REVIEW

SARCOMERE LENGTH OPERATING RANGE OF VERTEBRATE MUSCLES DURING MOVEMENT

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Summary

The force generated by skeletal muscle varies with sarcomere length and velocity. An understanding of the sarcomere length changes that occur during movement provides insights into the physiological importance of this relationship and may provide insights into the design of certain muscle/joint combinations. The purpose of this review is to summarize and analyze the available literature regarding published sarcomere length operating ranges reported for various species. Our secondary purpose is to apply analytical techniques to determine whether generalizations can be made regarding the 'normal' sarcomere length operating range of skeletal muscle. The analysis suggests that many muscles operate over a narrow range of sarcomere lengths, covering 94±13 % of optimal sarcomere length. Sarcomere length measurements are found to be systematically influenced by the rigor state and methods used to make these measurements.

Key words: locomotion, actin, myosin, myofilament, sarcomere, muscle design.

Introduction

It is difficult to hypothesize, *a priori*, the 'best' sarcomere length operating range of muscle. From a purely mechanical point of view, operation at or near the plateau of the active force/length relationship is appealing and is often tacitly presented as fact in physiology textbooks because this is the sarcomere length range that results in maximal force production. Indeed, the basic shape of the force/length relationship has a profound influence on the nature of force generation in skeletal muscle (Gordon et al., 1966). From a control point of view, sarcomere operation on the ascending limb of the force/length relationship might be considered appealing because this range is inherently mechanically stable: any length perturbation creates an opposing force that restores sarcomere length to a stable value (Julian and Morgan, 1979). Sarcomere operation on the descending limb of the force/length relationship may be less appealing since it has been stated that this portion of the curve is inherently unstable with increasing length, resulting in decreasing force, etc. (Hill, 1953).

That most muscles operate within a stereotypical sarcomere length range is implied by the fact that serial sarcomere number is very consistent for a given muscle among similar-sized, normal individuals of a species and that serial sarcomere number is highly plastic and tightly regulated. For example, Williams and Goldspink demonstrated that muscles immobilized for several weeks at a sarcomere length far from optimal added or removed sarcomeres to restore optimal sarcomere length at the length at which the muscle was immobilized (Williams and Goldspink, 1978). This work provided strong support for the simplifying assumption that muscles adapt to function on the plateau of the force/length curve, but it should be noted that this result does not exclude the possibility that other muscles may adapt such that they function over different stereotypical length ranges.

In this study, we anticipated that, by evaluating a large enough data set of sarcomere length operating ranges, some general trends or principles might be elucidated. To this end, we have created a broad survey of reported sarcomere lengths that range across a variety of species and muscle functions.

Materials and methods

Several methodological themes were apparent during the assembly of the data that comprise this review. Sarcomere lengths were generally measured either by laser diffraction (e.g. Cutts, 1988) or by counting sarcomeres under magnification (e.g. Dimery, 1985; Goulding et al., 1997). The range reported represents either the full range of motion through which the specimen could be manipulated or a more restricted 'locomotory' region identified by the analysis of

Table 1. *Filament lengths used in calculations of relative sarcomere length change*

Species	Thick filament length (µm)	Thin filament length (µm)	Optimal sarcomere length, L_0 (µm)
Carp	1.51	0.98	2.11
Cat	1.60*	1.12	2.43
Chicken	1.60	0.95	2.08
Frog	1.60	0.98	2.08
Human	1.60	1.27	2.64
Hummingbird	1.47	1.75	1.98
Monkey	1.60*	1.16	2.41
Rabbit	1.60*	1.09	2.27
Rat	1.60*	1.11	2.4
Wild rabbit	1.60	1.12	2.27

*The thick filament is assumed to be 1.60 µm long in this species. The value was not given in the original publication.

animal movement (Dimery, 1985). Some investigators did not allow muscles to go into rigor prior to sarcomere length measurement. Any of these methodological differences may result in a systematic difference in reported sarcomere lengths.

