

Mechanics Of Muscle Contraction Part Iii: Isokinetic Shortening Contraction

M Tsili

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Abstract

In this paper we applied a proposed theory (Tsili, 2013a) and we investigated the isokinetic shortening contraction of the sarcomer. We assumed that during contraction, the change of its cross-section area was negligible. Our model for special values of parameters, predicts the contraction speed measured by Faulkner et., al., (1986) at temperature 37°C. Also our findings that deal with nor-malized stress, force, length and volume of the sarcomer, are very closed to the results derived from statistical analysis on "raw" data taken from Gordon et., al., (1966); Spector et., al., (1980); Roy et., al., (1982); Powel et., al., (1984); Faulkner et., al., (1986); Pollack (1990); Epstein and Herzog (1998); Burkholder et., al., (2001); Makropoulou, (2009).

INTRODUCTION

The purpose of this paper is to study the problem of isokinetic shortening contraction of the sarcomer. For that reason we will base upon a recently developed theory (Tsili, 2013a). The main assumption of this work is that during contraction the change of cross-section area of the sarcomer is small and could be neglected.

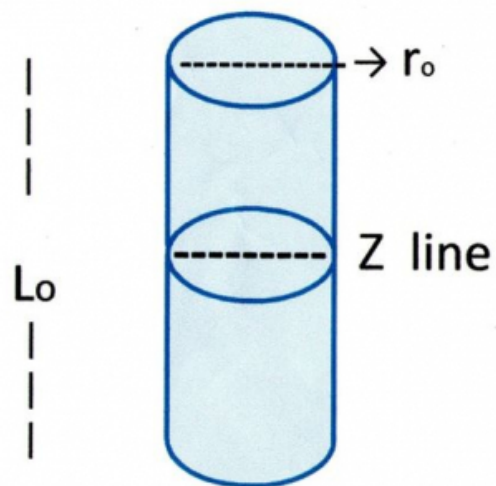
THE PHYSICAL APPROXIMATION OF THE PROBLEM

The basic equations of our theory are in our previous paper (Tsili, 2013a) and they will not be repeated here. We supposed that at $t < 0$, the sarcomer was free of stress. In resting state it had a length L_0 , a radius r_0 and a temperature ϑ_0 , as indicated in Fig. 1. Consequently its cross -section area and initial volume of sarcomer were S_0 and ϑ_0 , respectively, where:

$$S_0 = \pi r_0^2 \text{ and } \vartheta_0 = S_0 \cdot L_0 \quad (2.1)$$

Figure 1

In resting state the sarcomer had a length L_0 and a radius S_0

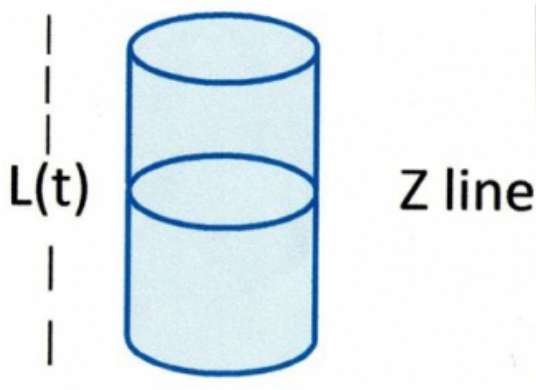


We assume that at $t=0$ the motor neuron sends a stimulative pulse to the motor unit, in order to start the process of muscle contraction. Due to the delay of the response, at $t_1 > 0$ a mechanical stress is produced. The last simultaneously displaces with constant speed upwards and downwards the material particles of the sarcomer that lie below and above the z line respectively. As a result of the above displacements, the sarcomer shortens (see Fig. 2.). The

process of shortening continues until a time t_s . At $t > t_s$ the contraction stops and the inverse process of relaxation starts.

