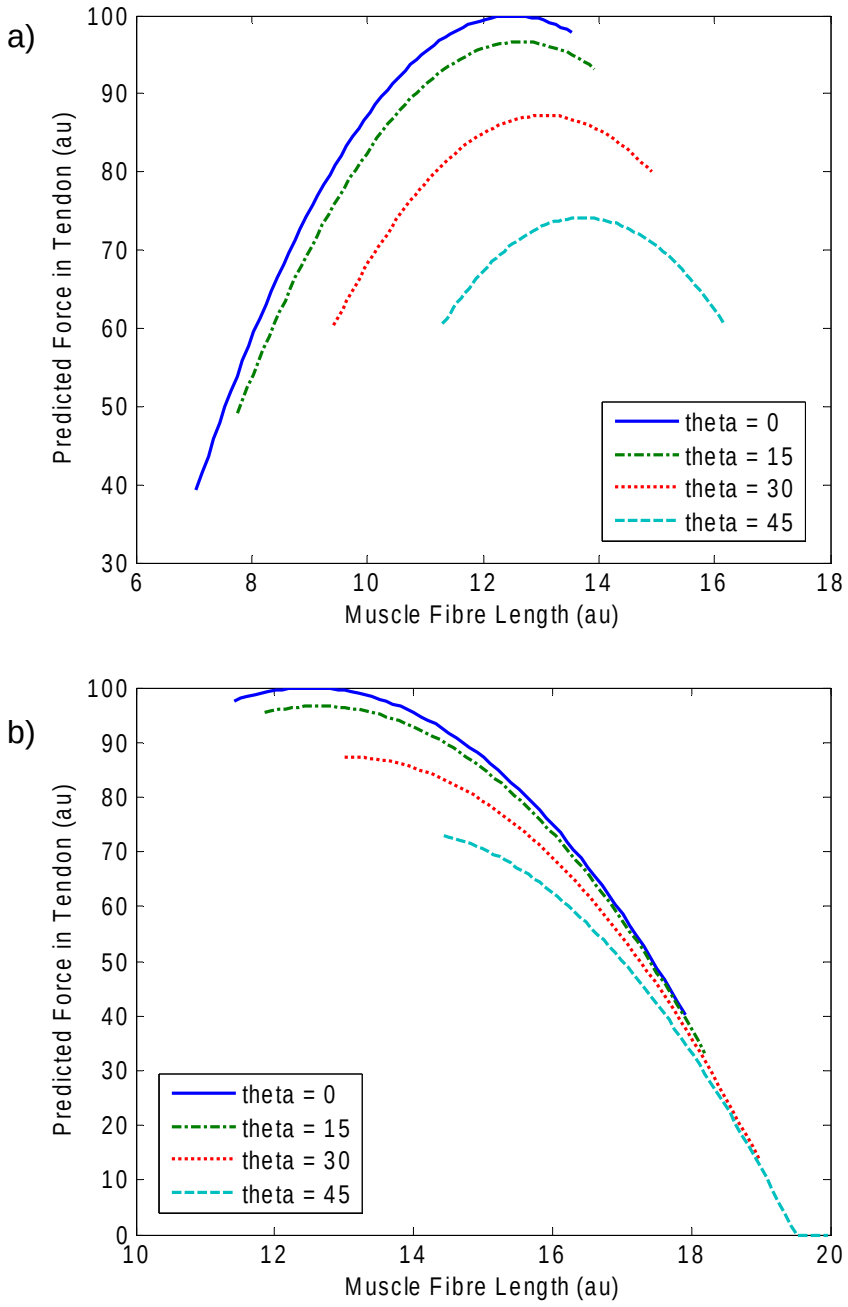

Figure **3.10**: The effect of muscle fibre pennation angle (θ_{PENN}) with the ratios L_{TR} / Lf_{OPT} and Lf_{OPT} / r equal to 3, c set at 0% and θ_{REF} set at a) 75 degrees, and, b) 15 degrees.

3.5 DISCUSSION

The model parameter that was most critical in allowing variability in the expressed section of the force-length relationship was the ratio L_{TR} / Lf_{OPT}. For high L_{TR} / Lf_{OPT} ratios, representing a long tendon and short muscle fibres, the whole of the force-length relationship was used due to the shortness of the muscle fibres. For very low ratios of L_{TR} / Lf_{OPT} the expressed section was always the plateau, unless the optimum length was set at a joint angle that was very far outside a physiologically realistic range of motion. The effect of changing the value of L_{TR} / Lf_{OPT}, however, was modified by the value of Lf_{OPT} / r. This is because for a fixed range of motion and a given value for the width of the force-length relationship, the inverse of Lf_{OPT} / r was proportional to the fraction of the force-length relationship that was used (Equation 3.12). For the range of motion and the width of the force-length curve used here only values of Lf_{OPT} / r above 1.5 resulted in only one limb of the force-length relationship being expressed. For intermediate values of L_{TR} / Lf_{OPT} and Lf_{OPT} / r the effect of increasing tendon compliance was to shift the expressed section to increasingly shorter lengths and the effect of increasing the pennation angle was to shift the expressed section to increasingly longer lengths.

Most models used in biomechanical analyses are of the phenomenological 'lumped single sarcomere' type used here. The intention of this study was to discover broad principles concerning the expression of the force-length relationship when considering the behaviour of the muscle-tendon complex as a whole. However, a complex three dimensional muscle architecture may be seen in vivo (Huijing, 1998) that may introduce subtleties that cannot be represented by the more simple model used here. For example, variability in the curvature and length of individual fascicles can cause fascicle strains that are not uniform throughout the muscle (Blemker et al., 2005). Nevertheless, very few

biomechanical models have attempted to include such detail and indeed it may be that the amount of inter-individual variation in muscle architecture when considered at this level prevents the drawing of general conclusions about muscle-tendon complex behaviour in vivo.

A second consideration is that the model parameters are inter-related and this means that changes in one parameter can affect the value of other parameters. For example, when an elastic tendon is assumed (c equal to or greater than 1%) then the absolute length change at maximum isometric force will depend on the value of L_{TR} / Lf_{OPT} since a long tendon extending by say 6% will extend more than a short tendon extending by 6%. For this reason an inextensible tendon was assumed when varying the other model parameters.

The findings from this study allow some predictions to be made about the amount of variability that may be expected in vivo for the five muscles considered as sources for the range of parameter values considered. The short head of the biceps femoris has a high value of 4.39 for Lf_{OPT} / r and a low value of 0.52 for L_{TR} / Lf_{OPT} (Table 3.1), meaning that this muscle is likely to operate entirely over the plateau region. The muscles ECRB, BR, and VL have intermediate values for Lf_{OPT} / r and L_{TR} / Lf_{OPT}, low tendon compliance and low to intermediate pennation angles making it likely that these muscles operate over one limb of the force-length relationship. Lieber & Friden (1998) measured ECRB sarcomere lengths using laser diffraction and muscle fibre lengths at different joint angles, and calculated from results averaged across 12 subjects that the ECRB would operate over the descending limb. Whether an individual operates over the ascending or descending limb will depend on the joint angle at which the optimum length occurs. In the model, varying the joint angle at which the optimum length (θ_{REF}) caused a small change in the length of the muscle tendon complex at a given joint angle. In vivo this inter-individual variability in muscle-

tendon complex lengths at a given joint angle could be caused in vivo by inter-individual differences in attachment sites, and therefore differences in the distance between origin and insertion sites. Such inter-individual differences in attachment sites have been reported, for example Duda et al. (1996) found that the coefficient of variation for the centroid of the attachment site of various muscles arising from and inserting onto the femur was 80%. Inter-individual variability in the limb of the force-length curve used for a given muscle could also arise in vivo due to small variations in L_{TR} / Lf_{OPT}. Variability in L_{TR} / Lf_{OPT} would mean that muscle-tendon complex lengths at a given joint angle may be similar between individuals but that differences in the expressed section could occur due to inter-individual differences in the tendon length or in the muscle fibre length at a given joint position. Different muscle fibre lengths at a given joint angle could occur in different subjects as a result of the addition or removal of sarcomeres, this has been shown to occur as a result of training in rats (Lynn et al., 1998).

The value of L_{TR} / Lf_{OPT} for SOL is high, and the value of Lf_{OPT} / r is low, which would indicate that most of the force-length relationship would be used. However, there is a fairly high amount of variability in the values reported for Lf_{OPT} / r by Maganaris et al. (2006). For subjects at the lower end of the range with a value of 0.5 for Lf_{OPT} / r the maximum joint range of motion that would be allowed by the force-length relationship assuming the width of the force-length relationship is 0.56 would be 0.56 radians or 32 degrees according to Equation 3.12. At the other end of the range, a subject with a value of 1.5 for Lf_{OPT} / r could achieve an ankle joint range of motion of 60 degrees and use only 62% of the force-length relationship. One of the problems with modelling the soleus is that the pennate muscle fibres have a long aponeurosis. The length of this aponeurosis is included in the estimate of the tendon resting length given by Hoy et al. (1990), yet the fact that the muscle belly extends along the series elastic component instead of sitting on top reduces the effective value of L_{TR} / Lf_{OPT}.

This would mean that SOL would be likely to operate over only part of the force-length relationship for most of the values of Lf_{OPT} / r quoted by Maganaris et al. (2006). Whether the muscle operates over the ascending or descending limb would be affected by the values of θ_{PENN} and c. Magnusson et al. (2001) report values of 4.4-5.6% for c. Increasing tendon compliance would shift the expressed section of the force-length relationship to shorter lengths. Given the long Achilles tendon and its relatively high strain value it would be expected that the majority of individuals would operate over the ascending limb. Nevertheless, Figures 3.7 and 3.9 demonstrate that it is possible that individuals with long SOL muscle bellies, and therefore lower effective values of L_{TR} / Lf_{OPT}, and tendons at the stiffer end of the range could still use the descending limb.

In conclusion, the value of L_{TR} / Lf_{OPT} seems important in determining the likely inter-individual variability in the expressed section of the force-length relationship, though the effect of L_{TR} / Lf_{OPT} is modified by the value of Lf_{OPT} / r. Low values of L_{TR} / Lf_{OPT} result in a muscle that operates over the plateau section, high values of L_{TR} / Lf_{OPT} result in a muscle that uses the whole of the force-length relationship. Intermediate values of L_{TR} / Lf_{OPT} allow a muscle to operate over one or other limb of the force-length relationship. Whether this is likely to be the ascending limb or the descending limb is then determined by the exact value of L_{TR} / Lf_{OPT} and the values of the remaining parameters: θ_{REF}, θ_{PENN} and c. It appears on the basis of values reported for these parameters in the literature that there is scope for inter-individual variation in the values of these parameters for different muscles, and that some inter-individual variability in the expressed section of the force-length relationship is possible, particularly for muscles with intermediate values of L_{TR} / Lf_{OPT} and Lf_{OPT} / r.

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CHAPTER 4

THE STEADINESS OF ISOMETRIC KNEE EXTENSION CONTRACTIONS IN YOUNG AND YOUNG-OLD ADULTS

4.1 ABSTRACT

Previous studies have identified that aging results in decreased steadiness during isometric force production at some effort levels, decreased steadiness has implications for force and movement control, and for the incidence of injury. In this study the knee resultant joint moment record was analyzed for young and young-old females at 25%, 50%, 75% and 100% of maximum effort. No difference in the magnitude of the fluctuations in the joint moment, as quantified by the coefficient of variation, was shown between the two age groups at any effort level. The young females demonstrated more complexity, quantified using Approximate Entropy, in the knee joint moment signal at all effort levels ranging between 100% and 25% of maximum compared to young-old females. A Detrended Fluctuation Analysis indicated different scaling behavior over shorter and longer timescales, suggesting that two or more different processes may be responsible for the fluctuations in the joint moment during isometric contractions. Young-old females generally demonstrated scaling characteristics that indicated more slowly repeating processes. Changes in the time-dependent structure of the fluctuations in the joint moment may reflect changes in neural activation strategies and muscle-tendon mechanical properties with age.

4.2 INTRODUCTION

When the resultant joint moment acting at a joint during an isometric contraction is measured it is not constant but rather it fluctuates (e.g., Lippold et al., 1957).

These fluctuations limit the steadiness of force production and affect the ability of an individual to maintain a desired force or to realize an intended limb trajectory (Harris & Wolpert, 1998). Steadiness is decreased in older adults for sub-maximal contractions (Tracy & Enoka, 2002). This reduced precision in force production may lead to movement errors and consequently an increased risk of injury in certain populations.

Muscle force is a consequence of motor unit activity and the mechanical properties of the muscle-tendon unit. Potential factors that could influence the fluctuations in force are: the properties of individual motor units, the behavior of motor unit populations, and the mechanical properties of the muscle-tendon unit that influence the force output namely the force-length and force-velocity relationships and the behavior of the parallel and series elastic components. Various changes in the properties of human muscle have been identified with aging that may be related to changes in the steadiness of force production. For example, there is a reduction in muscular strength (Frontera et al., 2000), a change in the relative fiber type distribution such that the proportion of slow twitch fibres increases (Lexell, 1995), and a reduction in the number of motor units (Galea, 1996). These changes are more marked in some muscles than others (Galea, 1996).

The size of the force or moment fluctuations has been quantified using the standard deviation (SD) and the coefficient of variation (CV) of the force (e.g., Tracy & Enoka, 2002; Enoka et al., 2003; Vaillancourt & Newell, 2003). However, use of the standard deviation and coefficient of variation is can give conflicting results when used for data that is not normally distributed, random, and independent. It has been shown that the fluctuations in the force or moment produced by a muscle or muscle group exhibits a structure that is not indicative of random white noise (Vaillancourt & Newell, 2003; Sosnoff et al., 2005). In these studies the Detrended Fluctuation Analysis (DFA) (Peng et al., 1994) was

used to determine the fractal scaling index (α) of the force signal. The scaling index gives information about how the value of a given variable varies with the timescale over which it is measured and indicates the presence or otherwise of long-term correlations. Challis (2006) analyzed isometric maximum effort ankle plantar flexion moments using Approximate Entropy (ApEn), which is a dimensionless measure varying between 0 (indicating a signal with high regularity such as a sine wave) and 2 (a signal with low regularity such as white noise) (Pincus, 1991). It was found that older male adults had greater regularity in the generation of a maximal plantar flexion moment than younger males. These studies suggest that the application of such biological signal processing techniques to the moment or force record may reveal more subtle differences between younger and older adults than is captured by using measures such as CV and SD. However, no systematic study of the effect of effort level or contraction intensity on the complexity or structure of the force signal has been made for the quadriceps.

The purpose of this study was to measure the knee moment generated during an isometric contraction at different effort levels in young and young-old women, and to analyze this moment record in order to assess differences between age groups in various aspects of the fluctuating moment time series. Specifically, the aim was to systematically examine the effect of contraction intensity and age on the complexity and structure of the force signal.

4.3 METHODS

Eight female subjects were recruited to a young age group (mean $\pm$ standard deviation: age 23.6 years $\pm$ 2.5 years; height 1.67 $\pm$ 0.06 m; mass 70.1 $\pm$ 11.9 kg), and eight other female subjects were recruited to a young-old age group (mean $\pm$ standard deviation: age 69.0 years $\pm$ 1.8 years; height 1.59 $\pm$ 0.04 m; mass 68.0 $\pm$ 8.9 kg). The age range for the young age group was 19 to 28

years and for the young-old age group was 66 to 71 years. Subjects were screened to ensure absence of obesity, cardio-vascular, lung, neurological and musculo-skeletal disorders. Subjects in the young-old age group underwent a DXA scan to ensure the absence of osteoporosis. All subjects were familiarized with the procedures and provided written informed consent before participating and the Institutional Review Board at The Pennsylvania State University approved all procedures.

Following a five minute cycle ergometer warm-up and three to four practice contractions, subjects performed isometric knee extension contractions using the right leg at a 90 degree hip angle and a 90 degree knee angle in a Biodex III dynamometer. The dynamometer position was manipulated so that the axis of rotation of the knee joint was aligned with the axis of rotation of the dynamometer. Straps were securely fastened and the subject's knee was positioned carefully to ensure minimal movement. Subjects performed three maximal voluntary isometric contractions with several minutes rest between each contraction; a minimum rest period of two minutes was enforced. Subjects then performed three contractions at each of the following levels: 75%, 50% and 25% of maximum, using visual feedback provided via a computer screen in a LabVIEW 7 environment. Each contraction was held for six seconds once the required torque was reached. The Biodex moment signal was sampled at 1600 Hz and low pass filtered at 20 Hz using Matlab 7. A 2.2 second window was selected from each of the joint moment records at each force level for analysis using a minimum variance criterion. This criterion was used in order to identify the steadiest part of each effort, although other criteria were tested and these gave similar results. The best trial at each effort level was selected for further analysis; this was defined as the trial at each effort level that was closest to the required moment value for the whole of the 2.2 second window. The size of the window (2.2 seconds) was chosen so that only the plateau section of the maximum effort contraction was selected.