In addition to methodological differences, another difficulty in comparing absolute sarcomere lengths among species is the variation in thin filament length and, hence, optimal sarcomere length (L_0) that occurs among species (Walker and Schrodt, 1973). As a result, comparisons among absolute sarcomere lengths are not instructive. (Optimal sarcomere length is defined as the sarcomere length at which maximum tetanic tension is generated.) For the comparisons reported here, all sarcomere lengths were first normalized to L_0 for that species. In cases where optimal length was not measured, L_0 was calculated from thin filament length (Table 1). In cases where thin filament length was unknown, sarcomere lengths from similar species were used. Optimal length was taken as twice thin filament length plus half the width of the bare zone. The width of the Z-disk, which varies with fiber type, was neglected and is not expected to affect the results of this study. The exception to this formula was the hummingbird, in which thin filament length was reported as the distance between opposing ends of both actin filaments bound to a Z-disk (Mathieu-Costello et al., 1992). This measure contains two actin filaments and the Z-disk. Furthermore, they report a thick filament length of 1.47 µm, which the present analysis assumed to represent fixation-induced shrinkage from the otherwise ubiquitous measure of 1.6 µm. The actin filament length calculated from their report (0.88 µm) was normalized to a thick filament length of 1.6 µm to calculate L_0. Thus, for hummingbird, this analysis uses a thin filament length of 0.95 µm and thick filament length of 1.6 µm, in contrast to the values of 1.75 µm and 1.47 µm, respectively, reported by Mathieu-Costello and co-workers (Mathieu-Costello et al., 1992).

Values were screened for normality using Bartlett's test in the cases where parametric statistics were applied. In cases where the data were non-normally distributed, they were log-transformed as a variance and skew stabilizing measure, and statistics were calculated on the basis of these values. Minimum, maximum and mean sarcomere lengths were compared among groups by one-way analysis of variance (ANOVA). Cluster analysis was performed on relative sarcomere maxima and minima to determine whether systematic variations among studies could be identified. Eighty-nine sarcomere length data sets were included in this analysis
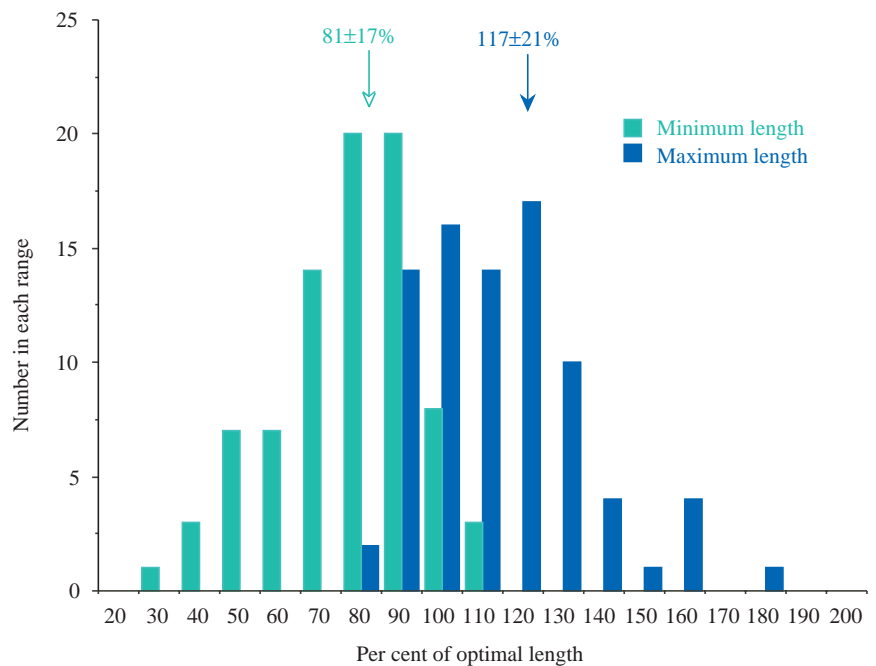

Fig. 1. Histogram showing the relative sarcomere lengths reported in the studies reviewed. Turquoise columns represent the minimum sarcomere length reported (reported as per cent optimal length, L_0) and blue columns represent the maximum sarcomere length reported. Mean minimum sarcomere length was 81 ± 17 L_0 (mean ± S.D., $N=91$) and mean maximum sarcomere length was 117 ± 21 %L_0.

and assigned into hierarchical groups in a stepwise fashion. Euclidean distances were used, and clustering was determined by centroid linkages. Significance level (P) was set to 0.05.

