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...
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 (L₀) 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 L₀ for that species. In cases where optimal length was not measured, L₀ 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 L₀. 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.

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

<table>
<thead>
<tr>
<th>Species</th>
<th>Thick filament length (μm)</th>
<th>Thin filament length (μm)</th>
<th>Optimal sarcomere length, L₀ (μm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carp</td>
<td>1.51</td>
<td>0.98</td>
<td>2.11</td>
</tr>
<tr>
<td>Cat</td>
<td>1.60*</td>
<td>1.12</td>
<td>2.43</td>
</tr>
<tr>
<td>Chicken</td>
<td>1.60</td>
<td>0.95</td>
<td>2.08</td>
</tr>
<tr>
<td>Frog</td>
<td>1.60</td>
<td>0.98</td>
<td>2.08</td>
</tr>
<tr>
<td>Human</td>
<td>1.60</td>
<td>1.27</td>
<td>2.64</td>
</tr>
<tr>
<td>Hummingbird</td>
<td>1.47</td>
<td>1.75</td>
<td>1.98</td>
</tr>
<tr>
<td>Monkey</td>
<td>1.60*</td>
<td>1.16</td>
<td>2.41</td>
</tr>
<tr>
<td>Rabbit</td>
<td>1.60*</td>
<td>1.09</td>
<td>2.27</td>
</tr>
<tr>
<td>Rat</td>
<td>1.60*</td>
<td>1.11</td>
<td>2.4</td>
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<tr>
<td>Wild rabbit</td>
<td>1.60</td>
<td>1.12</td>
<td>2.27</td>
</tr>
</tbody>
</table>

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

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, L₀) and blue columns represent the maximum sarcomere length reported. Mean minimum sarcomere length was 81±17 L₀ (mean ± s.d., N=91) and mean maximum sarcomere length was 117±21 %L₀.
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 $81\pm17\%$ (mean ± s.d., $N=90$) of optimal length ($L_0$) and a mean maximum length of $117\pm21\%L_0$. 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 $36\pm25\%L_0$ (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 $100\pm14\%L_0$ was more normally distributed, having a skewness of 0.38 and kurtosis of $-0.07$. This suggests that $L_0\pm14\%L_0$ 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 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

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**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, Wejs et al., 1982; 27, Wejs et al., 1983; 28, van Eijden and Raadsheer, 1992; 29, van Eijden et al., 1997.
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>
<thead>
<tr>
<th>Species</th>
<th>Muscle</th>
<th>Shortest sarcomere length reported ((\mu m))</th>
<th>Longest sarcomere length reported ((\mu m))</th>
<th>Final cluster (see Fig. 5)</th>
<th>Reference</th>
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</tr>
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</tr>
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<td>3.32</td>
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</table>
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., 1988).
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±12 %L₀ and a maximum sarcomere length of 114±15 %L₀, 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±15 %L₀; short, 27±16 %L₀; P=0.20), centered about different midranges (long, 114±5 %L₀; short, 94±7 %L₀; 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; Weis et al., 1982).

The high prevalence of non-rigor muscles in the long group suggests that these sarcomere lengths may be systematically underestimated 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±9 %L₀;
maximum 130±9%L0) and short (minimum 80±9%L0; maximum 107±12%L0) 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±12%L0 with an excursion of ±13%L0 centered around 94%L0. 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 swimming speeds. Similarly, the large power-producing muscle of the fish is optimized the muscle fiber/spinal curvature relationship such 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.

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References