The response variables (CV, nonparametric CV, the fractal scaling index alpha, and ApEn) were calculated for the 2.2 second window. The coefficient of variation is calculated by computing the standard deviation of the moment record over the time series and dividing it by the mean moment over this time period. Given that previous studies have shown that the data points in a sustained isometric contraction are not normally distributed (e.g. Vaillancourt & Newell, 2003), a non-parametric version of the coefficient of variation was also computed (Equation. **4.1**), this uses the inter quartile range and the median value.

$$CV_{NP} = \frac{0.75(IQR)}{\eta} \qquad [\mathbf{4.1}]$$

Where:

η is the median value, and

IQR is the difference between the value of the 25th percentile and the 75th percentile, i.e. the inter quartile range.

The α value gives information about the self-similarity of the time series. Self-similar processes have the property that they are composed of units, sub-units and sub-sub-units over multiple levels that statistically resemble the structure of the whole object. For a one dimensional times series, this means that when the x and y axes are expanded by similar factors, similar fluctuations are seen for many expansions. A problem with physiological processes is that they are bounded, that is they can adopt values only within certain ranges. Integration of a physiological time series maps the bounded process to an unbounded self-similar process (Peng et al., 1995) allowing the computation of the self-similarity or scaling parameter α.

To calculate α the Detrended Fluctuation Analysis algorithm was used (Peng et al., 1995). First, the time series of length N is integrated (Equation **4.2**),

$$y(k) = \sum_{i=1}^{k} \left[B(i) - B_{ave} \right] \qquad [\mathbf{4.2}]$$

where:

k is the number of data points,

$B(i)$ is the ith value of the time series, and

B_{ave} is the average value.

Next, the vertical characteristic scale of the integrated time series is measured. The integrated time series is divided into boxes of length n and a least-squares line is fitted, representing the trend in each box (Figure **4.1**). The y coordinate of the straight line segment is denoted by $y_n(k)$, and the integrated time series is detrended by subtracting the local trend in each box. For a given box size, n, the characteristic size of fluctuation for the integrated and detrended time series is computed using Equation **4.3**.

$$F(n) = \sqrt{\frac{1}{N} \sum_{k=1}^{N} \left[y(k) - y_n(k) \right]^2} \qquad [\mathbf{4.3}]$$

This computation is repeated over a range of time scales or box sizes, n, to provide a relationship between box size and F(n). The slope of the line relating the log of n to the log of F(n) determines the scaling parameter α. For this analysis a piecewise approach was taken in determining the scaling parameter. This was because it was clear that the straight line relationships were different for different intervals over the range of timescales (Figure **4.2**). A piecewise function with two sections was fitted to the data with the knot first occurring at data point 2. Then a new function was fitted using data point 3 as the knot and so on sequentially until data point (n-1). A least squares criterion was used in order to select the best fit from the (n-2) piecewise functions. The gradient of the first

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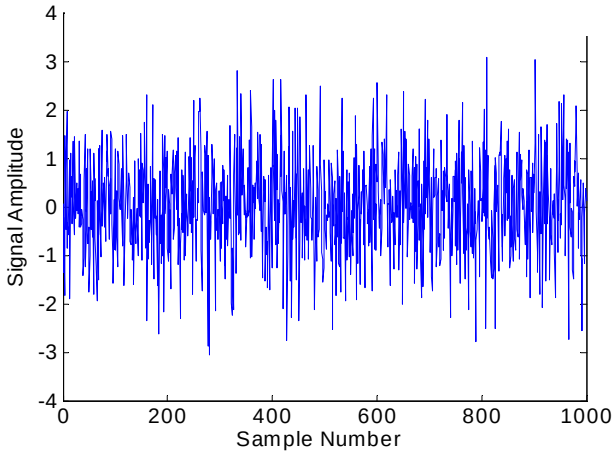

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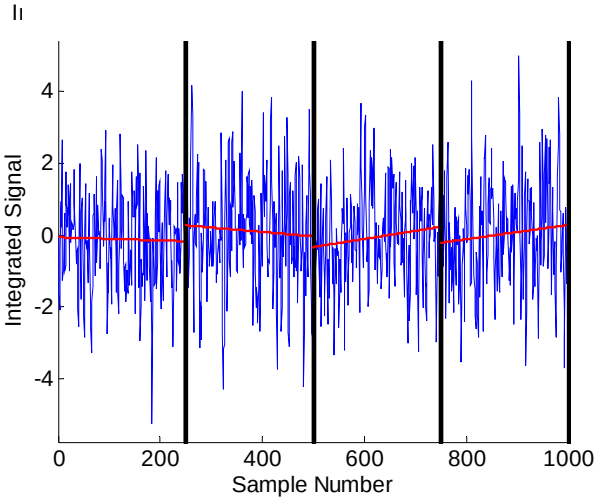

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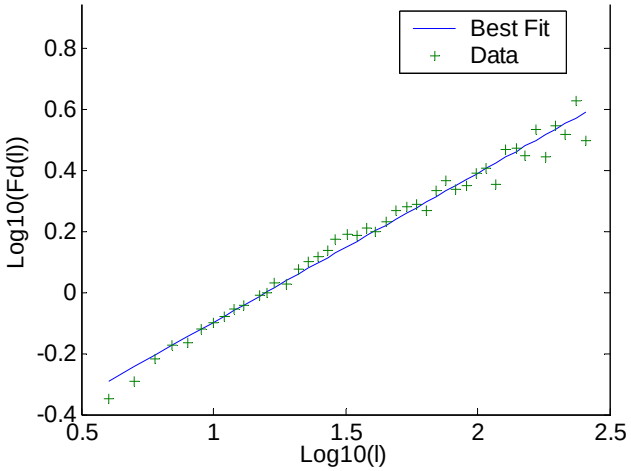

Figure **4.1**: Demonstration of the DFA procedure: a) white noise, b) integrated white noise with a linear trend identified, c) the slope of the log-log plot is the scaling parameter, α.

section of the function will be referred to as alpha$_1$, and the gradient of the second section will be referred to as alpha$_2$.

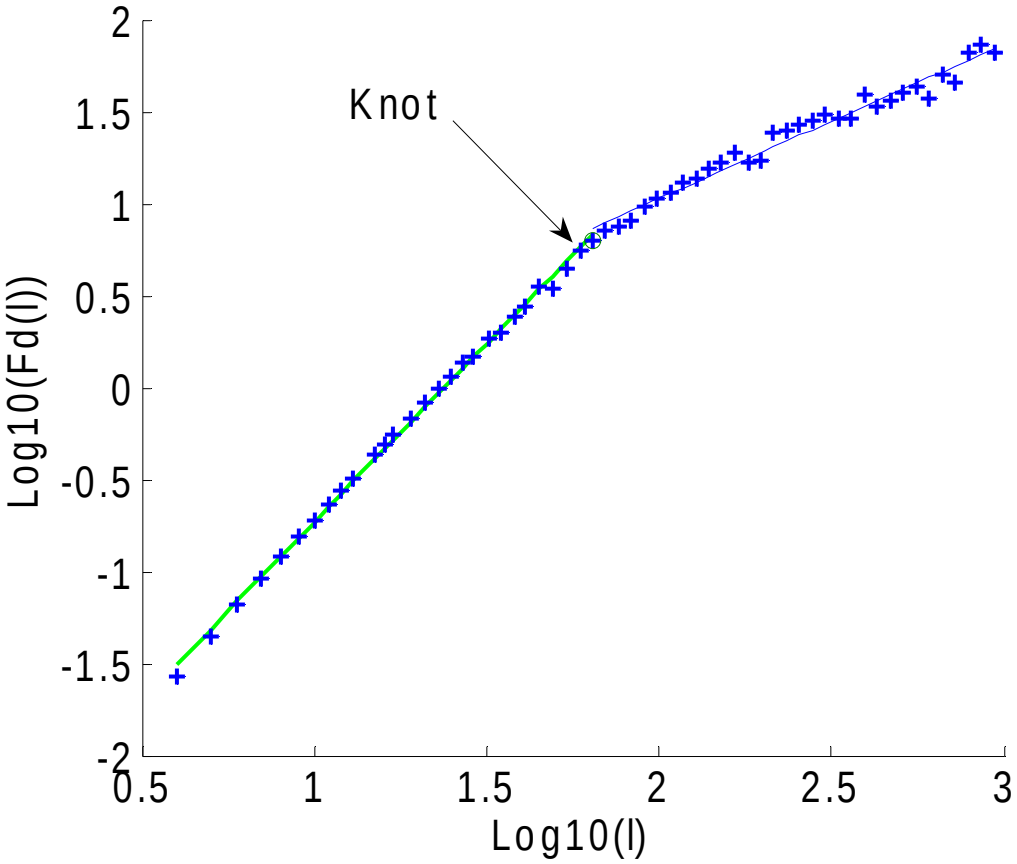

Figure **4.2**: Typical result of a piecewise DFA for one force record showing a knot and two different alpha values, one for shorter timescales (alpha$_1$) and one for longer timescales (alpha$_2$).

For uncorrelated, completely random white noise the integrated time series represents a random walk process and α=0.5. When 0<α<0.5 power law anti-correlations are present and when 0.5<α<1 power law correlations are present. When α>1, correlations exist but they cease to be of a power law form. Brown noise is indicated by α=1.5.

Signal complexity was quantified using Approximate Entropy (ApEn), using the algorithm of Pincus (1991). This determines the logarithmic likelihood that a sequence of m data points is similar to other sequences of data points in the data set. If the data set is regular then the value of ApEn is low and close to 0, if the data set is complex or irregular then the ApEn value is high and close to 2. The calculation of formal entropy theoretically requires perfectly noiseless data sets of infinite length. This algorithm was developed particularly for use with biological signals, which are noisy and of finite length; the tolerance of the ApEn algorithm for noise resides in its use of a range, r, within which the set of m points may be regarded as similar. This parameter r is set with reference to the anticipated noise in the data. Despite the name of the algorithm (Approximate Entropy), its value does not in fact approximate the formal entropy, but rather is designed for use as a comparative statistic when a fixed number of data points, and fixed values for m and r are used. The value used for r in this analysis is 0.1, this value was chosen on the basis of an analysis of the noise level of the Biodex signal, and the value m=2 as suggested by Pincus (1991). For a data set with N points, and for m=2, r=0.1, ApEn is computed as follows. Define a set of points in a two-dimensional space from successive pairs of values in the one-dimensional signal. The pair X_i, X_{i+1} then define a point in two-space, there are N-1 points in two dimensions. Obtain a measure of the distances between (X_i, X_{i+1}) and all other points (X_j, X_{j+1}), there are N-2 distances for each X_i in two-space. For each of the pairs of data points, X_i, find the fraction of the distances to the other points which are less than r, and let this fraction be called $C_i(r)$. This fraction is then a measure of the frequency of similar patterns between successive points in the two-dimensional plot. Find the average of the $C_i(r)$s for the N-1 fractions, and take the natural log, this value is defined as $\Phi(m=2,r=0.1)$. Repeat these steps using m=3, i.e. using X_i, X_{i+1}, X_{i+2} to define point positions in three-space, giving $\Phi(m=3,r=0.1)$. Then the measure ApEn (m=2, r=0.1, n=N) is defined in Equation **4.4**.

$$ApEn(m=2,r=0.1)=\Phi(m=2,r=0.1)-\Phi(m=3,r=0.1) \qquad [\mathbf{4.4}]$$

A surrogate analysis of the data was carried out and this showed that the ApEn and DFA values computed for the subject data were due to signal properties and not measurement system noise (Schreiber & Schmitz, 2000). Surrogate data were generated from the original data sets by computing the fast Fourier transform (FFT) of the data, and then computing the inverse FFT of the signal with the phase of the FFT randomized (Theiler et al., 1992). Statistical comparisons of the subject data were performed using a three way analysis of variance (age group, subject, effort level) with subject as a random factor nested in age.

4.4 RESULTS

A two-sample t-test assuming unequal variance indicated a significant difference in the moment achieved during the maximum effort trial for the two age groups ($t=-5.64$; d.f.=12; $p<0.001$) (Table **4-1**).

Table **4-1**: Mean and standard deviation of the moment achieved during the maximum effort trial for each age group.

Age Group	Mean Maximum Moment (N.m)	Standard Deviation (N.m)
Young	133.9	21.1
Young-Old	82.9	14.5

No statistically significant difference was seen between age groups for either CV or for the non-parametric version of coefficient of variation (CV_{NP}) for effort levels from 25% to 100% of maximum (Figure **4.3**).

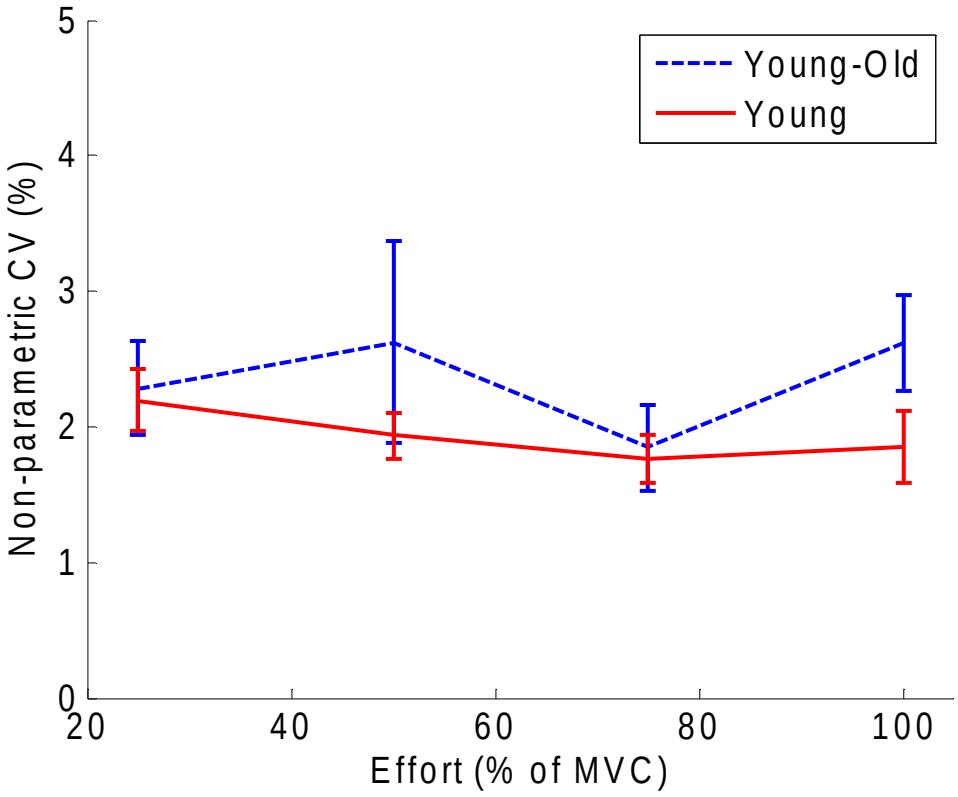

Figure **4.3**: Non-parametric coefficient of variation for young and young-old groups (mean ± SE).

A significant difference between age groups and force levels was seen for both the ApEn and alpha values (Figures **4.4** & **4.5**). ApEn tended to increase with increasing effort level ($F=70.28$; d.f.=3, 42; $p<0.001$), and was consistently lower at all force levels for the older females ($F=447.62$; d.f.=1, 14; $p<0.001$). There was a significant effort level by age interaction that was due to a reduced offset in the ApEn values between age groups at the 25% effort level (figure **4.4**). There was a significant difference between age group when the median force at each effort level was used as a covariate, suggesting that the difference in ApEn between age groups is not simply due to differences in the force produced by each age group.

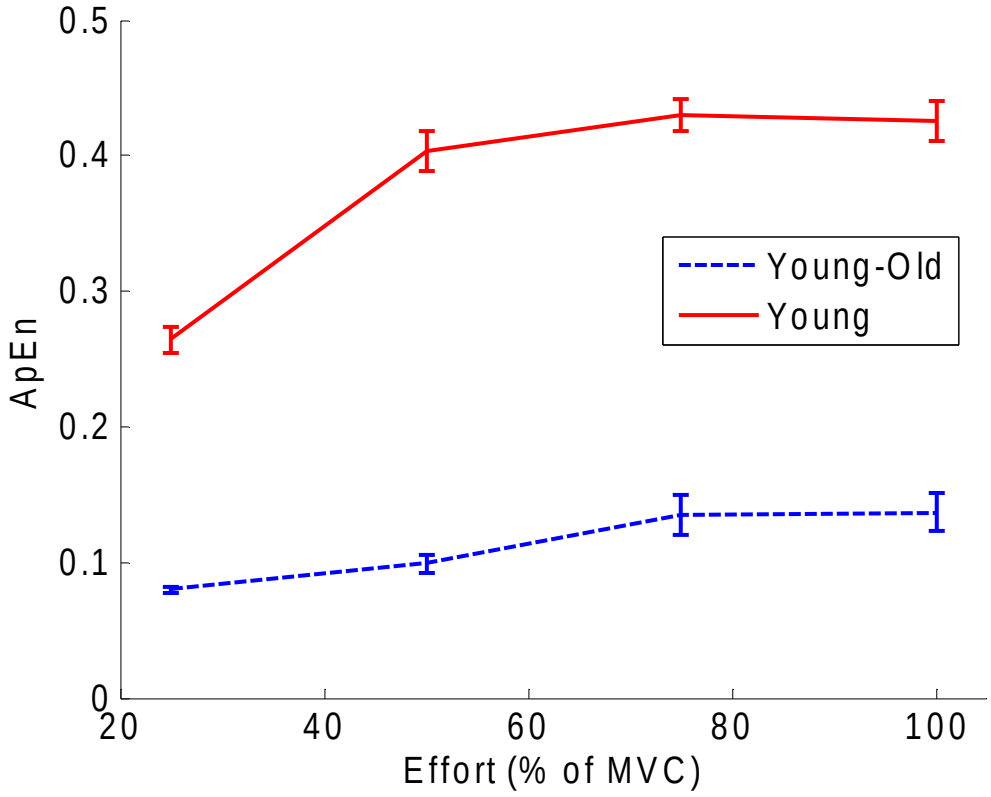

Figure **4.4**: ApEn values for young and young-old groups (mean ± SE).