Results and discussion

This survey includes muscles reported in 36 separate studies covering 51 different muscles from eight different species, yielding a total of 90 data sets. Specifically, the data were obtained from studies of six bird, 10 cat, three fish, eight frog, one horse, 23 human, 13 mouse, 17 rabbit and 9 rat muscles. The minimum and maximum sarcomere lengths of these muscles are reported in Table 2, displayed as a histogram in Fig. 1, and some are superimposed on a normalized force/length curve in Fig. 2. The summarized reports yield a mean minimum sarcomere length of 81±17 % (mean ± s.d., $N=90$) of optimal length (L_0) and a mean maximum length of 117±21 %L_0. Of the reported minimum sarcomere lengths, 90 % were within the range of 50–110 %L_0. Of maximum sarcomere lengths, 90 % fell within 92–167 %L_0. On average, sarcomere length operating range was 36±25 %L_0 (Fig. 3), centered at 100 %L_0. The distribution of operating ranges was highly skewed (skew 1.48, kurtosis 2.31), with 90 % of the samples falling within an operating range of 9–90 %L_0. The mean sarcomere length of

100±14 %L_0 was more normally distributed, having a skewness of 0.38 and kurtosis of −0.07. This suggests that L_0±14 %L_0 would make a reasonable first approximation for a 'generic' muscle in the absence of other data.

A few systematic differences in sarcomere length estimates attributable to methodology were identified by one-way ANOVA. For example, maximum sarcomere length was significantly ($P<0.01$) shorter if the analysis range was restricted to locomotory muscle lengths. Interestingly, there was no apparent difference in the minimum sarcomere length during locomotion and minimum observable sarcomere length. Minimum sarcomere lengths, estimated by extrapolation outside the measured range using a