Figure 2

The sarcomer at time $t \geq t_1$ during shortening. Accordingly to all that we stated in previous paragraph, the displacements are: $u_r = u_\theta = 0$ and $u_z = a\dot{\theta}t$ (2.2)1-2-3



Accordingly to all that we stated in previous paragraph, the displacements are:

$$u_r = u_\theta = 0 \text{ and } u_z = a\dot{\theta}t \text{ (2.2)1-2-3}$$

where a is an unknown constant. Therefore the velocity of the material particle of sarcomer is:

$$v_r = du_r/dt = 0 \quad v_\theta = du_\theta/dt = 0 \text{ and } v_z = du_z/dt = a\dot{\theta} \text{ (2.3)1-2-3}$$

Then strain-displacement equations become:

$$E_{rr} = E_{\theta\theta} = \epsilon_{rr} = \epsilon_{\theta\theta} = \epsilon_{rz} = 0 \text{ and } E_{zz} = a\dot{\theta}t \text{ (2.4)1-2-3-4-5-6}$$

Substituting the above into stress - strain equation (see Tsili, 2013a) it follows that all stresses vanish:

$$T_{rr} = T_{\theta\theta} = \epsilon_{rz} = T_{rz} = T_{r\theta} = 0 \text{ (2.5)1-2-3-4-5}$$

except from the axial stress:

$$T_{zz} = c_{33}a\dot{\theta}t + a_z + a_{zz}a\dot{\theta} \text{ (2.6)}$$

CALCULATION OF STRESS, FORCE, LENGTH AND VOLUME OF THE SARCOMER, USING "RAW" DATA

Spector et., al., (1980); Roy et., al., (1982); Powel et., al., (1984) calculated the maximal isometric stress P_o :

$$P_o = 225 \text{ KN/m}^2 \text{ (3.1)}$$

Accordingly to Gordon et., al., (1966) and to Pollack (1990),

the initial length and diameter of sarcomer are :

$$L_o = 2.22 \text{ }\mu\text{m} \text{ and } d_o = 2r_o = 1 \text{ }\mu\text{m} \text{ (3.2)}_{1,2} \text{ respectively (1}\mu\text{m} = 10^{-6}\text{m)}. \text{ Therefore:}$$

$$S_o = \pi r_o^2 = 0.7854 \text{ }\mu\text{m}^2 \text{ and } V_o = S_o \cdot L_o = 1.7436 \text{ }\mu\text{m}^3 \text{ (3.3)}_{1,2}$$

The maximum isometric force F_o could be calculated by replacing (3.1) and (3.3)₂ into:

$$F_o = P_o \cdot S_o = 176.715 \times 10^9 \text{ N (3.4)}$$

Burkholder and Lieber (2001, p.1531) superimposed data taken from 36 studies for bird, cat, rat, rabbit, mouse, frog, horse, human and derived a general normalized force-length relation for the sarcomer. Accordingly to their graph, the ascend limb of this relation is :

$$\begin{cases} 4.73k - 2.6156 \text{ for } 0.572 \leq k \leq 0.736 & f = |1.185k - 0.122 \text{ for } 0.736 \leq k \leq 0.947 \\ 1 \text{ for } 0.947 \leq k \end{cases} \quad f = \frac{F}{F_o} \quad k = \frac{L}{L_o} \text{ (3.5)}$$

where $f = F/F_o$ and $k = L/L_o$. It has been shown (Pollack 1990, p.3; Epstein and Herzog, 1998, p.76) that during shortening the length of the sarcomer linearly decreases :

$$L(t) = At + B \text{ for } t_1 \leq t \leq t_s \text{ in units of } \mu\text{m} \text{ (3.6)}$$

Then the contraction speed is:

$$v_z = du_z/dt = d(L_o - L(t))/dt = -A \text{ (3.7)}$$

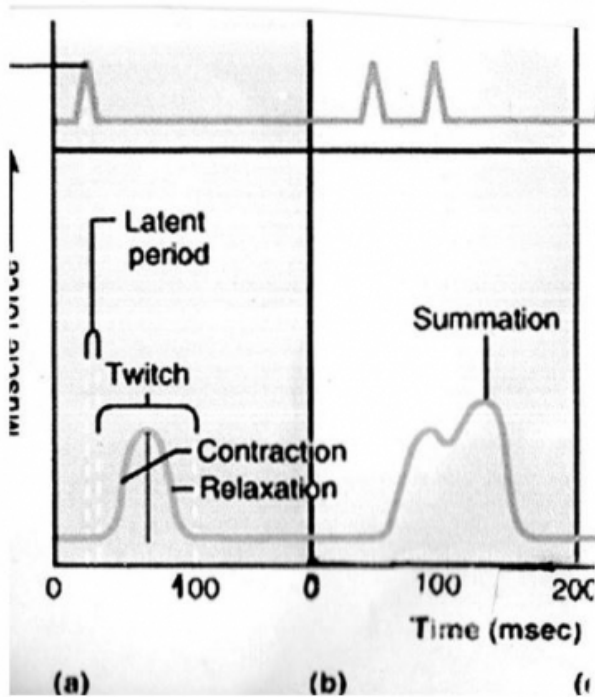
Faulkner et., al., (1986) reported values for the contraction velocity 6 lengths/sec and 2 lengths/sec for fast and slow fibres respectively at temperature 37°C. We assume that we have to do only with fast fibres. Then from (3.7), it results:

$$A = 6 \text{ }\mu\text{m/sec} \text{ (3.8)}$$

In addition for fast- fibres $t_1 = 0.02 \text{ sec}$ (see for example Makropoulou, 2009, p.16).

Figure 3

Electromyograph for muscle contraction. Taken from Makropoulou (2009)



Substituting the initial condition $L(t_1=0.02) = L_o = 2.22\mu\text{m}$ into (3.6), it follows:

$$L(t) = 6t + 2.34 \text{ in units of } \mu\text{m} \quad (3.9)$$

Consequently by the help of (3.1), (3.2), (3.3), (3.4), (3.5) and (3.9) it is possible to calculate the normalized stresses, forces, lengths and volumes of the sarcomer, for various time moments. All results are concentrated in Table 1. Also Table 2. contains the results derived from linear regression analysis on data of Table 1. Particularly the forces and the lengths have been calculated by:

$$f = F/F_o = (P.S_o)/(P_o.S_o) = P/P_o = 1.4 - 6.933t \text{ and}$$

$$k = L/L_o = (V/S_o)/(V_o/S_o) = V/V_o = 1.0542 - 2.705t \quad (3.10)_{1,2}$$

THEORETICAL RESULTS FOR CONTRACTION SPEED AND FOR NORMALIZED STRESS, FORCE, LENGTH AND VOLUME OF THE SARCOMER

In (2.2)₃ we restrict z to a constant z_1 such that:

$$z_1 = 0.00954 \times 10^9 \quad (4.1) \text{ and we choose:}$$

$$a = 17 \times 10^9 \text{ and } T = 37^\circ\text{C} \quad (4.2)_{1,2}$$

Table 1

All results for stresses, forces, lengths and volumes of the sarcomer, for various time moments of isokinetic contraction. The initial data are $P_o = 225 \text{KN/m}^2$, $F_o = 176.715 \text{N} \times 10^9$, $S_o = 0.7854 \mu\text{m}^2$, $V_o = 1.7436 \mu\text{m}^3$, $L_o = 2.22 \mu\text{m}$ and are picked from cites refered in the text.

P/P_o	F/F_o	L/L_o	V/V_o	t
1	1	1	1	$t_1=0.02\text{s}$
0.918	0.918	0.878	0.878	$t_2=0.065\text{s}$
0.892	0.892	0.856	0.856	$t_3=0.073\text{s}$
0.865	0.865	0.833	0.833	$t_4=0.082\text{s}$
0.839	0.839	0.811	0.811	$t_5=0.09\text{s}$
0.812	0.812	0.788	0.788	$t_6=0.098\text{s}$
0.786	0.786	0.766	0.766	$t_7=0.107\text{s}$
0.758	0.758	0.743	0.743	$t_8=0.115\text{s}$
0.682	0.682	0.721	0.721	$t_9=0.123\text{s}$
0.577	0.577	0.698	0.698	$t_{10}=0.132\text{s}$
0.476	0.476	0.676	0.676	$t_{11}=0.14\text{s}$
0.371	0.371	0.653	0.653	$t_{12}=0.148\text{s}$
0.27	0.27	0.631	0.631	$t_{13}=0.157\text{s}$
0.165	0.165	0.608	0.608	$t_{14}=0.165\text{s}$
0.06	0.06	0.585	0.585	$t_{15}=0.173\text{s}$
0	0	0.572	0.572	$t_{16}=0.178\text{s}$

Table 2

All results for stresses, forces, lengths and volumes of the sarcomer de-rived by linear regression analysis $F/F_o = 1.4 - 6.933t$ and $L/L_o = 1.0542 - 2.705t$ on data of Table 1.