The alpha values were consistently lower at all force levels and over all time scales for the younger females. The alpha value for the first section of the piecewise function fitted to the log-log plot ($alpha_1$) was significantly higher for the older subjects (F=7.58; d.f.=1, 14; p=0.016) and increased with increasing force level (F=4.64; d.f.=3, 14; p=0.0187) (Figure **4.5**). The knot position changed such that it was lower with increasing force level and was lower for older adults (Figure **4.5**). The alpha value for the second section of the piecewise function fitted to the log-log plot ($alpha_2$) was significantly higher for the older subjects (F=10.42; d.f.=1, 14; p=0.006) and increased with increasing force level (F=6.77; d.f.=3, 14; p=0.005) (Figure **4.5**).

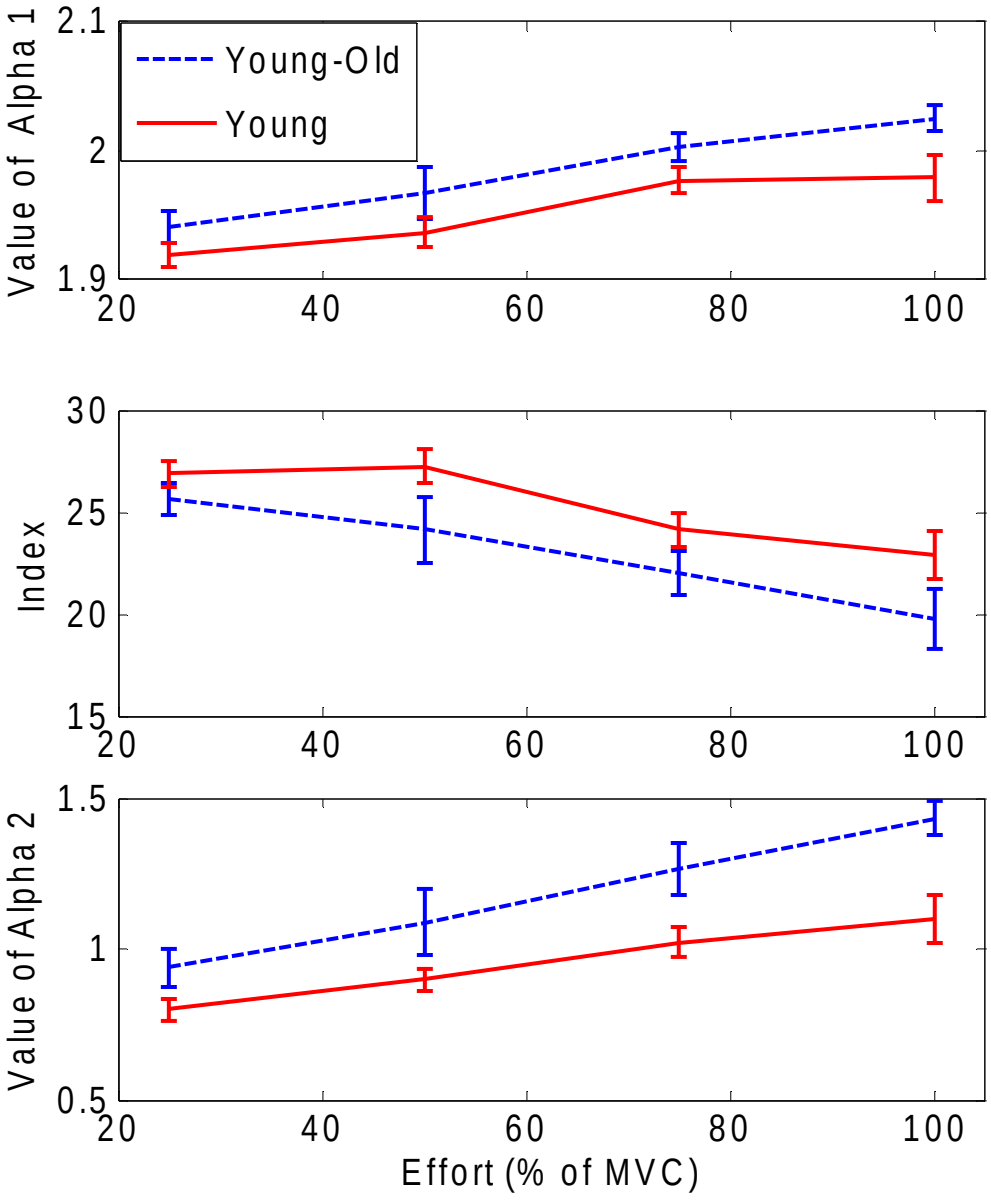

Figure **4.5**: Values of alpha$_1$, knot position (index) and alpha$_2$ for young and young-old groups at different force levels (mean ± SE).

4.5 DISCUSSION

The lower ApEn values for the older females compared with the young females indicates reduced regularity or reduced signal complexity in the isometric force output at all effort levels for the young-old age group. A more complex signal may be caused by two different types of process: a signal that is more random, or a signal that is highly deterministic but that reflects the integration of several processes. In either case, the reduced complexity seen in the force output of the older females is consistent with an alteration, often a down regulation, of one or more processes with aging (Lipsitz & Goldberger, 1992). The decrease in complexity with aging is also consistent with the age-related changes in homeostatic processes (Vaillancourt & Newell, 2002); isometric force production at a desired or specified effort level can be considered a homeostatic process. One change associated with aging muscle that has been identified is a de-nervation re-nervation process that results in fewer, larger motor units (Galea, 1996). During this process some muscle fibres, typically fast twitch muscle fibres are de-nervated and then re-nervated via outgrowths from axons innervating existing slow twitch muscle fibres. This process results in a more slowly contracting muscle in older adults. It may be that the reduced number of motor units in older muscle results in a less complex force signal (Challis, 2006).

The results of the DFA analysis generally indicate a shift in the power of the frequency spectrum to lower frequencies with increasing effort level for both age groups, and a shift to slower frequencies at each effort level with increased age. The alpha values over the first part of the piecewise function were similar and close to 2 but generally lower for the young females than for the young-old females. Alpha values close to 2 indicate a very slowly repeating process. The young group had alpha values over the second part of the piecewise function ($alpha_2$ values) that indicated power law scaling relationships for effort levels at 75% of maximum and below, that is the alpha values were between 0.5 and 1.

The $alpha_2$ values at maximum effort were greater than 1, and this means that long term correlations exist, however they are no longer of a power law form. That is, only lower frequencies are present rather than power law scaling over the whole frequency spectrum. The older group only exhibited power law scaling at an effort level of 25%. At effort levels of 50% of maximum and above, the $alpha_2$ values were greater than 1 and were equal to 1.5 at 100% effort. An alpha value of 1.5 is indicative of brown noise. The two stage nature of the alpha values is suggestive of different processes operating over different timescales. At shorter timescales the dominant process may repeat more slowly than a second process that is dominant at longer timescales.

The results of the DFA analysis indicate a non-stationary process. One of the features of a non-stationary process is that statistical measures such as the standard deviation will not be the same all the way along the time series. This means that measures of variability dependent on such statistics should be used with caution since the value will depend on the length of the interval used and how far along the time series the interval is taken. This means that measures of variability such as SD and CV are at best only comparable where an identical time interval and an identical procedure for selecting this time interval have been used. This suggests that some of the contradictory evidence found in studies of steadiness (reviewed by Enoka et al., 2003) may be explained by the non-stationarity of the force time-series.

The lower entropy of the force signal of the older adults and the higher alpha values, indicating more slowly varying time dependent processes suggests that, although measures of variability such as CV and SD may indicate that older adults have a higher variability, instead there is less randomness in the signal. This means that less ‘states’ are accessible to the older adults, and that in fact there is less variability in the force output of older muscles. This suggests that

older muscles are less able to adapt to changing requirements or produce precise control.

In this study two age groups were recruited based on the age group definitions of Spirduso (1995). While it is appreciated that chronological age does not necessarily reflect the time course of the biological processes associated with aging, the prior medical screening ensured that both groups were healthy. This means that age is the major potential reason for the differences identified between the two groups. One factor which can potentially influence steadiness is the level of co-contraction of agonists and antagonists (Selen et al., 2005), but there is evidence in the literature that is no difference between the young and old in co-contraction over a range of effort levels during isometric contractions (Burnett et al., 2000).

In summary, it has been shown that there is no difference between young and young-old females in the magnitude of the fluctuations in joint moment during isometric knee extensions as quantified by CV and a non-parametric equivalent of CV. There no difference between the results of the analysis when using the parametric compared to the non-parametric version of CV. Although there was little difference between the age groups in the magnitude of the fluctuations, there are striking differences between the two age groups in terms of the complexity and scaling characteristics of the fluctuations. It has been shown for the first time that young adult females demonstrate more complexity in the knee joint moment signal at all effort levels ranging between 25% and 100% of maximum compared to young-old females. A DFA indicated different scaling behavior over shorter and longer timescales, suggesting that two or more different processes may be responsible for the fluctuations in the joint moment during isometric contractions. Young-old females demonstrated scaling characteristics that indicated more slowly repeating processes. Changes in the time-dependent structure of the fluctuations in the joint moment may reflect

changes in neural activation strategies and muscle-tendon mechanical properties with age.

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CHAPTER 5

THE STEADINESS OF ISOMETRIC KNEE EXTENSION CONTRACTIONS IN YOUNG AND YOUNG-OLD ADULTS FOLLOWING STRENGTH TRAINING

5.1 ABSTRACT

The steadiness of isometric force or moment production has implications for the successful control of muscle force and movement. There is some evidence that steadiness is reduced at certain effort levels in older adults, this may affect the incidence of injury in this population. The effect of a ten week program of strength training on the steadiness of the knee joint moment during isometric knee extension contractions was studied in young (18-28 years) and older (65-74 years) females at 25%, 50%, 75% and 100% of maximum effort. Strength training produced a small decrease in the coefficient of variation (CV) but not the standard deviation (SD) of the moment record in both the young and the older age groups. The complexity of the joint moment record as quantified by Sample Entropy (SampEn), and the behavior of the scaling parameter, alpha, as determined by a Detrended Fluctuation Analysis was unchanged. It may be that the aspects of the time dependent structure of the joint moment record that are characterized by SampEn and alpha relate to a training-resistant, aging-related deterioration in the calcium release-reuptake kinetics at the level of the sarcoplasmic reticulum.

5.2 INTRODUCTION

The ability to produce a desired force is fundamental to successful movement performance. The steadiness of the force produced has significant implications

for the ability of an individual to maintain a desired force or to realize an intended limb trajectory (Harris & Wolpert, 1998).

The steadiness of isometric contractions appears to change with aging such that the coefficient of variation (CV) of the force or moment record is increased in older adults under certain submaximal conditions (Enoka et al., 2003). This reduced precision in force production may lead to movement errors making performance of activities of daily living difficult and leading to an increased risk of injury in older populations. Previous studies have determined that these differences are greatest at low forces of around 2.5-15% of maximum effort (e.g. Keen et al., 1994; Tracy & Enoka, 2002; Galganski et al., 1993). These differences in the CV with age disappeared following a strength training program for the first dorsal interosseus (Keen et al., 1994). A strength training program did not remove age-related differences in the CV for force for sub-maximal isometric contractions in the quadriceps (Tracy et al., 2004). However, strength training did result in a decreased CV for acceleration during sub-maximal dynamic quadriceps contractions in older adults (Tracy et al., 2004).

Some studies have used algorithms from the fields of statistical mechanics and non-linear dynamics to quantify the time dependent structure of the fluctuations in the force or moment record. Although it appears there is no difference in the CV for force with aging above 20% of MVC (Enoka et al., 2003), studies using Approximate Entropy (ApEn) (e.g. Challis, 2006), and the Detrended Fluctuation Analysis (DFA) (e.g. Vaillancourt & Newell, 2003) have shown that consistent and significant differences exist between age groups in the time dependent structure of the force or moment record at some effort levels.

A previous study (Chapter 4) has shown that the moment recorded during isometric quadriceps contractions demonstrates consistent differences in ApEn and the alpha values (the output of the DFA) between age groups at effort levels ranging from 25% to 100% of MVC. The lower ApEn values seen in the older age group are consistent with the hypothesis that homeostatic processes such as isometric muscle contraction demonstrate a decrease in complexity with aging (Lipsitz & Goldberger, 1992; Vaillancourt & Newell, 2002). Challis (2006) suggested that the reduced complexity during isometric contractions seen in a 65-74 year old age group compared to an 18-27 year old age group may be related to decreases in the number of motor units with aging after the age of 60 (Galea, 1996). This decrease in the number of motor units results from a de-nervation re-nervation process that results in a reduced number of motor units, and a shift in the fibre type population such that the proportion of slow or type I fibres is increased. If these are responsible for the differences in the entropy and alpha values between age groups then the differences between age groups should be retained even after strength training. The purpose of this study was therefore to test whether changes occur with strength training in the magnitude and structure of the fluctuations of the knee joint moment recorded during isometric knee extension contractions.

5.3 METHODS

Eight female subjects were recruited to a young age group (mean ± standard deviation: age 23.6 years ± 2.5 years; height 1.67 ± 0.06 m; mass 70.1 ± 11.9 kg), and eight other female subjects were recruited to a young-old age group (mean ± standard deviation: age 69.0 years ± 1.8 years; height 1.59 ± 0.04 m; mass 68.0 ± 8.9 kg). The age range for the young age group was 19 to 28 years and for the young-old age group was 66 to 71 years. Subjects were screened to ensure absence of obesity, cardio-vascular, lung, neurological and musculo-skeletal disorders. Subjects in the young-old age group underwent a

DXA scan to ensure the absence of osteoporosis. All subjects were familiarized with the procedures and provided written informed consent before participating and the Institutional Review Board at The Pennsylvania State University approved all procedures.

Testing sessions were carried out before and after ten weeks of strength training both took the following format. After a five minute cycle ergometer warm-up and three to four practice contractions, subjects performed isometric knee extension contractions using their right leg at a 90 degree hip angle and a 90 degree knee angle in a Biodex III dynamometer. The dynamometer position was manipulated so that the axis of rotation of the knee joint was aligned with the axis of rotation of the dynamometer. Straps were securely fastened across the body and the subject's knee was positioned carefully to ensure minimal movement. Subjects performed three maximal voluntary isometric contractions with several minutes rest between each contraction; a minimum rest period of two minutes was enforced. Subjects then performed three contractions at each of the following levels: 75%, 50% and 25% of maximum, using visual feedback provided via a computer screen in a LabVIEW 7 environment. Each contraction was held for six seconds once the required torque was reached. The Biodex moment signal was sampled at 1,600 Hz and low pass filtered at 20 Hz in both directions with a second order Butterworth filter in Matlab 7.

Subjects performed ten weeks of strength training during which time they attended training sessions three times a week. Subjects were supervised while performing a whole body workout that included bi-lateral squats performed with dumbbells, uni-lateral leg extensions, uni-lateral leg curls and bi-lateral loaded plantar flexions. Subjects performed three sets of eight repetitions of each exercise. The first set was performed at 50% of maximum effort, the second set at 75% of maximum effort and the third set at 100% of maximum effort. The loading was increased whenever the subject was able to extend the third set to

ten repetitions. The magnitude of the increase depended on the relative strength of the subject for that exercise but was typically around 5 or 10 pounds. Where subjects had to miss training sessions due to illness, the training period was extended beyond ten weeks so that all subjects performed at least 28 training sessions.

At the end of the training period subjects were re-tested using the protocol described above. The sub-maximal effort contractions were performed at 75%, 50%, and 25% of the new maximum effort level.

A 2.2 second window was selected from each of the joint moment records at each force level for analysis using a minimum variance criterion. This criterion was used in order to identify the steadiest part of each effort, although other criteria were tested and these gave similar results. The best trial at each effort level was selected for further analysis; this was defined as the trial at each effort level that was closest to the required moment value for the whole of the 2.2 second window. For the maximum effort trial, the trial at which the maximum torque was achieved was used. For these trials the size of the window (2.2 seconds) was chosen so that only the plateau section of the maximum effort contraction was selected for all of the subjects, i.e. before fatigue reduced the recorded torque by more than 10%.

The response variables (SD, CV, fractal scaling index (alpha), and Sample Entropy) were calculated for the 2.2 second window. The CV is calculated by computing the SD of the moment record over the time series and dividing it by the mean moment over this time period.