mathematical model or using measured muscle lengths, were shorter by 26 % and 22 %, respectively, than those measured in muscles fixed at the 'short' length. Furthermore, maximum sarcomere lengths estimated by extrapolation to muscle lengths predicted by a mathematical model were significantly longer ($P<0.01$) than those either extrapolated to measured muscle lengths or actually measured at the long extreme. Neither method of sarcomere length determination (diffraction *versus* counting *via* microscopy) nor rigor state had a significant effect on reported sarcomere length.

Comparing among species, frog sarcomere lengths were

Fig. 2. Reported sarcomere length operating ranges, graphically superimposed upon a normalized sarcomere force/length curve. The ranges are ordered from minimum length to maximum length within a study and are color-coded according to the species from which the data were obtained. L_0, optimal sarcomere length; P_0, maximum tetanic tension. 1, Ashmore et al., 1988; 2, Brown et al., 1996; 3, Chanaud et al., 1991; 4, Cutts, 1986; 5, Cutts, 1988; 6, Dimery, 1985; 7, Fleeter et al., 1985; 8, Goulding et al., 1997; 9, Griffiths, 1991; 10, Grimm et al., 1983; 11, Hamrell and Hultgren 1992; 12, James et al., 1995; 13, Ledvina and Segal, 1994; 14, Lieber and Brown, 1993; 15, Lieber et al., 1994; 16, Lieber et al., 1992; 17, Lieber and Fridén, 1997; 18, Lutz and Rome, 1996a; 19, Mathieu-Costello, 1991; 20, Mathieu-Costello et al., 1998; 21, Nordstrom et al., 1974; 22, Poole et al., 1994; 23, Rack and Westbury, 1969; 24, Rome and Sosnicki, 1991; 25, Tardieu et al., 1977; 26, Weijs et al., 1982; 27, Weijs et al., 1983; 28, van Eijden and Raadsheer, 1992; 29, van Eijden et al., 1997.
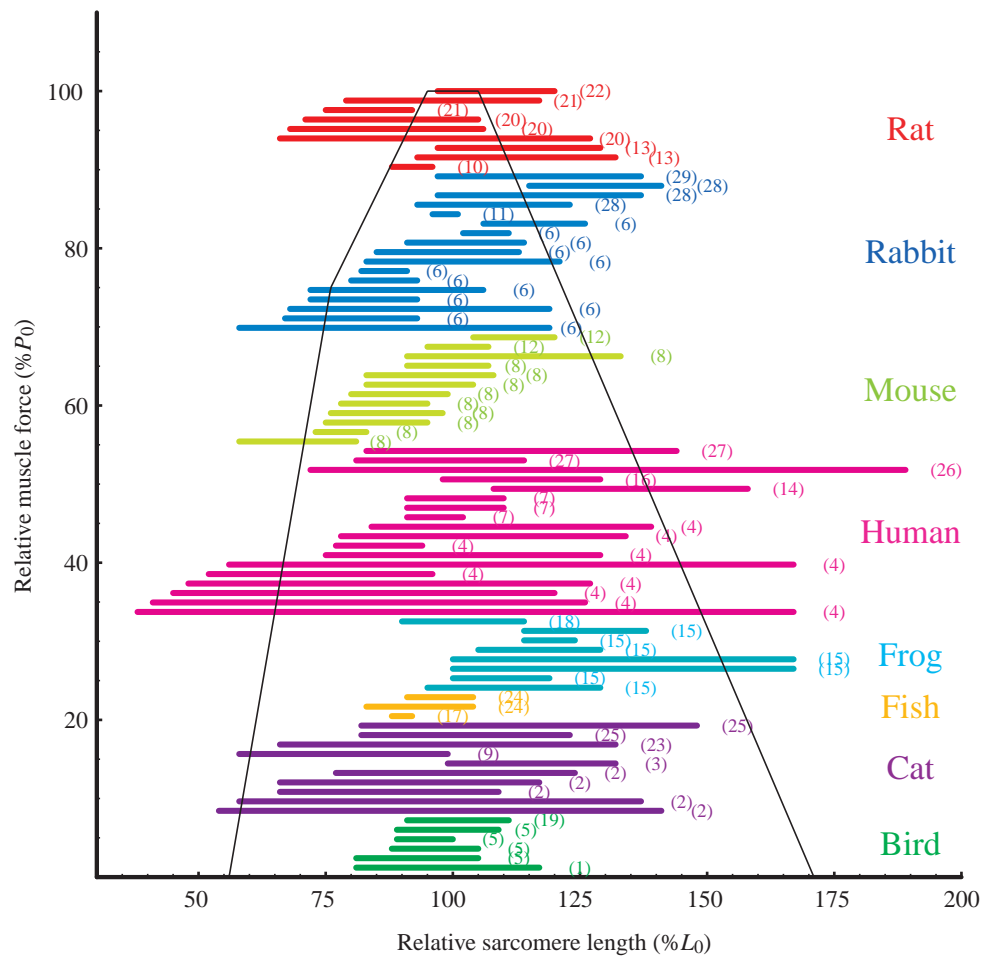
Table 2. *Sarcomere length ranges reported in different species*

Species	Muscle	Shortest sarcomere length reported (μm)	Shortest sarcomere length reported (L_0)	Longest sarcomere length reported (μm)	Longest sarcomere length reported (L_0)	Final cluster (see Fig. 5)	Reference
Bird	Patagialis	1.69	0.81	2.44	1.17	Short	Ashmore et al., 1988
Bird	Pectoralis	1.80	0.91	2.20	1.11	Short	Mathieu-Costello, 1991
Bird	Pectoralis major	1.69	0.81	2.19	1.05	Short	Cutts, 1986
Bird	Pectoralis major	1.85	0.89	2.26	1.09	Short	Cutts, 1986
Bird	Supracoracoideus	1.85	0.89	2.07	1.00	Short	Cutts, 1986
Bird	Supracoracoideus	1.84	0.88	2.19	1.05	Short	Cutts, 1986
Cat	Biceps femoris	1.60	0.66	2.84	1.17	Short	Brown et al., 1996
Cat	Biceps femoris	2.40	0.99	3.20	1.32	Long	Chanaud et al., 1991
Cat	Caudofemoralis	1.60	0.66	2.64	1.09	Short	Brown et al., 1996
Cat	Medial gastrocnemius	1.40	0.58	2.40	0.99	None	Griffiths, 1991
Cat	Sartorius	1.41	0.58	3.34	1.37	None	Brown et al., 1996
Cat	Soleus	2.00	0.82	3.60	1.48	Long	Tardieu et al., 1977
Cat	Soleus	1.60	0.66	3.20	1.32	Short	Rack and Westbury, 1969
Cat	Semitendinosus	1.32	0.54	3.42	1.41	None	Brown et al., 1996
Cat	Tibialis anterior	2.00	0.82	3.00	1.23	Short	Tardieu et al., 1977
Cat	Tenuissimus	1.87	0.77	3.01	1.24	Short	Brown et al., 1996
Fish	Red	1.91	0.91	2.20	1.04	Short	Rome and Sosnicki, 1991
Fish	White	1.75	0.83	2.20	1.04	Short	Rome and Sosnicki, 1991
Fish	?	1.85	0.88	1.95	0.92	Short	Lieber et al., 1992
Frog	Cruralis	2.00	0.95	2.70	1.29	Long	Lieber and Brown, 1993
Frog	Gastrocnemius	2.40	1.14	2.90	1.38	Long	Lieber and Brown, 1993
Frog	Gluteus magnus	2.40	1.14	2.60	1.24	Long	Lieber and Brown, 1993
Frog	Gracilis	2.20	1.05	2.70	1.29	Long	Lieber and Brown, 1993
Frog	Iliacus internus	2.10	1.00	2.50	1.19	Long	Lieber and Brown, 1993
Frog	Semimembranosus	2.10	1.00	3.50	1.67	None	Lieber and Brown, 1993
Frog	Semimembranosus	1.90	0.90	2.40	1.14	Short	Lutz and Rome, 1996a
Frog	Semitendinosus	2.10	1.00	3.50	1.67	None	Lieber and Brown, 1993
Horse	Semitendinosus	1.85	–	3.00	–	None	Mermod et al., 1988
Human	Biceps femoris	1.20	0.45	3.17	1.20	None	Cutts, 1988
Human	Digastric	2.15	0.81	3.00	1.14	Short	van Eijden et al., 1997
Human	ECRB	2.00	0.76	3.10	1.17	Short	Loren et al., 1996
Human	ECRB	2.60	0.98	3.40	1.29	Long	Lieber et al., 1994
Human	ECRL	2.30	0.87	2.60	0.98	Short	Loren et al., 1996
Human	ECU	2.20	0.83	2.60	0.98	Short	Loren et al., 1996
Human	EDC	2.40	0.91	2.90	1.10	Short	Fleeter et al., 1985
Human	FCR	1.20	0.45	2.40	0.91	None	Loren et al., 1996
Human	FCU	1.10	0.42	2.40	0.91	None	Loren et al., 1996
Human	FCU	2.84	1.08	4.16	1.58	None	Lieber et al., 1996
Human	FCU	2.40	0.91	2.90	1.10	Short	Fleeter et al., 1985
Human	Gastrocnemius	1.01	0.38	4.41	1.67	None	Cutts, 1988
Human	Masseter	1.90	0.72	5.00	1.89	None	van Eijden and Raadsheer, 1992
Human	Palmaris longus	2.40	0.91	2.70	1.02	Short	Fleeter et al., 1985
Human	Rectus femoris	1.37	0.52	2.54	0.96	None	Cutts, 1988
Human	Semimembranosus	1.48	0.56	4.41	1.67	None	Cutts, 1988
Human	Soleus	1.26	0.48	3.36	1.27	None	Cutts, 1988
Human	Semitendinosus	2.23	0.84	3.67	1.39	Long	Cutts, 1988
Human	Tibialis anterior	1.09	0.41	3.32	1.26	None	Cutts, 1988