Sample Entropy (SampEn) was calculated using the algorithm of Richman and Moorman (2000), which determines the logarithmic likelihood that a sequence of m data points is similar to other sequences of data points in the data set. If the

data set is regular then the value of SampEn is low and close to 0, if the data set is complex or irregular then the SampEn value is high. The calculation of formal entropy theoretically requires perfectly noiseless data sets of infinite length (Richman & Moorman, 2000). The SampEn algorithm was developed particularly for use with biological signals, which are noisy and of finite length; the tolerance of the SampEn algorithm for noise resides in its use of a range, r, within which the set of m points may be regarded as similar. This parameter r is set with reference to the anticipated noise in the signal. The value used for r in this analysis is 0.1, this value was chosen on the basis of an analysis of the noise level of the Biodex signal, and the value m=2 as suggested by Richman and Moorman (2000).

To calculate alpha the Detrended Fluctuation Analysis algorithm was used (Peng et al., 1994). This procedure is particularly suited to biological signals since it maps the raw bounded process to an unbounded self-similar process via integration of the time series (Peng et al., 1995). For uncorrelated, completely random white noise the integrated time series represents a random walk process and α=0.5. When 0<α<0.5 power law anti-correlations are present and when 0.5<α<1 power law correlations are present. When α>1, correlations exist but they cease to be of a power law form. Brown noise is indicated by α=1.5. For this analysis a piecewise approach was taken in determining the scaling behavior. This was because it was clear that the straight line relationships were different for different intervals over the range of timescales (Chapter 4). A piecewise function with two sections was fitted, the gradient of the first section of the function will be referred to as $alpha_1$, and the gradient of the second section will be referred to as $alpha_2$.

A surrogate analysis of the data was carried out and this showed that the SampEn and DFA values computed for the subject data were due to signal properties and not measurement system noise (Schreiber & Schmitz, 2000).

Surrogate data were generated from the original data sets by computing the fast Fourier transform (FFT) of the data, and then computing the inverse FFT of the signal with the phase of the FFT randomized (Theiler et al., 1992). Statistical comparisons of the subject data were performed using a four way analysis of variance (age group, subject, training status, effort level) with subject as a random factor nested in age. Variance stabilizing log transforms were applied to SD and CV prior to the statistical analysis.

5.4 RESULTS

The mean increase in the maximum knee joint moment as a consequence of training for the young age group was (mean $\pm$ standard error) 14.0 $\pm$5.5 Nm, and for the old age group was 9.7 $\pm$ 2.4 Nm. Both of these changes were statistically significant ($p<0.05$).

There were significant effects on SD for the age group ($F=37.24$, $p<0.001$) and effort level ($F=128.40$, $p<0.001$), however there was also a significant age group by effort level interaction ($F=3.54$, $p=0.023$), and an age group by training status interaction that approached significance ($F=3.56$, $p=0.082$).

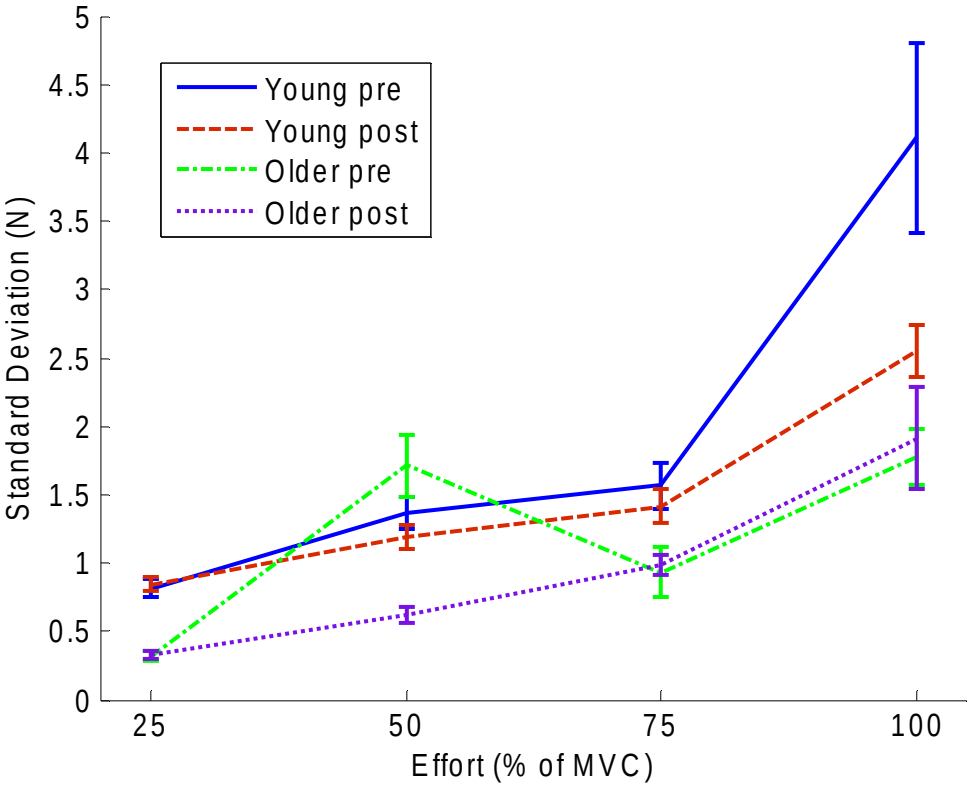

Figure **5.1**: Standard deviation values for young and older groups before and after strength training (mean ± SE).

Generally the SD increased for both age groups with effort level (Figure **5.1**). The young age group tended to have a higher SD at all force levels, and strength training tended not to affect the SD for either age group. There were two exceptions to these trends that are likely to have caused the significant interactions. The 50% effort level for the older age group before strength training was associated with a particularly high mean SD that was caused by one subject. The 100% effort level for the young age group before strength training was also associated with a particularly high SD; this was due to four subjects.

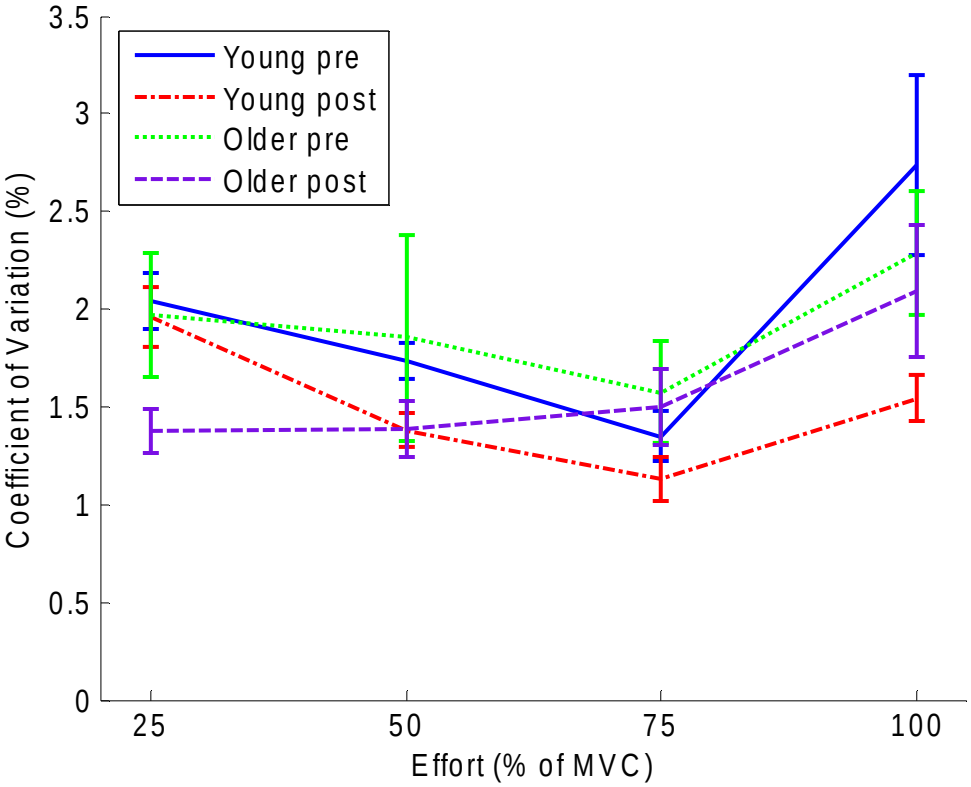

Figure **5.2**: Coefficient of variation values for young and older groups before and after strength training (mean ± SE).

When the magnitude of the fluctuations was quantified using CV, which essentially normalizes the SD to the mean force during the trial, the effect of training status became significant (F=10.69, p=0.006). The CV typically decreased across all effort levels after strength training (Figure **5.2**). The effect of effort level was significant (F=11.57, p<0.001), and there was an age group by effort level interaction term that approached significance (F=2.73, p=0.057). This was due to differences between the age groups at the 25% and 75% effort levels: the CV for the younger group was much higher than that of the older group at 25% and was much lower at 75%.

The effect of strength training on SampEn was not significant (F=1.03, p=0.329), however the values for SampEn were significantly lower for the older group than for the younger group (F=18.29, p=0.001) (Figure **5.3**). The value of SampEn decreased with force level for both age groups (Figure 5.3).

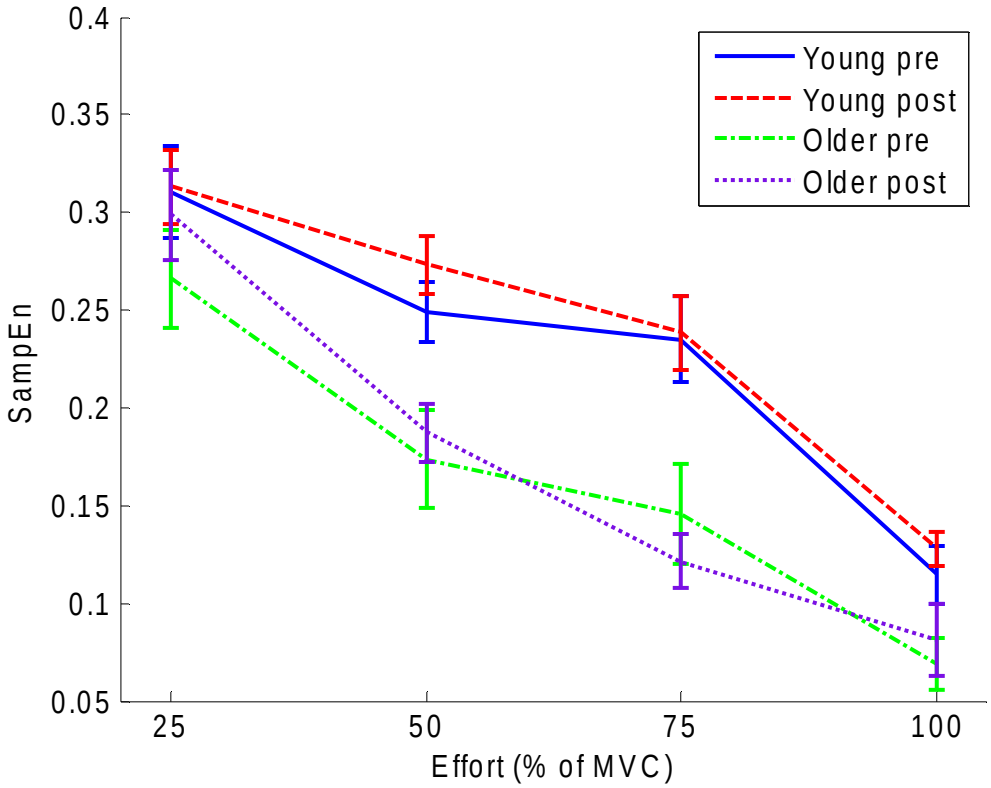

Figure **5.3**: SampEn values for young and older groups before and after strength training (mean ± SE).

The values of alpha$_1$ (Figure **5.4**) and alpha$_2$ (Figure **5.5**) were significantly higher for the older age group compared with the younger age group (F=5.31, p=0.031 and F=15.63, p=0.002 respectively). Both the alpha$_1$ and the alpha$_2$ values tended to increase with increasing effort level (F=30.68, p<0.001 and F=40.86, p<0.001 respectively). Tukey post-hoc comparisons showed that all effort levels were significantly different from each other for both alpha values; the only

exception was that the 50% and 75% effort levels were not significantly different from each other. There was no effect of strength training for either age group on either $alpha_1$ (F=0.54, p=0.465), or on $alpha_2$ (F=F=0.87, p=0.35).

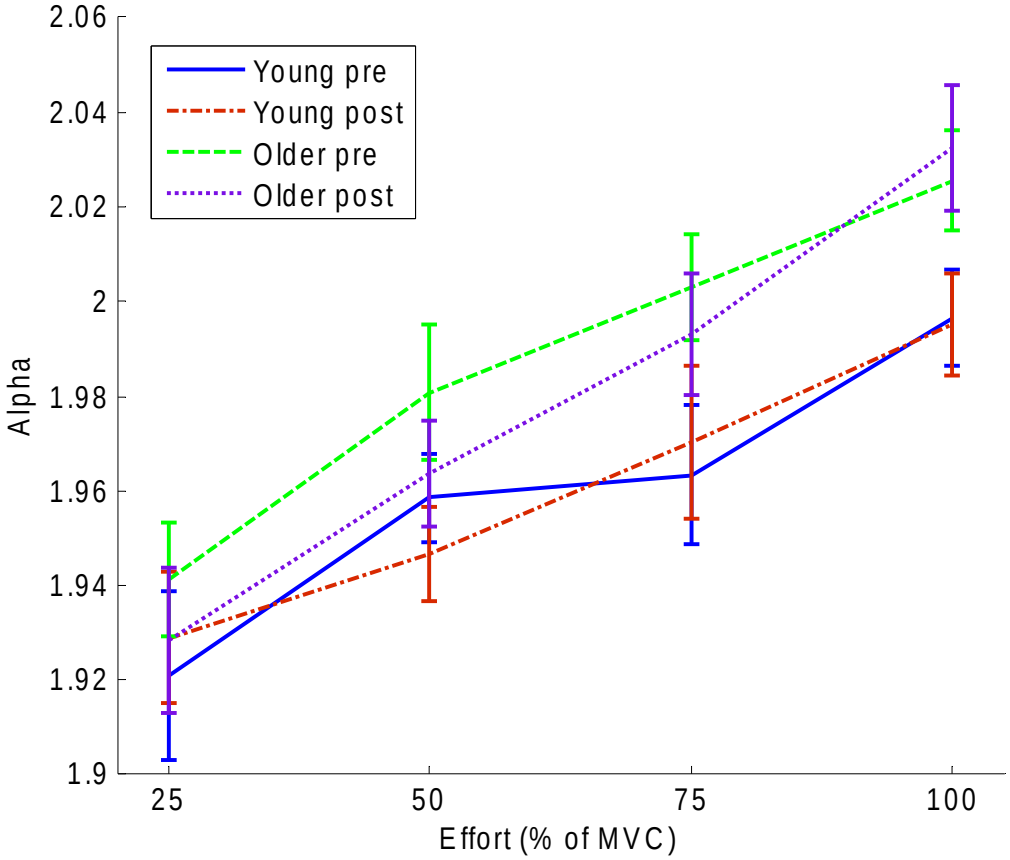

Figure **5.4**: $Alpha_1$ values for young and older groups before and after strength training (mean ± SE).

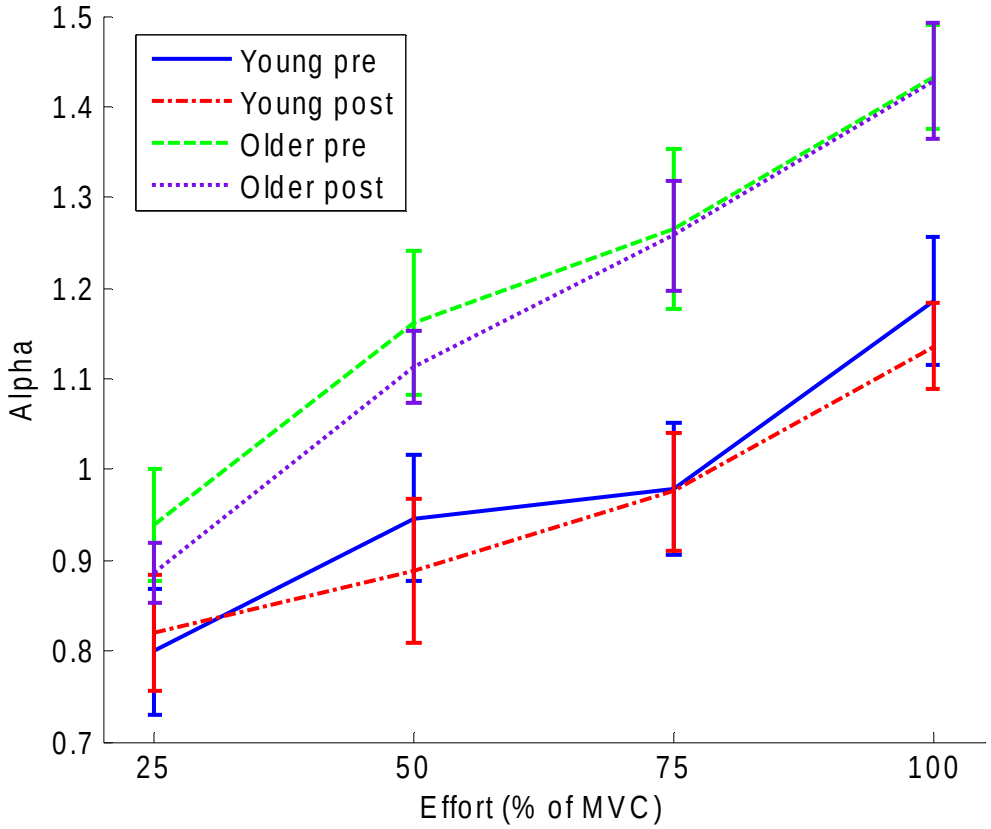

Figure **5.5**: $Alpha_2$ values for young and older groups before and after strength training (mean ± SE).