systematically longer than those of all other species ($P<0.003$), having a mean length of $120\%L_0$. Reported human sarcomere lengths covered the widest range, with the shortest lengths comparable with those of cats ($70\%L_0$) and the longest reported lengths ($130\%L_0$) approaching those of frogs ($135\%L_0$).

Cluster analysis yielded no functionally identifiable groupings. The first three clusters identified might be considered outliers from the main group (Fig. 4) for technical reasons. Cluster 4 is composed of intraoperative measurement of the flexor carpi ulnaris (Lieber and Fridén, 1997) and *in situ* measurements of biarticular semimembranosus and

Table 2. *Continued*

Species	Muscle	Shortest sarcomere length reported		Longest sarcomere length reported		Final cluster (see Fig. 5)	Reference
		(μm)	(L_0)	(μm)	(L_0)		
Human	Temporalis	2.20	0.83	3.80	1.44	Long	van Eijden et al., 1997
Human	Vastus intermedius	2.03	0.77	2.48	0.94	Short	Cutts, 1988
Human	Vastus lateralis	2.07	0.78	3.53	1.34	Short	Cutts, 1988
Human	Vastus medialis	1.99	0.75	3.40	1.29	Short	Cutts, 1988
Mouse	Biceps brachii	1.98	0.83	2.50	1.04	Short	Goulding et al., 1997
Mouse	EDL	2.49	1.04	2.88	1.20	Long	James et al., 1995
Mouse	Gastrocnemius	1.83	0.76	2.34	0.97	Short	Goulding et al., 1997
Mouse	Longissimus dorsi, lumbar	1.74	0.72	2.00	0.83	Short	Goulding et al., 1997
Mouse	Longissimus dorsi, thoracic	2.19	0.91	2.57	1.07	Short	Goulding et al., 1997
Mouse	Pectoralis major	1.92	0.80	2.37	0.99	Short	Goulding et al., 1997
Mouse	Psoas	2.18	0.91	3.18	1.33	Long	Goulding et al., 1997
Mouse	Rectus femoris	1.81	0.75	2.28	0.95	Short	Goulding et al., 1997
Mouse	Soleus	2.28	0.95	2.57	1.07	Short	James et al., 1995
Mouse	Soleus	2.08	0.87	2.43	1.01	Short	Williams and Goldspink, 1978
Mouse	Soleus	2.00	0.83	2.60	1.08	Short	Goulding et al., 1997
Mouse	Trapezius	1.40	0.58	1.95	0.81	None	Goulding et al., 1997
Mouse	Triceps brachii	1.88	0.78	2.28	0.95	Short	Goulding et al., 1997
Rabbit	Adductor longus	1.64	0.72	2.11	0.93	Short	Dimery, 1985
Rabbit	Adductor magnus	1.81	0.80	2.11	0.93	Short	Dimery, 1985
Rabbit	BF1	1.94	0.85	2.56	1.13	Short	Dimery, 1985
Rabbit	BF2	2.06	0.91	2.59	1.14	Short	Dimery, 1985
Rabbit	Digastric	2.60	1.15	3.20	1.41	Long	Weijs et al., 1982
Rabbit	Gluteus maximus	1.53	0.67	2.11	0.93	Short	Dimery, 1985
Rabbit	Lateral gastrocnemius	1.55	0.68	2.69	1.19	Short	Dimery, 1985
Rabbit	Masseter	2.20	0.97	3.10	1.37	Long	Weijs et al., 1983
Rabbit	Medial gastrocnemius	1.63	0.72	2.40	1.06	Short	Dimery, 1985
Rabbit	Papillary	2.17	0.96	2.29	1.01	Short	Hamrell and Hultgren, 1992
Rabbit	Pterygoid	2.20	0.97	3.10	1.37	Long	Weijs et al., 1982
Rabbit	Rectus femoris	1.32	0.58	2.71	1.19	Short	Dimery, 1985
Rabbit	Semimembranosus	1.86	0.82	2.06	0.91	Short	Dimery, 1985
Rabbit	Tibialis anterior	1.88	0.83	2.75	1.21	Short	Dimery, 1985
Rabbit	Temporal	2.10	0.93	2.80	1.23	Long	Weijs et al., 1982
Rabbit	Tensor fascia latae	2.31	1.02	2.52	1.11	Long	Dimery, 1985
Rabbit	Vastus lateralis	2.41	1.06	2.86	1.26	Long	Dimery, 1985
Rat	Diaphragm	2.32	0.97	2.88	1.20	Long	Poole et al., 1994
Rat	EDL	2.33	0.97	3.09	1.29	Long	Ledvina and Segal, 1994
Rat	Gastrocnemius	1.58	0.66	3.05	1.27	Short	Mathieu-Costello et al., 1988
Rat	Gracilis	1.71	0.71	2.53	1.05	Short	Mathieu-Costello et al., 1988
Rat	Masseter	1.90	0.79	2.80	1.17	Short	Nordstrom et al., 1974
Rat	Soleus	2.22	0.93	3.17	1.32	Long	Ledvina and Segal, 1994
Rat	Soleus	1.62	0.68	2.55	1.06	Short	Mathieu-Costello et al., 1988
Rat	Temporal	1.80	0.75	2.20	0.92	Short	Nordstrom et al., 1974
Rat	Ventricle	2.01	0.88	2.19	0.96	Short	Grimm et al., 1983

BF, biceps femoris; ECRB, extensor carpi radialis brevis; ECRL, extensor carpi radialis longus; ECU, extensor carpi ulnaris; EDC, extensor digitorum communis; EDL, extensor digitorum longus; FCR, flexor carpi radialis; FCU, flexor carpi ulnaris.

semitendinosus muscles of the frog (Lieber and Brown, 1993). These techniques measure sarcomere length in fresh tissue and may have slightly distorted the muscle. Cluster 3 consists of estimates of human gastrocnemius and semimembranosus, both biarticular muscles that would be particularly susceptible

to errors in extrapolation in the mathematical model used (Cutts, 1988) and estimation of human masseter, another complex muscle approximated by a model (van Eijden and Raadsheer, 1992). Cluster 2 consists of six more estimates from mathematical models of two-joint muscles (Brown et al.,
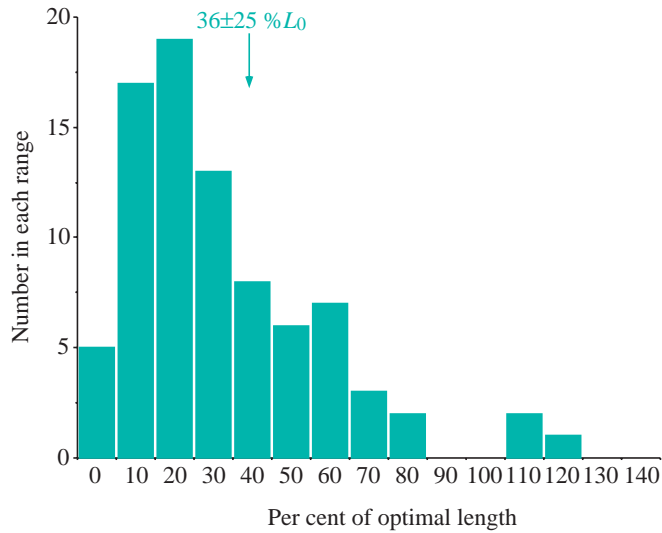
Fig. 3. Histogram showing the range of sarcomere lengths over which each muscle studied operated in the 91 data sets reviewed. Note that the distribution is highly skewed (skewness 1.48, kurtosis 2.31) towards small lengths, with the mean operating range being $36\pm25\,\%L_0$, where L_0 is optimal sarcomere length.
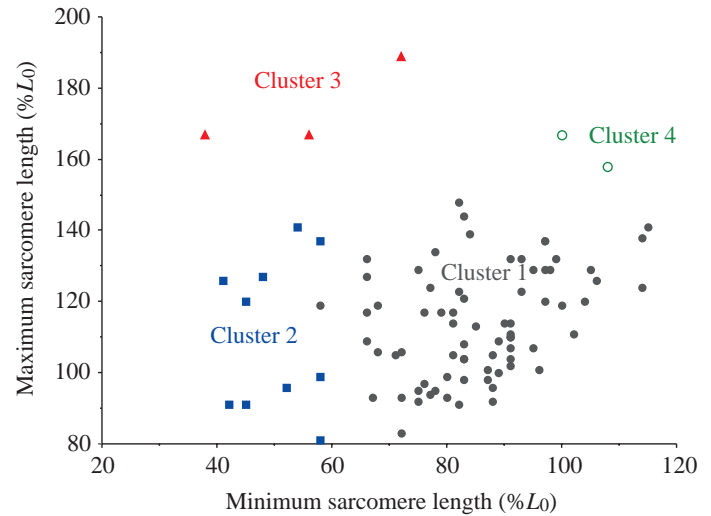

Fig. 4. Initial clustering of 89 out of the 90 data sets reviewed. Two could not be included because of incomplete data. Each cluster is represented by a specific symbol and color. While the data can be classified statistically into four clusters, technical details justify considering cluster 1 (black circles) in the absence of the outlying clusters, numbered 2–4. Cluster 1 is further subdivided in Fig. 5. L_0, optimal sarcomere length.

1996; Griffiths, 1991), technically challenging ultrasound measurements (Griffiths, 1991) and mouse trapezius (Goulding et al., 1997), which is described as 'prone to supercontraction'. The remaining muscles form a single group, with a mean minimum sarcomere length of $86\pm12\,\%L_0$ and a maximum sarcomere length of $114\pm15\,\%L_0$, which will be referred to as the 'main group.'

Further clustering within the main group was not as easily attributed to methodology, nor was any pattern obvious. Most clusters contained both anti-gravity (or power-producing) and non-antigravity muscles through at least six further divisions. Both fast-contracting and slow-contracting muscles could be found in most clusters. The most apparent division of the primary group was into two clusters (Fig. 5). Group 2 (referred to as 'long') could be considered to be muscles with substantial operating range on the descending limb of the force/length curve, while group 1 (referred to as 'short') could be considered to be muscles that operate more on the ascending limb and plateau region of the force/length curve. Both groups display similar operating ranges (long, $32\pm15\,\%L_0$; short, $27\pm16\,\%L_0$; $P=0.20$), centered about different midranges (long, $114\pm5\,\%L_0$, short, $94\pm7\,\%L_0$; $P<0.001$). The short group contains almost all the muscles measured over the 'locomotory' range, with the exception of the rabbit vastus lateralis and tensor fascia latae muscles (Dimery, 1985) and the mouse extensor digitorum longus muscle (James et al., 1995). The long group consists primarily of sarcomere lengths measured at the extremes, as opposed to extrapolated, in specimens fixed or held at those extremes without rigor (e.g. Lieber and Brown, 1993; Weijs et al., 1982).