5.5 DISCUSSION

It was found that the CV but not the SD of the fluctuations in the joint moment during isometric knee extension contractions decreased in both young and older females following 10 weeks of strength training. The mean decrease across all force levels was 0.25% for the older group and 0.39% for the younger group. This study confirmed previous findings (Chapter 4) that the entropy of the moment record, as quantified by SampEn, is reduced with aging. For the first time it has been shown that ten weeks of strength training does not alter the

entropy of the moment record in either young or older females for effort levels at 25%, 50%, 75% and 100% of maximum. As in previous work (Chapter 4) a two phase pattern was found for the scaling parameter using the DFA that indicated a slowly repeating process operating over short time scales and a more rapidly repeating process operating over longer time scales. The values of the scaling parameter for the two phases were unchanged following strength training in both the young and the older group.

The quadriceps muscle was chosen for this study since there is evidence that both young and older subjects groups are able to activate this muscle almost completely (Roos et al., 1999). Subjects were allowed a period of familiarization with the protocol and subjects were allowed three attempts to produce their maximum effort, the trial that resulted in the highest moment being recorded was selected for further analysis. The size of the data window used for the analysis was chosen so that only the steady part of the maximum effort contraction was used for all subjects.

The changes in the structure of the moment record with aging identified previously (Chapter 4) appear to be irreversible with strength training despite significant strength increases in both groups. The DFA values and SampEn values seem to be highly characteristic for a given age group: the standard error within an age group for SampEn, $alpha_1$ and $alpha_2$ at each effort were very small. During pilot work it was noted that the SampEn and alpha values recorded for a subject were highly reliable across different days. Here it is shown that the values for a given subject were very similar despite being measured ten weeks apart and with a period of strength training in between. Since the values do not change following an increase in strength it is unlikely that the differences in the alpha values and SampEn values between the age groups are due to strength differences. The Biodex signal was also recorded while unloaded and while passively loaded at levels similar to those applied by the subjects during

testing. These records were shown to have very different SampEn and alpha values to those generated by the subjects indicating that it was not a signal generated by the measurement system that was being analyzed.

It would be interesting to determine at what point in the life cycle these changes in the structure of the joint moment data occur. Using SampEn and the DFA may prove useful as a non-invasive method of identifying the point at which aging-related muscular degeneration occurs, and in testing the effectiveness of interventions to prevent this degeneration.

The neuromuscular changes that are believed to occur with strength training are: muscle fibre hypertrophy, transient increases in mean motor unit firing rate, increases in the rate of tension development associated with doublet firing and possibly motor unit synchronization although changes in motor unit synchronization have not been consistently shown to occur with strength training (Duchateau et al., 2006). Since only the steady section of the moment record was used for analysis the doublet firing during tension development is not relevant here. Since SampEn and the alpha values do not change in either age group with strength training it would seem that the differences between the age groups are not related to differences in muscle fibre size, transient fluctuations in firing rates or the degree of motor unit synchronization since these factors do change with strength training.

The knot position marking the transition between the two alpha values occurs at a time scale of 50 ms, which would equate to a frequency of around 20 Hz. The alpha values at time scales above 50 ms (the $alpha_2$ values) range between 0.58 and 1.71, and range between 1.85 and 2.10 at time scales below this (the $alpha_1$ values). An alpha value of 0.5 reflects random white noise, so a value of 0.58 represents a process that is fairly close to random. These lower $alpha_2$ values occur at the lowest effort levels, at these effort levels only slow motor units with

low firing rates would be recruited. It is possible that at these low levels there would be incomplete fusion of the muscle force since the firing rate is low enough that at least partial reuptake of calcium into the sarcoplasmic reticulum could occur (Lippold, 1952). This would lead to nearly random fluctuations in the muscle force. Almost all of the force gradation in the quadriceps occurs via motor unit recruitment (Roos et al., 1999). At higher effort levels faster, higher frequency motor units are recruited and at these firing rates a more complete fusion of muscle force would occur due to the calcium release-reuptake kinetics. The $alpha_2$ values were higher in the older group at all effort levels, this may be due to a slowing of the calcium reuptake process with age (Narayanan et al., 1996) that would result in a more complete fusion of the muscle force at lower effort levels. It is unlikely that changes in this process would change a great deal in response to strength training. At time scales below 50ms ($alpha_1$ values) it may be that the muscle force response to motor unit firing is further damped by the interactions between the muscle and tendon mechanical properties. Although the $alpha_1$ values were still statistically significantly higher for the older age group, the differences between the two age groups were much smaller for the $alpha_1$ values than for the $alpha_2$ values.

In summary, ten weeks of strength training resulted in a small decrease in the CV of the knee joint moment during isometric knee extension contractions in both young (18-28 years) and older (65-74 years) groups of females. The complexity of the joint moment record as quantified by SampEn, and the behavior of the scaling parameter, alpha, as determined by the DFA was unchanged. It may be that the aspects of the time dependent structure of the joint moment record that are characterized by SampEn and alpha relate to a training resistant deterioration in the calcium kinetics at the level of the sarcoplasmic reticulum.

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CHAPTER 6

MUSCLE LENGTH DEPENDENT STEADINESS DURING ISOMETRIC FINGER ABDUCTION CONTRACTIONS

6.1 ABSTRACT

The steadiness of isometric force production at different effort levels was examined for different muscle lengths in the First Dorsal Interosseus (FDI). Subjects produced isometric contractions at long, medium and short muscle lengths at 5%, 10%, 25%, 50%, 75% and 100% of maximum in each finger position by targeting a force displayed on a computer monitor. A minimum variance criterion was used to select a window for further analysis from the force record. A Detrended Fluctuation Analysis (DFA) indicated different scaling behavior over shorter and longer timescales, suggesting that two or more different processes may be responsible for the fluctuations in the force produced during isometric contractions. The magnitude, as quantified by the coefficient of variation (CV), of the fluctuations in force produced during isometric index finger abduction contractions over all force levels was increased at short muscle lengths, and that the structure of the fluctuations is also altered at short muscle lengths. This may be due to different motor unit firing characteristics required to achieve full activation at short muscle lengths. The relationship between the magnitude of the fluctuations and effort level, and between the results of the DFA and effort level were explained by the relative contributions of motor unit recruitment and rate coding to force gradation in the FDI. These findings have implications for the accurate control of movement and force production.

6.2 INTRODUCTION

The force produced during an isometric muscle action is not constant but rather it fluctuates (Lippold et al., 1957). The steadiness of the force produced during sustained isometric contractions has important implications for successful movement performance and the accurate control of muscle force. The steadiness of isometric force production has been examined for different muscle groups (e.g. Hamilton et al., 2004), age groups (e.g. Enoka et al., 2003) and for subjects before and after strength training (Keen et al., 1994). However there has been no systematic evaluation of the effect of muscle length on the fluctuations in force during an isometric contraction. It is reasonable to suppose that aspects of the force fluctuations may be different for different muscle lengths since there is evidence that the optimal stimulation pattern of muscle is different for different muscle lengths (Mela et al., 2002; Rack & Westbury, 1969). In order to effectively study the relationship between the nature of the force fluctuations and muscle length in vivo it is preferable to study a joint action that is caused by a single muscle. In the human body there are a limited number of such joint actions, in this study abduction of the index finger will be studied as it caused by only one muscle, the first dorsal interosseus (FDI) (Masquelet, 1968).

Previous work (Chapters 4 and 5) using a Detrended Fluctuation Analysis (DFA) (Peng et al., 1994) to analyze the force or moment records during a sustained isometric contraction indicated different processes operating over different timescales. The output of the DFA is a scaling parameter, alpha, which gives information about the long term correlations present in a time series. The DFA showed that during isometric knee extension contractions there was a dominant process at shorter timescales that repeated more slowly than a second process that was dominant at longer timescales. It was suggested that the slowly repeating process at the shorter timescales could be due to damping of the system response to neural firing by the interactions of the muscle and tendon

(Chapter 5). The DFA indicated that there was a shift in the power of the frequency spectrum to lower frequencies with increasing effort level, and there was also a shift of power to slower frequencies with increased aging. The differences between force levels were highly consistent for all subjects within an age group. These differences in the values of the scaling parameter between force levels and age groups were evident even though there were no differences in the magnitude of the fluctuations as quantified by the coefficient of variation. It was suggested that the differences between age groups in the values of the scaling factor were due to differences between the age groups in the number of motor units and the characteristic firing frequencies of the motor units (Chapter 4). These differences in the number of motor units and their firing rates arise because aging is associated with a de-nervation re-nervation process that results in a reduced number of motor units, and a shift in the fibre type population such that the proportion of slow or type I fibres is increased (Galea, 1996). The DFA therefore seems well suited to identify differences in the force output arising due to variations in the dynamical system that results from the integration of the neural, physiological and mechanical properties of the motor system.

The purpose of this study was to quantify the magnitude of the fluctuations in force during sustained isometric finger abduction contractions, and to identify the long term correlation properties of the fluctuations, at different muscle lengths. This was done using a range of effort levels for each muscle length. It was hypothesized that length dependent differences in the neural recruitment strategy would show up as differences in the long term correlation properties identified by the DFA.

6.3 METHODS

Twelve subjects, five females and seven males were recruited; mean age 26 years $\pm$ 6 years, mean mass 72.5 kg $\pm$ 16.7 kg, mean height 1.72 m $\pm$ 0.1 m.

All subjects were familiarized with the procedures and provided written informed consent before participating and the Institutional Review Board at The Pennsylvania State University approved all procedures. The Edinburgh Handedness Inventory was used to identify the dominant hand of each subject and this hand was used for the testing procedure (Oldfield, 1971). A custom built rig was used to restrain the hand and wrist. The thumb was restrained at an approximate 80 degree angle to the index finger and the wrist was restrained using Velcro straps at a roughly 45 degree angle to the hand. A uni-axial force transducer (PCB 208-C01) was placed against the distal phalangeal head of the proximal phalanx of the index finger in order to measure the force due to isometric index finger abduction. Testing was carried out over two testing sessions: one trial at each force level in each finger position was carried out at the first session and the entire procedure was repeated at the second testing session. Care was taken to align the axis of the force transducer with line of action of the force applied by the finger.

Subjects performed familiarization contractions then performed isometric finger abduction contractions in three finger positions: with the index finger in a normal position lying next to the middle finger (‘long’ muscle length), with the finger abducted 10 degrees from the normal position (‘medium’ muscle length) and with the finger abducted 20 degrees from the normal position (‘short’ muscle length). For most subjects the ‘short’ position was a few degrees before the end of the range of motion of abduction of the index finger. The distance between the centre of the force transducer and the base of the proximal phalanx was recorded for each subject and each position. The finger, wrist, hand and force transducer position was marked onto paper underneath the hand so that the same position could be used for the second test session.

In each finger position a maximum effort contraction was produced. After a rest period of at least one minute a second maximum effort contraction was produced

while square wave percutaneous muscle stimulation was applied at a frequency of 100Hz to the motor point using a Sys Stim 270A neuromuscular stimulator. The voltage for the stimulation was set at a level that was tolerable for the subject but that produced a rapid finger abduction movement on application of the stimulation. The highest force produced during these two contractions was taken to be the maximum force level for that muscle length. Motor point stimulation is preferable to ulnar nerve stimulation since it is more targeted and does not seem to result in spread of the stimulation to the antagonist muscles (Davies et al., 1985).

Subjects then performed sustained isometric contractions at 100%, 75%, 50%, 25%, 10% and 5% of the maximum force level. A target line was displayed on a computer monitor and subjects were instructed to increase the force until the force signal met the target line and to then hold the contraction at this force level as steadily as possible. A single trial was performed at each force level and subjects were instructed to hold the contractions for four to five seconds. Seven contractions were therefore performed at each muscle length; this procedure was then repeated in the other finger positions. A total of twenty one contractions were performed with five minutes rest between each set of seven contractions. Subjects returned to perform the entire testing procedure on a second visit three to five days after the initial test.

The force transducer data was sampled at 160 Hz and low pass filtered at 20Hz in both directions using a second order Butterworth filter. The data were interpolated using a cubic spline and re-sampled at a frequency of 1,600 Hz. A 2.2 second window was selected from each of the force records at each force level using a minimum variance criterion; this window was used for further analysis. The minimum variance criterion was used in order to identify the steadiest part of each effort, other criteria were tested and these gave similar

results. The size of the window (2.2 seconds) was chosen so that only the plateau section of the maximum effort contraction was selected.

The fractal scaling index, alpha, was calculated for the 2.2 second window using the DFA algorithm of Peng et al. (1994). For this analysis a piecewise approach was taken in determining the scaling parameter. This was because it was clear that the straight line relationships were different for different intervals over the range of timescales (Figure **6.1**). A piecewise function with two sections was fitted to the data consisting of n data points with the knot first occurring at data point 2. Then a new function was fitted using data point 3 as the knot and so on sequentially until data point (n-1). A least squares criterion was used in order to select the best fit from the (n-2) piecewise functions. The gradient of the first section of the function will be referred to as $alpha_1$, and the gradient of the second section will be referred to as $alpha_2$. For uncorrelated, completely random white noise the integrated time series represents a random walk process and α=0.5. When 0<α<0.5 power law anti-correlations are present and when 0.5<α<1 power law correlations are present. When α>1, correlations exist but they cease to be of a power law form. Brown noise is indicated by α=1.5.

A surrogate analysis of the data was carried out and this showed that the DFA values computed for the subject data were due to signal properties and not measurement system noise (Schreiber & Schmitz, 2000). Surrogate data were generated from the original data sets by computing the fast Fourier transform (FFT) of the data, and then computing the inverse FFT of the signal with the phase of the FFT randomized (Theiler et al., 1992).

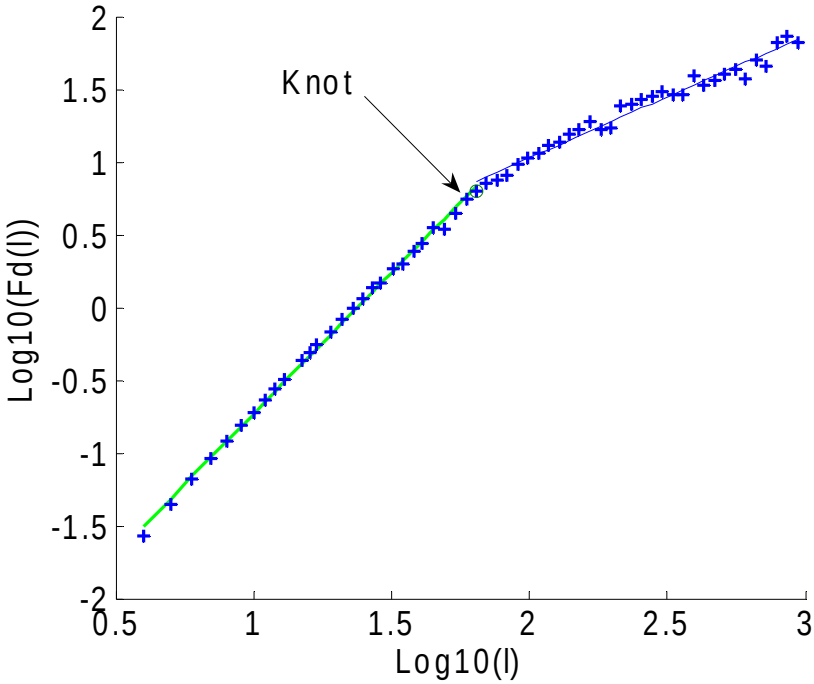

Figure **6.1**: Typical result of a piecewise DFA for one force record showing a knot and two different alpha values, one for shorter timescales ($alpha_1$) and one for longer timescales ($alpha_2$).

Previous work (Chapters 4 and 5) has shown that in some trials, particularly at the higher effort levels, the standard deviation (SD) is artificially inflated by low frequency, high amplitude fluctuations that represent small corrections made by the subject. Since these trends are related to targeting and not to the steadiness of the sustained contraction force they were removed using a high pass second order Butterworth filter applied in both directions with a cut off of 1 Hz (Figure **6.2**). Other ways of removing the trend such removing the trend using a moving average and other cut off levels were assessed. However the high pass filter with a 1 Hz cut off was felt to retain the important aspects of the signal while removing trends that could over inflate the measure of steadiness given by the SD based on the autocorrelation functions and the frequency spectra of the data

before and after filtering. The SD of the high pass filtered data was computed and this was then used as a measure of the magnitude of the fluctuations. The coefficient of variation was computed as the standard deviation of the high pass filtered force record divided by the mean force taken from the non-high pass filtered data over the same time period.

A cross over design was used so that the study was balanced for order effects across muscle length and force level. An analysis of variance model was performed using a 0.05 significance level and Tukey post-hoc comparisons were computed where statistically significant results were found.

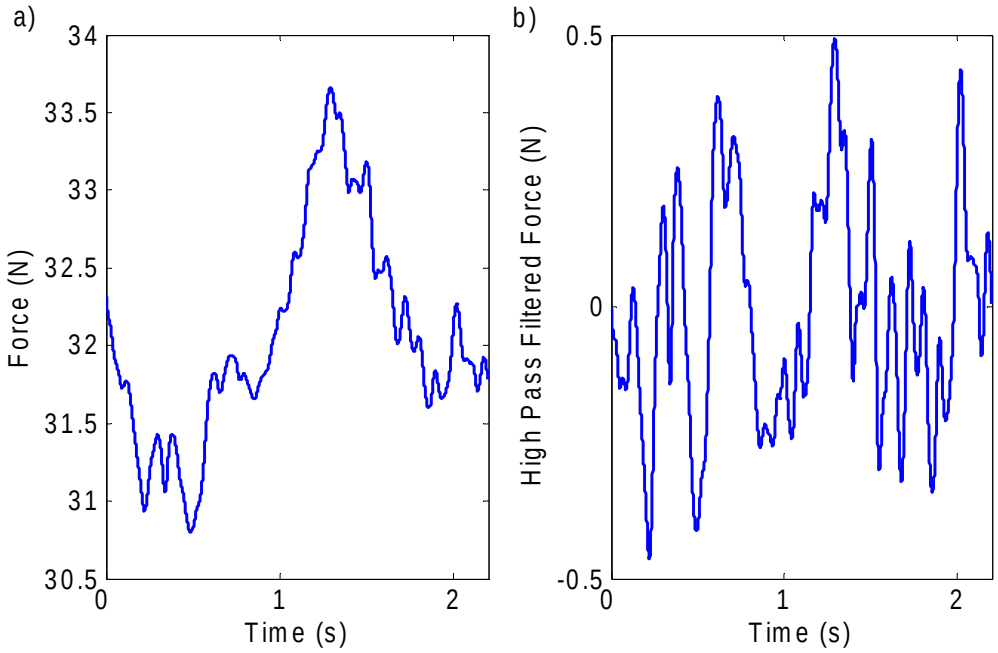

Figure **6.2**: A 75% effort trial for one subject showing a) the original minimum variance window, and b) the high pass filtered data. The subject was targeting thirty two Newtons.

6.4 RESULTS

There was no statistically significant increase in the peak force for the MVC effort with stimulation compared to the peak force during the MVC effort without stimulation (p=0.99). For the trials where there was an increase in the peak force with stimulation there was no trend in the trials for which an increase occurred for any particular position, day or subject. Subjects showed no consistent pattern across the different positions in terms of the peak force produced and the effect of position on the peak force produced was not significant (F=2.30, p=0.123). The peak forces produced ranged from 19.6 to 46.7N (mean = 34.1N, standard deviation = 7.5N).

The SD of the high pass filtered data and the CV, calculated as the SD over the mean non-high pass filtered force, were used as measures of the magnitude of the variability in force during a contraction. A log transform was applied to SD and CV prior to the statistical analysis to ensure that the response variable in each case was normally distributed. The effect of position on SD was not statistically significant (F=1.55, p=0.214). This was the case regardless of whether the statistical model used the force level as a factor or whether the mean force during the contraction was used as a covariate. However, the effect of position was significant when CV was used as the measure of variability (F=4.46, p=0.012). Tukey post-hoc comparisons showed that the short position was associated with a significantly higher CV than either the medium or long positions (Figure **6.3**).

The effect of force level on SD was statistically significant (F=757.95, p<0.001). The SD generally increased with the force level (Figure **6.4**). The effect of force level on CV was also significant (F=10.63, p<0.001). The peak mean values for CV across all subjects occurred at 50% and 5%, the lowest cell mean values occurred at 25%, 75% and 100% of MVC (Figure 6.3).

The force level had a significant effect on the values of $alpha_1$ ($F=9.18$, $p<0.001$) (Figure **6.5)** and $alpha_2$ ($F=8.12$, $p<0.001$) (Figure **6.6**), and on the knot location ($F=8.91$, $p<0.001$). The muscle length had a significant effect on the knot location ($F=4.24$, $p=0.028$) and on $alpha_2$ ($F=5.69$, $p=0.010$), but did not have a significant effect on the value of $alpha_1$ ($F=2.21$, $p=0.134$).

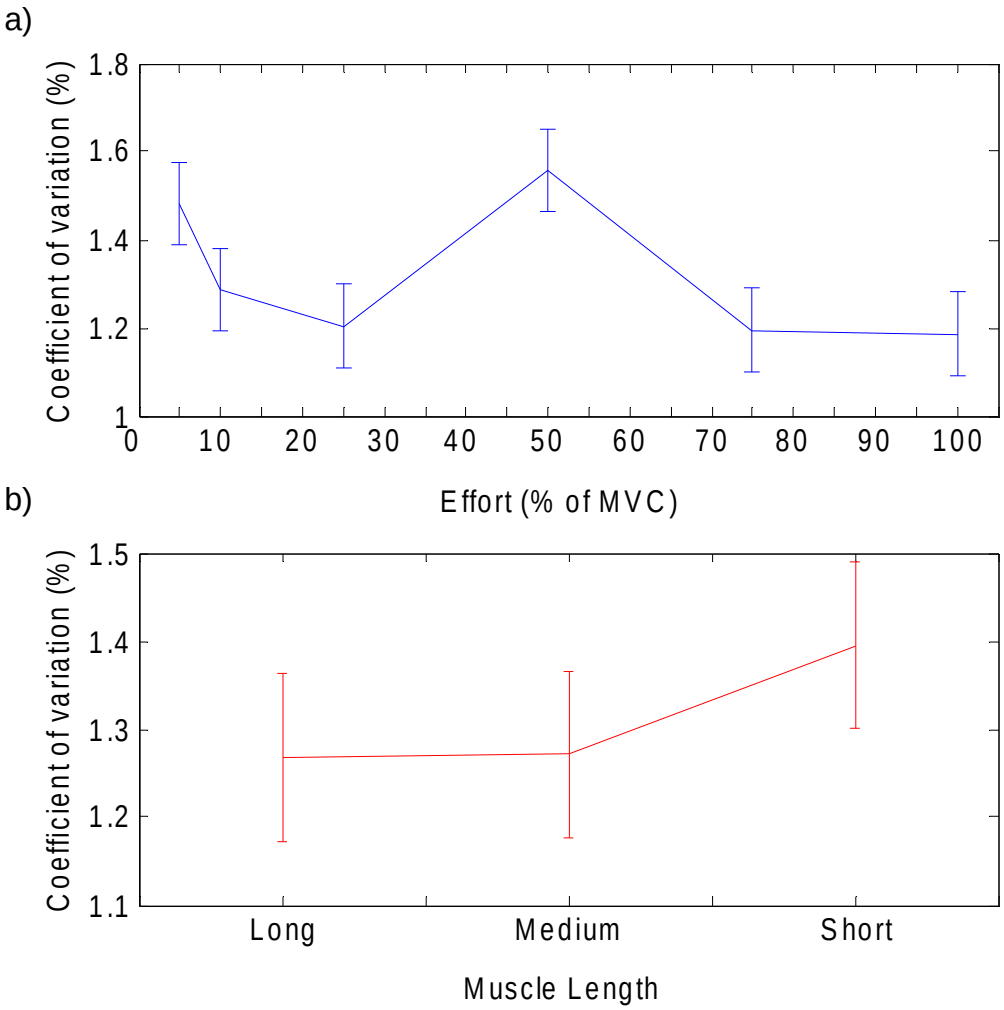

Figure **6.3**: Mean coefficient of variation (bars show standard error) for a) each effort level, means is taken across all muscle lengths and subjects, and b) each muscle length. The means are taken across all effort levels and subjects.

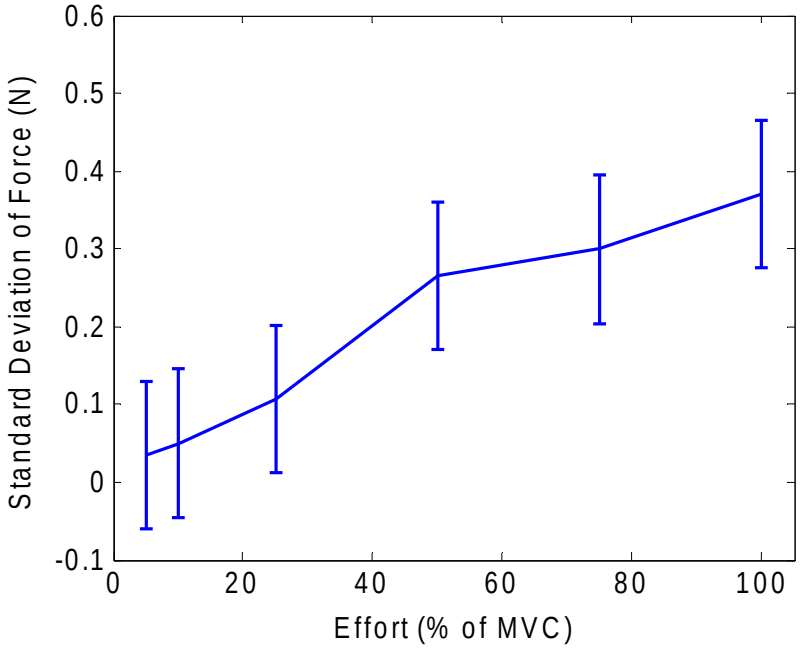

Figure **6.4**: The mean standard deviation of the force during the sustained contraction against each effort level (bars show standard error). The means are taken across all positions and subjects.

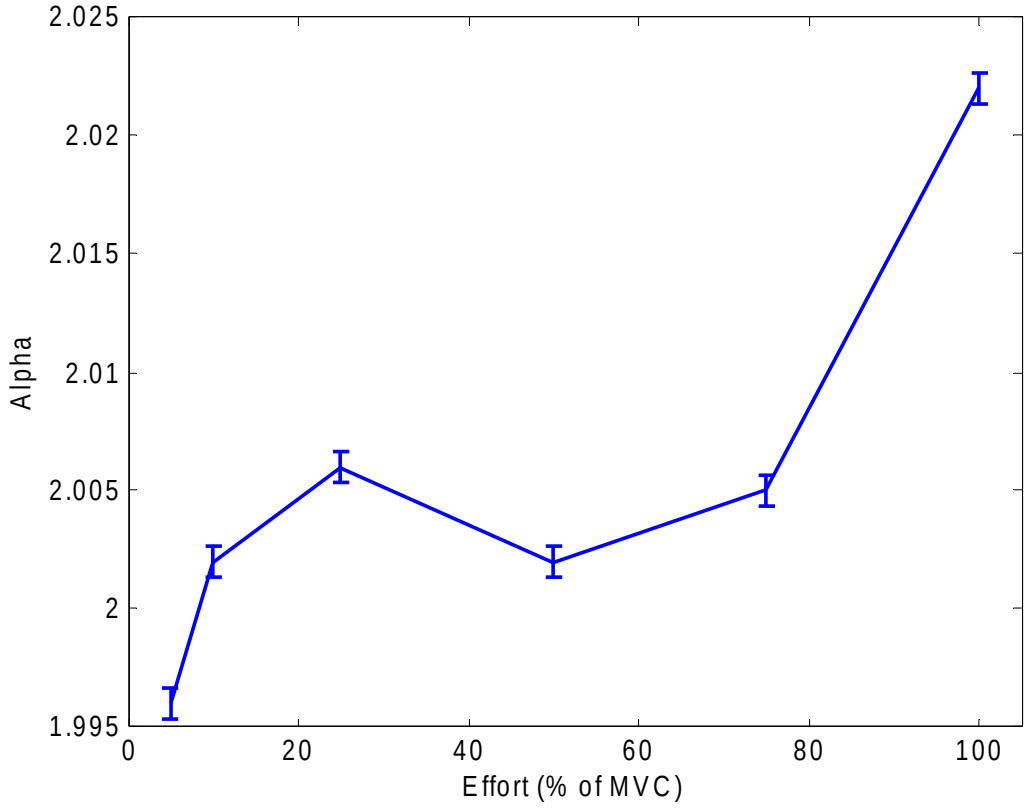

Figure **6.5**: The mean alpha$_1$ values against each effort level (bars show standard error). The means are taken across all positions and subjects.

Tukey post-hoc comparisons showed that the knot location for the short muscle length was significantly larger than the knot location for the medium muscle length; however the difference between the two means equated to only 3 milliseconds. The knot location for the 100% effort level was significantly lower than for all other force levels, i.e. the knot location occurred at smaller timescales for the 100% effort level. The timescales associated with the knot location varied between 34 milliseconds for the 100% effort level and 57 milliseconds for the 50% effort level.

The Tukey multiple comparisons also showed that the alpha$_1$ and alpha$_2$ values for the 100% effort level were significantly different from all other effort levels.

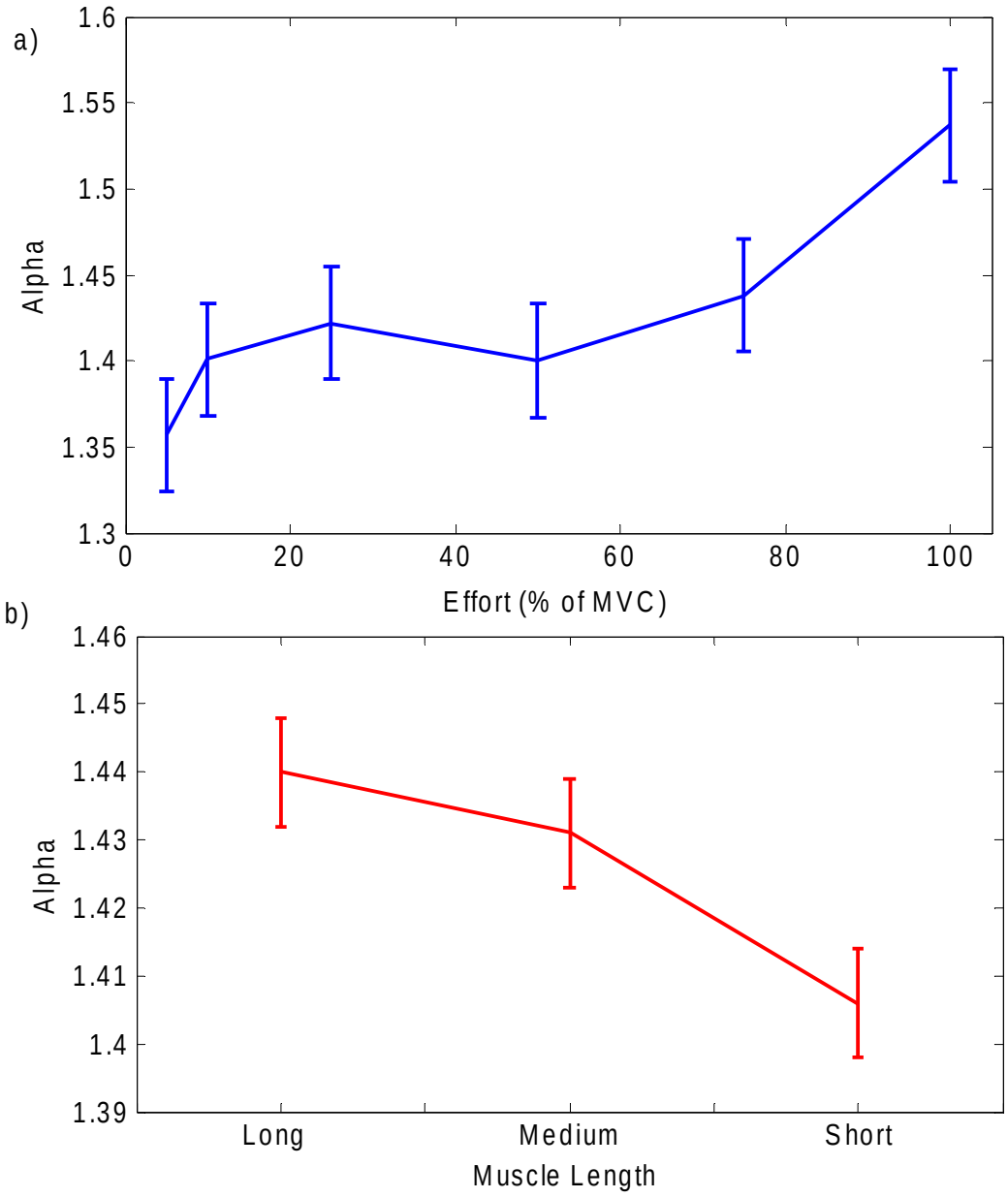

Figure **6.6**: Mean alpha$_2$ values (bars show standard error) for a) each effort level, mean is taken across all subjects and positions, and b) each muscle length. The means are taken across all subjects and effort levels.

6.5 DISCUSSION

It has been shown previously that there is a systematic variation in the structure of the fluctuations in force during an isometric quadriceps contraction with the effort level (Chapters 4 and 5). This study has confirmed this trend for the first dorsal interosseus. It has been shown here for the first time that the magnitude and time dependent structure of the fluctuations in force also depend on the length of the muscle at which the isometric contraction is performed.