The high prevalence of non-rigor muscles in the long group suggests that these sarcomere lengths may be systematically overestimated or that rigor results in systematic

underestimation of actual sarcomere lengths. Despite the lack of significance of rigor state as an influence on either endpoint measure in the complete data set, there is a significant ($P<0.001$) difference between the long (minimum $98\pm9\,\%L_0$;
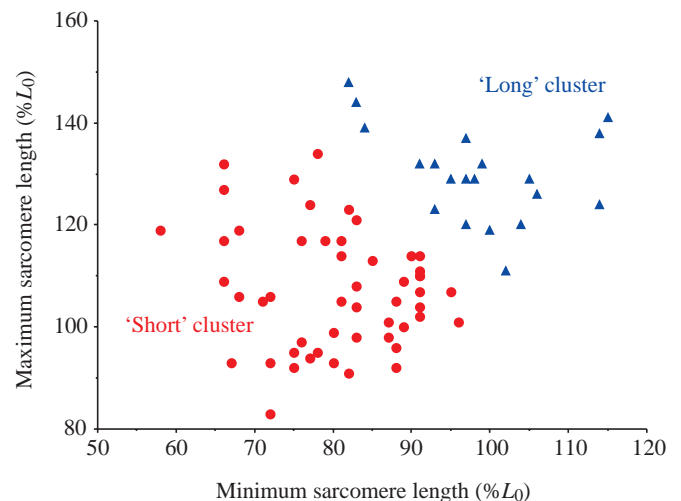

Fig. 5. The first division of cluster 1 from Fig. 4, representing 73 of the 90 data sets reviewed. This subdivision illustrates the separation of the cluster into two separate groups of measurements, characterized by the rigor state of the muscles at the time of sarcomere length measurement. Both minimum and maximum sarcomere length are longer in the cluster for which sarcomere length measurements were made prior to the muscles entering rigor ($N=21$) compared with the cluster for which sarcomere length measurements were made after permitting the muscles to enter rigor ($N=52$). L_0, optimal sarcomere length.

maximum $130\pm9\,\%L_0$) and short (minimum $80\pm9\,\%L_0$; maximum $107\pm12\,\%L_0$) groups.

The main objective of this work was to assemble the published sarcomere length operating ranges of different animals. We then attempted to examine these reports critically to determine a 'typical' range. Starting with 90 muscles, 16 were discarded as methodological or technical outliers, leaving the main group of 73. Cluster analysis revealed that a further 21 reports could be considered statistical outliers, leaving a final population of 52 muscles whose lengths span from 80 ± 9 to $107\pm12\,\%L_0$ with an excursion of $\pm13\,\%L_0$ centered around $94\,\%L_0$. This range represents a substantial portion of the ascending limb, the entire plateau and a small region of the descending limb of the force/length curve. It should be noted that this description does not accurately describe each individual muscle. Even within the short group, muscles operating on a substantial portion of the descending limb could be found.

Sarcomere length operation over a restricted, near-optimal range has been reported in fish muscle during steady swimming in red muscle and during the startle response in white muscle (Rome et al., 1992; Rome and Sosnicki, 1991; Rome et al., 1993). The results of these studies suggest that fish have optimized the muscle fiber/spinal curvature relationship such that swimming produces sarcomere length changes and sarcomere contraction velocities very close to optimal across a variety of swimming speeds. The differences in muscle design between the red and white muscles of the fish are complemented by the differences in activation of the muscles at various swimming speeds. Similarly, the large power-producing muscle of the frog, the semimembranosus, appears to be constrained by muscle fiber length and knee joint angle such that near-optimal sarcomere lengths and powers are produced during hopping (Lutz and Rome, 1996a; Lutz and Rome, 1996b). In spite of the agreement among some studies, the 'take-home' message may be that there is not simply a single stereotypical operating range for skeletal muscle that applies to all muscles, movements and species. Rather, the musculoskeletal system seems to tailor itself to the particular functional task. When raw power production is necessary, systems are in place to maximize power production. However, when joint stability or control is the major consideration, musculoskeletal systems may be arranged to provide this stability even if it is accompanied by losses in power. As a first approximation, our survey of the literature indicates that the 'typical' muscle operates over the range $94\pm13\,\%L_0$. Of course, future studies are required to determine the extent and nature of the design principles that govern sarcomere length operating range in general.

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