The FDI is the sole agonist for index finger abduction, this made it an ideal muscle to use for this study, however finger abduction is not a particularly common movement in daily living. Nevertheless, subjects still seemed able to recruit the muscle well given that the superimposed neuromuscular stimulation did not result in an increased maximal force for most trials. The neuromuscular stimulation was at a level that was sufficient to increase force where subjects were not able to fully recruit the muscle voluntarily. Whichever trial (stimulated or non-stimulated) produced the highest force was taken to be the maximum force achievable in that position. Where the subjects were not able to fully activate the muscle they tended not to be able to reach the 100% target, however in all cases the actual force produced during the 100% trial was greater than that produced during the 75% effort. Using the mean force produced during the trial as a covariate did not change the conclusions from the statistical analysis. There was no trend within subjects or between subjects in terms of the muscle length at which subjects were not able to fully activate the muscle. Since a training study (Chapter 5) did not produce changes in the DFA values for a given force level it can be assumed that familiarity with the protocol would not change the DFA values seen here.

If there was spread of the stimulation to the antagonist muscle then this would reduce the force recorded during a stimulation trial. However Davies et al.

(1985) presented evidence for the FDI that motor point stimulation of the type used here does not result in spread of the stimulation to other muscles including the antagonist. The motor point neuromuscular stimulation precluded the use of electromyography to measure activation patterns of the agonist and antagonist during trials.

It is possible that fatigue could have affected the results. However, the experimental design was balanced for order effects across muscle length and effort level, this design allows order effects to be separated from the effects of muscle length and effort level. There was never a significant interaction between effort level order and effort level, or between position level order and position for any of the dependent variables measured. Such an interaction would indicate that the effect of muscle length or effort level depended on the order in which the conditions were presented. Generally the muscle length order and effort level order effects were not significant, where they were significant there was no consistent pattern in the cell means that could indicate a fatigue related trend: instead the means varied randomly over the order. The maximum difference between means was less than 5% of the differences due to effort levels or muscle lengths, i.e. the differences were not practically significant.

Subjects were advised to build up the force to the target level fairly slowly at the beginning of each trial, and then to hold the contraction at the target level. This procedure was followed in order to reduce the occurrence of high amplitude, low frequency fluctuations that are related to targeting rather than reflecting fluctuations that occur during a steady contraction. Some large amplitude low frequency fluctuations did still appear in the force record. In order to avoid over-inflating the standard deviation of the force they were removed by high pass filtering the data before computing the standard deviation. Previous studies using SD as a measure of the magnitude of the fluctuations in force (e.g. Vaillancourt & Newell, 2003; Enoka et al., 2003) have not carried out such a

procedure, over-inflation of the SD by such trends may explain the occasionally conflicting results reported in these studies. Other methods of removing the trends were tried, such as a moving average technique. However, these techniques removed virtually all of the autocorrelation within the signal and therefore removed all of the characteristic behavior of the fluctuations.

The SD generally increased with increasing force level, but there was no position effect. This was the case even when the mean force produced during the trial was used a covariate. When the SD was normalized to the mean force produced during the trial as the CV the position effect was significant. This suggests that the effect of position on the magnitude of the fluctuations was not simply explained by the different forces produced at different muscle lengths by the subjects. The CV was largest for the short muscle length and was similar for the long and medium muscle lengths. Higher stimulation frequencies are generally required to attain the maximum tension at short muscle lengths (Mela et al., 2002; Rack & Westbury, 1969). There was no consistent difference across subjects in the maximum force at the different muscle lengths, however the higher firing frequencies required to attain full activation at the short muscle length may explain the increased fluctuations as quantified by CV seen in this position.

There was no difference in the $alpha_1$ values seen at different muscle lengths; however the $alpha_2$ values were significantly lower for short muscle lengths compared to long and medium muscle lengths. This finding reinforces the idea that the $alpha_1$ values are due to muscle-tendon interactions, whereas the $alpha_2$ values are related to neural factors. It would be expected that the higher firing frequencies expected at short muscle lengths would result in changes in the $alpha_2$ value but would not affect the $alpha_1$ value unless a different force was produced at maximum activation at the short muscle length. Since this was not the case, no change in the $alpha_1$ value was seen between muscle lengths.

Both the $alpha_1$ values and the $alpha_2$ values changed with changing effort level. The relationship between effort level and the two alpha values was different for the FDI compared to that seen for the quadriceps (Chapter 4). A positive linear relationship between the two alpha values and increasing effort level was seen for the quadriceps, whereas a cubic-like relationship was seen for the FDI. These different relationships may be explained by different recruitment and rate coding strategies for the two muscles. Typically recruitment accounts for the whole range of force gradation from 0 to 100% of maximum in the quadriceps (Roos et al., 1999), however recruitment only accounts for the first 30 to 40% of force gradation in the FDI and rate coding (increased neural firing rates) accounts for force gradation thereafter (Milner-Brown et al., 1973). Generally the $alpha_2$ values were higher for the FDI than they were for the quadriceps over the range of effort levels studied: the $alpha_2$ values ranged between 1.3 and 1.55 for the FDI but were between 0.8 and 1.3 for the quadriceps. Higher neural firing frequencies result in more fused muscle force responses due to the calcium ion release-reuptake kinetics of the sarcoplasmic reticulum (Bigland & Lippold, 1954). Increased fusion would lead to more slowly varying fluctuations in the muscle force response. Since fast motor units with their higher frequency recruitment thresholds would be recruited earlier for the FDI the force response of this muscle would vary more slowly at lower effort levels compared with the quadriceps group. This pattern of activation is reflected in the higher $alpha_2$ values seen in the FDI compared to the quadriceps.

It has been demonstrated that the DFA allows differentiation between effort levels, muscle lengths, age groups and recruitment strategies by analyzing the structure of the fluctuations in the force or moment produced during an isometric contraction (Chapter 4 and this chapter). Use of the DFA may allow tracking of age related muscular and neural changes throughout the lifespan. It may also allow identification of the activation level during contractions, this may be of use

for example during rehabilitation. The finding that muscle length affects the structure of the fluctuations is likely to have implications for the control of force and movement over different sections of the range of motion of a joint.

In summary, this study has found that the magnitude, as quantified by CV, of the fluctuations in force produced during isometric index finger abduction contractions increases at short muscle lengths, and that the structure of the fluctuations is also altered at short muscle lengths. This may be due to the higher firing frequencies required to achieve full activation at short muscle lengths. This finding has implications for the accurate control of movement and force production.

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CHAPTER 7

GENERAL DISCUSSION

7.1 INTRODUCTION

This chapter will recap the most significant findings from the four experimental chapters (Chapters 3 through 6). The limitations of the four studies will be addressed. Possible future research will be discussed and finally general conclusions from the work will be presented.

7.2 SUMMARY OF FINDINGS

The specific aims of this work were to:

5. Assess the variability in the expressed section of the force-length curve in different muscles and identify potential factors that may explain the differences in this variability with respect to the parameters typically used in a muscle model.
6. Quantify the differences between young and young-old groups of females in the magnitude and time dependent structure of the fluctuations in the knee resultant joint moment during maximal and sub-maximal contractions.
7. Assess the effect of strength training in young and young-old females on the fluctuations in the resultant joint moment produced at the knee.
8. Assess the influence of muscle length on the fluctuations in force produced by the first dorsal interosseus.

In Chapter 3 a generalized model of a mono-articular muscle-tendon complex was used to examine the effect of various model parameters on the section of the force-length relationship operated over for a 90 degree joint range of motion. The model parameters investigated were: the ratio of tendon resting length to muscle fibre optimum length (L_{TR} / Lf_{OPT}), the ratio of muscle fibre optimum length to average moment arm (Lf_{OPT} / r), the normalized tendon strain at maximum isometric force (c), the muscle fibre pennation angle (θ_{PENN}), and the joint angle at which the optimum muscle fibre length occurred (θ_{REF}). Each parameter was varied systematically through a range of values determined from parameter values reported in the literature for various muscles. It was shown that L_{TR} / Lf_{OPT} was important in determining the amount of variability in the section of the force-length relationship that the muscle operated over. The effect of this ratio was modulated by Lf_{OPT} / r. The muscle operated over only one limb at intermediate values of these two ratios, whether this was the ascending or descending limb was determined by the relative values of c, θ_{PENN}, θ_{REF}, and L_{TR} / Lf_{OPT}. This chapter addressed the first specific aim.

In Chapter 4, the knee resultant joint moment record was analyzed for young and young-old females at 25%, 50%, 75% and 100% of maximum effort. No difference in the magnitude of the fluctuations in the joint moment, as quantified by the coefficient of variation, was shown between the two age groups at any effort level. The young females demonstrated more complexity, assessed using Approximate Entropy (Pincus, 1991), in the knee joint moment signal at all effort levels ranging between 100% and 25% of maximum compared to young-old females. A Detrended Fluctuation Analysis (DFA) indicated different scaling behavior over shorter and longer timescales, suggesting that two or more different processes may be responsible for the fluctuations in the joint moment during isometric contractions. Young-old females generally demonstrated

scaling characteristics that indicated more slowly repeating processes. This chapter addressed the second specific aim.

The work in Chapter 4 was extended in Chapter 5 by examining the effect of a ten week program of strength training on the steadiness of the knee joint moment during isometric knee extension contractions was studied in young (18-28 years) and older (65-74 years) females at 25%, 50%, 75% and 100% of maximum effort. Strength training produced a small decrease in the coefficient of variation (CV) but not the standard deviation (SD) of the moment record in both the young and the older age groups. The complexity of the joint moment record as quantified by SampEn, and the behavior of the scaling parameter, alpha, as determined by the DFA was unchanged. This chapter addressed the third specific aim.

In Chapter 6 the steadiness of isometric force production at different effort levels was examined for different muscle lengths in the First Dorsal Interosseus. Subjects produced isometric contractions at long, medium and short muscle lengths at 5%, 10%, 25%, 50%, 75% and 100% of maximum in each finger position by targeting a force displayed on a computer monitor. A DFA indicated different scaling behavior over shorter and longer timescales, suggesting that two or more different processes may be responsible for the fluctuations in the force produced during isometric contractions. The magnitude, as quantified by CV, of the fluctuations in force produced during isometric index finger abduction contractions over all force levels was increased at short muscle lengths, and that the structure of the fluctuations is also altered at short muscle lengths. This may be due to different motor unit firing characteristics required to achieve full activation at short muscle lengths. The relationship between the magnitude of the fluctuations and effort level, and between the results of the DFA and effort level were explained by the relative contributions of motor unit recruitment and

rate coding to force gradation in the FDI. This chapter addressed the fourth specific aim.

7.3 LIMITATIONS

In Chapter 3 it was shown that muscles with moderate L_{TR} / Lf_{OPT} and Lf_{OPT} / r ratios would demonstrate a lot of variability in the expressed section of the force-length relationship. The FDI is one such muscle, and indeed the 12 subjects tested did demonstrate variability in the gradient of the relationship between muscle length and muscle force. While it was determined that there was a significant effect of muscle length on the alpha values determined by the DFA, the variability in the expressed section of the force-length relationship meant that it was not possible to assess whether the position on the force-length relationship also affected $alpha_1$ and $alpha_2$. A future study with a greater number of subjects may be able to elucidate if such an effect exists.

One possible problem with the quantification of steadiness in vivo is the ability of the subjects to maximally activate the muscle. The quadriceps muscle was chosen to investigate the effects of strength training on steadiness (Chapter 5) since there is evidence that both young and older age groups are able to voluntarily activate this muscle to 94-96% of full activation as shown by superimposed electrical stimulation (Roos et al., 1999). However, the quadriceps muscle group is not ideal when examining the effect of muscle length on the steadiness of isometric contractions since it is made up of more than one muscle. The first dorsal interosseus was used in Chapter 6 to investigate the effect of muscle length on the structure of the force record during an isometric contraction since it is the only muscle responsible for the joint action it produces. In this latter study electrical stimulation was superimposed on a maximum voluntary contraction to ensure that the maximum force measured represented the force

produced at full activation. For 50 out of the 72 trials of maximum effort trials superimposed stimulation did not produce an increase in force, and for those trials where superimposed stimulation did result in an increase the mean increase was only 2.4 N. This suggests that subjects were able to fully, or nearly fully activate the FDI under voluntary control. In addition there was no pattern of incomplete activation in certain positions: of the 22 trials that resulted in an increase in the maximum force produced with stimulation, seven were in the long position, eight were in the medium position and seven were in the short position.

If the antagonist muscles were co-activated during testing of the quadriceps or the FDI this could reduce the maximum force or joint moment recorded and could affect the steadiness of the contraction. However, for isometric contractions in the middle of the range of motion of a muscle and following a period of familiarization there is no evidence of significant co-activation in the hamstrings. For example, Beltman et al. (2003) showed that fatigue in the hamstrings that reduced the knee flexion moment by more than 50% did not affect the maximum knee extension moment. The antagonist of the FDI is the second palmar interosseus: intramuscular EMG has shown that the amount of co-activation of this muscle was small for young subjects (Laidlaw et al., 2002). It has also been shown that changes in the amount of co-activation do not correlate with changes in the steadiness of isometric finger abduction contractions (Laidlaw et al., 2002). This suggests that a limited amount of co-activation does not seem to affect the steadiness of the force or moment produced by the agonist.

The potential for error in the results caused by various experimental factors such as incomplete activation and co-activation often leads researchers to use models such as that used in Chapter 3. However, any model is only an approximation of reality. Often there is a compromise to be made between a simple model that is less realistic but easily interpretable and a complex model that is more realistic but less easily interpretable. The model used in Chapter 3 treated the muscle as

though it were a single lumped fibre, this does not account for common architectural features such as compartmentalized fibres (Finni et al., 2003) and fibres that do not extend the length of the muscle (Trotter, 2002). Accounting for such architectural features may alter the conclusions drawn from the model. However since these architectural features are highly muscle group and subject specific it would not have been possible to generalize the model as was the case in Chapter 3.

7.4 DISCUSSION

A generalized muscle model was used to investigate variability in the expression of the force-length relationship. The value of L_{TR} / Lf_{OPT} was found to be of critical importance in determining how much variability in the expression of the force-length relationship was possible. A muscle tendon complex with a value for L_{TR} / Lf_{OPT} of around 3 could operate solely over one section of the force-length relationship, i.e. either the ascending limb, or the plateau, or the descending limb. Muscle-tendon complexes with lower values would use only the plateau section of the force-length relationship, and those with higher values would use most of the force-length relationship. This may explain an earlier finding that there is more variability in the expression of the force-length relationship in vivo in the rectus femoris, a muscle with a L_{TR} / Lf_{OPT} ratio close to 3, than in the gastrocnemius, a muscle with a L_{TR} / Lf_{OPT} ratio of around 11 (Winter, 2004).

The force-length relationship of a muscle is determined in vivo by producing a series of isometric contractions at different muscle lengths. However, during an isometric contraction the force fluctuates. It was found that the complexity and fractal scaling behavior of these fluctuations is highly dependent on the age of the subject, the effort level of the contraction and the muscle length. Differences in the complexity and scaling behavior of these fluctuations between muscle

groups may reflect differences in the number of motor units, the relative proportions of slow and fast twitch fibres, and differences in the relative contributions of motor unit recruitment and neural rate coding strategies.

It has been shown in Chapters 4, 5, and 6 that algorithms from the fields of statistical mechanics (ApEn and SampEn) and non-linear dynamics (the fractal scaling parameter alpha) are useful in identifying differences in the structure of the fluctuations in isometric force records for different age groups and muscle lengths even where there is no difference in the magnitude of the fluctuations. The identification of these differences in the complexity and scaling behavior can give important insights into age and length dependent neuro-muscular characteristics that would not be possible by studying the CV or SD of the force or moment record alone.

Older females were shown to have a reduced complexity and more slowly repeating patterns of fluctuations in their isometric force at all effort levels compared to young females, these differences were not due to differences in the magnitude of the force produced between age groups since the values did not change in either group despite increased strength gains following strength training. Although the magnitude of the fluctuations was not different between age groups, the reduced complexity and more slowly repeating fluctuations may present a challenge to the control of movement when rapid adjustments in force are required. Although it might be anticipated that an ability to produce a steady force would reflect improved control, it may be that such a steady force would require so much damping of motor noise that adjustments in response to unexpected perturbations become impossible.

The fluctuations in isometric force measured at short muscle lengths were shown to have a lower CV, but not SD, for force, and were shown to have lower alpha values reflecting more rapidly repeating processes. However, there was no

evidence that these length related differences in the magnitude and structure of the fluctuations reflected an incomplete activation at short muscle lengths. There was no pattern of reduced force production at short muscle lengths, indeed several subjects produced their maximum force at the shortest muscle length. Chapter 3 illustrates that for a muscle with the architecture of the FDI it is likely different subjects work on different portions of the force-length relationship. In addition it was found that of the 22 trials that resulted in an increase in the maximum force produced with stimulation, seven trials were at the long position, eight were in the medium position, and seven were in the short position. This suggests that subjects were as good at activating their muscle at short muscle lengths as at any other muscle length. This finding is important since the determination of the muscle force-length relationship in vivo involves producing a series of maximum effort contractions at different muscle lengths. If reduced activation typically occurred at certain muscle lengths then it would not be possible to determine the force-length relationship from such a series of contractions.

Biomechanical muscle models typically assume that all muscles operate over either the whole or the plateau of the force-length relationship, and that the force output of the muscle is constant. It has been shown here that in vivo neither of these assumptions are valid. It would be interesting to investigate whether the inclusion of these two effects could alter the conclusions drawn from such muscle models.

7.5 FUTURE RESEARCH

Chapters 4 and 5 showed that there were consistent age related differences in SampEn and in the scaling behavior as quantified by the alpha values for isometric force production. It was suggested that these differences may be due to aging-related changes in the number and type of the motor units in the muscle,

and to changes in the calcium release-reuptake kinetics in the sarcoplasmic reticulum. It would be interesting to test subjects from each decade of life in order to determine at what point in the lifespan these changes occur. It may be that suitably timed interventions could delay or prevent these changes. Although no changes in SampEn and alpha were seen in Chapter 5 it may be that longer periods of strength training are successful in reversing age-related reductions in the motor unit population.

The work in Chapters 4, 5, and 6 has been done using isometric or static contractions. Steadiness during isometric contractions has implications for the accuracy of limb trajectories during movement since, depending on the inertia of the limb, it would be anticipated that fluctuations in muscle force would lead to fluctuations in the joint angular acceleration. However, it may be that the motor unit recruitment or firing rate characteristics change during movement, so it would be interesting to test whether age and effort level related differences in SampEn and the alpha values are retained when analyzing the fluctuations in the acceleration profile of segments during movement.

Fuglevand et al. (1993) formulated a model of a motor unit pool that was used to investigate the fluctuations in force produced as a result of changes in firing rate and motor unit recruitment. However, this model did not include the mechanical properties of the muscle tendon unit. In Chapters 4, 5, and 6 there was consistent evidence of two processes operating over different timescales and it was suggested that the more slowly repeating behavior at shorter timescales was due to damping of the fluctuations by the interactions between the muscle and tendon. It would be interesting to extend the model of Fuglevand et al. (1993) to test this hypothesis.

7.6 CONCLUSIONS

In summary, it has been shown that:

1. The value of the ratio of tendon resting length to muscle fibre optimum length was found to be of critical importance in determining how much variability in the expression of the force-length relationship was possible. A muscle tendon complex with a ratio of tendon resting length to muscle fibre optimum length of around 3 could operate solely over one section of the force-length relationship, i.e. either the ascending limb, or the plateau, or the descending limb. Muscle-tendon complexes with lower values would use only the plateau section of the force-length relationship, and those with higher values would use most of the force-length relationship.

2. The complexity and scaling behavior of the fluctuations in the force or moment produced during an isometric contraction are highly dependent on the age of the subject and the intensity or effort level of the contraction. Older females exhibit a less complex joint moment pattern with more slowly repeating fluctuations compared with young females.

3. The complexity and scaling behavior of these fluctuations does not change with strength training in either young or older females.

4. The scaling behavior of the fluctuations in the force or moment produced during an isometric contraction is also dependent on muscle length such that at short muscle lengths the fluctuations occur more rapidly.

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APPENDIX A

INFORMED CONSENT FORM IRB #23684

Title of Project: Quantification of Force-Fluctuations during Isometric Quadriceps Contractions

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1. Purpose of the Study: The purpose of this research is to learn more about measures relating to muscle movement. The muscle group that will be studied, the quadriceps, is the muscle in the front top part of your leg that is used to straighten the knee.

2. Procedures to be followed: You will be asked to perform a five minute warm up using a cycle ergometer and will be able to do as much stretching as you wish before performing the test procedure. For the test, you will use a machine that is used to measure the force produced by a muscle. This type of machine is often used by physical therapists. Straps will be placed around your

chest, waist, thigh and lower leg in order to limit unnecessary movement. You will practice three or four times to get used to the feeling of the machine. You will be asked to try to straighten your knee; the machine, however, will not allow you to actually move. All tests will be performed in a sitting position. You will be asked to do three trials and then three trials at lower workloads. Feedback will be provided via a computer monitor to help you. Each movement will last up to ten seconds. You will be given rest periods between the movements.

3. Discomforts and Risks: During testing, there is a slight risk of muscle strain, sprains, or muscle soreness that will go away within approximately 48 hours following exercise. This soreness may temporarily limit your natural movement patterns. The likelihood of these discomforts occuring can be reduced by performing the warm up and practice contractions. You may ask to stop at any time during the test procedure. There is an unlikely possibility of bone fracture (broken bone).

4. Benefits: The benefits to you are none.

The benefits to society include increased understanding of the work muscles can do.

5. Duration/Time: Your participation in this study will last for half an hour; this includes the warm up time.

6. Statement of Confidentiality: Your participation in this research is confidential. Only the person in charge, and his/her assistants, will know your identity. The data will be stored and secured in the office of the Principal Investigator in the Biomechanics Laboratory in a password protected file using numeric codes as subject identifiers on a computer server. A list of participant names and the corresponding numeric identifiers will be stored in a locked filing

cabinet in a locked office in the Biomechanics laboratory accessible only by the Principal Investigator and the Faculty Advisor. The following may review and copy records related to this research: The Office of Human Research Protections in the U.S. Department of Health and Human Services, the Biomedical Institutional Review Board, the Food and Drug Administration (FDA), and the PSU Office for Research Protections. In the event of a publication or presentation resulting from the research, no personally identifiable information will be shared.

7. Right to Ask Questions: You can ask questions about this research. Contact Samantha Winter at (814) 865-3445 with questions. You can also call this number if you have complaints or concerns about this research. If you have questions about your rights as a research participant, or you have concerns or general questions about the research, contact Penn State University's Office for Research Protections at (814) 865-1775. You may also call this number if you cannot reach the research team or wish to talk to someone else.

8. Payment for participation: You will receive $5 for your participation in this study.

9. Voluntary Participation: Your decision to be in this research is voluntary. You can stop at any time. You do not have to answer any questions you do not want to answer. Refusal to take part in or withdrawing from this study will involve no penalty or loss of benefits you would receive otherwise.

In the unlikely event you become injured as a result of your participation in this study, medical care is available but neither financial compensation nor free medical treatment is provided. By signing this document, you are not waiving any rights that you have against The Pennsylvania State University for injury resulting from negligence of the University or its investigators.

You must be 18 years of age or older to consent to take part in this research study. If you agree to take part in this research study and the information outlined above, please sign your name and indicate the date below.

You will be given a copy of this signed and dated consent form for your records.

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Participant Signature Date

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Person Obtaining Consent Date

APPENDIX B

INFORMED CONSENT FORM IRB #23684 REVISED

Title of Project: Quantification of Force-Fluctuations during Isometric Quadriceps Contractions

Principal Investigator: Samantha Winter
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1. Purpose of the Study: The purpose of this research is to learn more about measures relating to muscle movement. The muscle group that will be studied, the quadriceps, is the muscle in the front top part of your leg that is used to straighten the knee.

2. Procedures to be followed: You will be asked to perform a five minute warm up using a cycle ergometer and will be able to do as much stretching as you wish before performing the test procedure. For the test, you will use a machine that is used to measure the force produced by a muscle. This type of machine is often used by physical therapists. Straps will be placed around your

chest, waist, thigh and lower leg in order to limit unnecessary movement. You will practice three or four times to get used to the feeling of the machine. You will be asked to try to straighten your knee; the machine, however, will not allow you to actually move. All tests will be performed in a sitting position. You will be asked to do three maximum effort trials and then three trials at each of three lower workloads (25%, 50%, 75% of maximum). Feedback will be provided via a computer monitor to help you. Each effort will last up to ten seconds. You will be given rest periods between the movements.

You will then be asked to participate in ten weeks of strength training. Each session will begin with a five to ten minute warm-up on a stationary exercise bike or equivalent aerobic exercise and stretching exercises as necessary. You will be asked to attend the fitness room in the Noll Laboratory three times a week in order to carry out the programme. The PI will present during each of the training sessions. The following exercises will be performed:

Unilateral leg extension performed on both legs (straightening legs one at a time against a weight using a machine)
Bi-lateral leg press (pushing with both legs against a weight using a machine)
Leg curl performed on both legs (bending legs against a weight using a machine)
Bi-lateral calf raises (raising heels off the ground against a weight using a machine)
Bench Press (raising a weight while lying back using the chest and arm muscles using dumb bells)
Horizontal row (raising a weight using a rowing action using a machine)
Shoulder Press (raising a weight overhead while seated using the arm and shoulder muscles using dumb bells)
Dumb Bell Curl (raising a dum bell using the arms only)
Stomach Crunches (sit ups)
Cool down stretching

Three sets of eight repetitions will be performed of each exercise, each with a progressively higher weight. Ideally, you will increase weight if you are able to extend the third set of repetitions to ten repetitions. However, this may be modified slightly on a personal basis in order to avoid injury or excessive pain. You will be asked to attend three one hour long sessions per week.

If you are participating in a strength training class (Kines 068) the certified instructor may suggest other exercises to try as part of the class syllabus and these will be performed under the instructor's supervision. However, the unilateral leg extension and bi-lateral leg press will be performed on each occasion. This training will be carried out in the IM building and will be supervised by the class instructor.

At the end of the ten weeks you will be re-tested using the same testing prcedures given above.

3. Discomforts and Risks: During the testing and during the strength training, there is a slight risk of muscle strain, sprains, or muscle soreness that will go away within approximately 48 hours following exercise. This soreness may temporarily limit your natural movement patterns. The likelihood of these discomforts occuring can be reduced by performing the warm up and practice contractions. You may ask to stop at any time during the test procedure or during the strength training. There is an unlikely possibility of bone fracture (broken bone).

4. Benefits: The benefits to you are that you may receive some health benefits from participation in the strength training programme. You may be motivated to complete the training by having to go to the gym at a pre-set time each week and work out with other people..

The benefits to society include increased understanding of the work muscles can do.

5. Duration/Time: Your participation in the testing phase of the study will last for an hour; this includes the two half hour testing sessions before and after the strength training. The duration of the study is twelve weeks, including the ten weeks of strength training. Over the ten week strength training programme you will be asked to complete three one hour sessions a week.

6. Statement of Confidentiality: Your participation in this research is confidential. Only the person in charge, and his/her assistants, will know your identity. The data will be stored and secured in the office of the Principal Investigator in the Biomechanics Laboratory in a password protected file using numeric codes as subject identifiers on a computer server. A list of participant names and the corresponding numeric identifiers will be stored in a locked office in the Biomechanics laboratory accessible only by the Principal Investigator and the Faculty Advisor. The following may review and copy records related to this research: The Office of Human Research Protections in the U.S. Department of Health and Human Services, the Biomedical Institutional Review Board, the Food and Drug Administration (FDA), and the PSU Office for Research Protections. In the event of a publication or presentation resulting from the research, no personally identifiable information will be shared.

7. Right to Ask Questions: You can ask questions about this research. Contact Samantha Winter at (814) 865-3445 with questions. You can also call this number if you have complaints or concerns about this research. If you have questions about your rights as a research participant, or you have concerns or general questions about the research, contact Penn State University's Office for Research Protections at (814) 865-1775. You may also call this number if you cannot reach the research team or wish to talk to someone else.

8. Payment for participation: You will receive $10 for your participation in this study. This will be pro-rated at the rate of $5 per test session if you do not complete the study.

9. Voluntary Participation: Your decision to be in this research is voluntary. You can stop at any time. You do not have to answer any questions you do not want to answer. Refusal to take part in or withdrawing from this study will involve no penalty or loss of benefits you would receive otherwise.

In the unlikely event you become injured as a result of your participation in this study, medical care is available but neither financial compensation nor free medical treatment is provided. By signing this document, you are not waiving any rights that you have against The Pennsylvania State University for injury resulting from negligence of the University or its investigators.

You must be 18 years of age or older to consent to take part in this research study. If you agree to take part in this research study and the information outlined above, please sign your name and indicate the date below.

You will be given a copy of this signed and dated consent form for your records.

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Participant Signature Date

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Person Obtaining Consent Date

APPENDIX C

INFORMED CONSENT FORM IRB #23685

Title of Project: Force-Fluctuations during Isometric Contractions in the First Dorsal Interrosseus

Principal Investigator: Samantha Winter
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1. Purpose of the Study: The purpose of this research is to learn more about measures relating to muscle movement. The muscle group that will be studied, the first dorsal interrosseus, is the muscle in the hand that is used to move the index finger towards the thumb when the hand is flat.

2. Procedures to be followed: During your first visit, you will be asked to complete a short questionnaire that will identify which hand you use to perform certain tasks. A special piece of equipment will be used to measure movement of your hand/fingers. Straps will be placed around your wrist, thumb and middle fingers and a recording device that measures force will be placed against your

index finger tip. You will have a chance to practice three or four times to get used to the machine. You will be asked to try and move your finger; the machine, however, will prevent this from occurring. You will be asked to do three trials of this movement. perform three maximum effort static finger abduction muscle contractions. During these trials, electrical stimulation will be used via electrodes placed on the skin. The electrical current will not cause you any harm and will be set at a level that is comfortable for you. Some describe the sensation similar to pins and needles. You may ask to stop at any time during the test procedure.

You will then be asked to perform one movement without the electrical stimulation and then several more movements at a lower workload. Feedback will be provided via a computer monitor to help you. You will be asked to hold each movement for ten seconds. You will be given rest periods between the movements. This procedure will be repeated for three different finger positions. The whole procedure will be repeated on the other hand. This will last approximately one hour. You will then come back at another time to repeat the entire procedure, as described above.

3. Discomforts and Risks: During testing, there is a slight risk of muscle strain, sprains, or muscle soreness that will go away within approximately 48 hours following exercise. This soreness may temporarily limit your natural movement patterns. The likelihood of these discomforts occuring can be reduced by resting between efforts. Some skin redness and irritation may develop at the site where the electrodes (patches) will be placed. The stimulator produces a sensation similar to pins and needles. You may ask to stop at any time during the test procedure.

4. Benefits: We do not expect you to experience any benefits as a result of participating in this project.

The benefits to society include increased understanding of the mechanism by which the fluctuations in force during a contraction arise. The fluctuations in force have implications for understanding how muscle forces and any resulting movement may be produced accurately.

5. Duration/Time: Your participation in this study will take a total two hours; one hour per day on two separate days.

6. Statement of Confidentiality: Your participation in this research is confidential. Only the person in charge, and his/her assistants, will know your identity. The data will be stored and secured in the office of the Principal Investigator in the Biomechanics Laboratory in a password protected file using numeric codes as subject identifiers on a computer server. A list of participant names and the corresponding numeric identifiers will be stored in a locked filing cabinet in a locked office in the Biomechanics laboratory accessible only by the Principal Investigator and the Faculty Advisor. The following may review and copy records related to this research: The Office of Human Research Protections in the U.S. Department of Health and Human Services, the Biomedical Institutional Review Board and the PSU Office for Research Protections. In the event of a publication or presentation resulting from the research, no personally identifiable information will be shared.

7. Right to Ask Questions: You can ask questions about this research. Contact Samantha Winter at (814) 865-3445 with questions. You can also call this number if you have complaints or concerns about this research. If you have questions about your rights as a research participant, or you have concerns or general questions about the research, contact Penn State University's Office for Research Protections at (814) 865-1775. You may also call this number if you cannot reach the research team or wish to talk to someone else.

8. Payment for participation: If you complete all research activities, you will receive $20. For any time less than this, you will be compensated $5 for every thirty (30) minutes spent in research activities.

9. Voluntary Participation: Your decision to be in this research is voluntary. You can stop at any time. You do not have to answer any questions you do not want to answer. Refusal to take part in or withdrawing from this study will involve no penalty or loss of benefits you would receive otherwise.

In the unlikely event you become injured as a result of your participation in this study, medical care is available but neither financial compensation nor free medical treatment is provided. By signing this document, you are not waiving any rights that you have against The Pennsylvania State University for injury resulting from negligence of the University or its investigators.

You must be 18 years of age or older to consent to take part in this research study. If you agree to take part in this research study and the information outlined above, please sign your name and indicate the date below.

You will be given a copy of this signed and dated consent form for your records.

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Participant Signature Date

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Person Obtaining Consent Date

VITA

Samantha L. Winter

EDUCATION

2004 to date	Ph.D. Kinesiology (Biomechanics), Masters in Applied Statistics. ***The Pennsylvania State University***.
2003-2004	M.S., Kinesiology (Biomechanics), ***The Pennsylvania State University***. Date of graduation: August 2004
1993-1996	First Class B.Sc. (Honors), Sport and Exercise Sciences, ***The University of Birmingham***. Date of graduation: July 1996

THESES

Masters Thesis, 2004 – "In vivo measurement of the force-length curves of the rectus femoris and gastrocnemius." (The Pennsylvania State University).

Honors Thesis, 1996 – "An examination of extended knee jumping." (The University of Birmingham).

PUBLICATIONS

Challis, J.H., Murdoch, C., and Winter, S.L. (in press) Mechanical properties of the human heel pad: a comparison between populations. *Journal of Applied Biomechanics*

Infantalino, B, W., Gales, D.J., Winter, S.L., and Challis, J.H. (in press) The validity of ultrasound estimation of muscle volumes. *Journal of Applied Biomechanics*

Winter, S.L., and Challis, J.H. (in press) Reconstruction of the human gastrocnemius force-length curve in vivo: Part 1, model based validation of method. *Journal of Applied Biomechanics*

Winter, S.L., and Challis, J.H. (in press) Reconstruction of the human gastrocnemius force length curve in vivo: Part 2, experimental results. *Journal of Applied Biomechanics*