P/P_o	F/F_o	L/L_o	V/V_o	t
1.26	1.26	1	1	$t_1=0.02$
1.005	1.005	0.9	0.9	$t_2=0.057\text{s}$
0.893	0.893	0.857	0.857	$t_3=0.073\text{s}$
0.831	0.831	0.832	0.832	$t_4=0.082\text{s}$
0.776	0.776	0.811	0.811	$t_5=0.09\text{s}$
0.721	0.721	0.789	0.789	$t_6=0.098\text{s}$
0.658	0.658	0.765	0.765	$t_7=0.107\text{s}$
0.603	0.603	0.743	0.743	$t_8=0.115\text{s}$
0.547	0.547	0.721	0.721	$t_9=0.123\text{s}$
0.485	0.485	0.697	0.697	$t_{10}=0.132\text{s}$
0.43	0.43	0.676	0.676	$t_{11}=0.14\text{s}$
0.374	0.374	0.651	0.651	$t_{12}=0.148\text{s}$
0.3115	0.3115	0.630	0.630	$t_{13}=0.157\text{s}$
0.256	0.256	0.608	0.608	$t_{14}=0.165\text{s}$
0.2	0.2	0.586	0.586	$t_{15}=0.173\text{s}$
0.166	0.166	0.573	0.573	$t_{16}=0.178\text{s}$

Replacing (4.1) and (4.2) into (2.2)₃ and (2.3)₃, it implies:

$$u_z = 6t \text{ in units of } \mu\text{m and } v_z = 6 \mu\text{m/sec} \quad (4.3)_{1,2}$$

respectively. The theoretical result (4.3)₂ predicts the measurement of Faulkner et., al., (1986) for the contraction speed of fast fibres.

We normalize sarcomer's length:

$$k = L(t)/L_o = L_o u_z / L_o = 2.22 \mu\text{m} / 2.22 = (V/S_o) / (V_o/L_o) = V/V_o \quad (4.4)$$

where we have used (3.3)₂ and (4.3)₁. At continuity we divide (2.6) with the maximum isometric stress (3.1) and we account that the coefficient a_z coincides with P_o (Tsili, 2013b. p.3). Then it implies:

$T_{zz}/P_o = P/P_o = c_{33} a_z t / P_o + 1 + a_{zz} a_z / P_o$ (4.5) Hatta et., al. (1984) measured the elastic constant of muscle c_{33} in active state:

$$c_{33} = 2.47 \times 10^9 \text{ N/m}^2 \quad (4.6)$$

and concluded that muscle elastically lies near an unstable state. Therefore more implicit situations such viscoelasticity are unstable. The last means that it is rather impossible to compute a standard value for the viscoelastic coefficient a_{zz} .

We only could predict the order of the magnitude of the above parameter. We choose:

$$a_{zz} = 0.143 \times 10^9 \text{ N/m}^2 \quad (4.7)$$

Then (4.4) because of (3.1), (3.2)₁, (4.2), (4.6) and (4.7) concludes to:

$$P/P_o = 1.4 \mu\text{m} / 6.905 \mu\text{m} = (F/S_o) / (F_o/S_o) = F/F_o \quad (4.8)$$

Therefore using (4.4) and (4.8) it is possible to calculate all values for normalized stresses, forces, lengths and volumes for the sarcomer for the same time moments as we did earlier. All these results are found in Table 3.

DISCUSSION

Our model for proper choice of the unknown parameters, i) it predicts the contraction speed for fast fibres measured by Faulkner et., al., (1986) and ii) it is very closed to results for normalized stresses, forces, lengths and volumes of the sarcomer derived from statistical analysis on "raw" data (Table 2.), picked by Spector et., al., (1980); Roy et., al., (1982); (1982); Powel et., al., (1984); Gordon et., al., (1966); Pollack (1990), Burkholder and Lieber (2001); Faulkner et., al., (1986), Epstein and Herzog (1998); Hatta et., al., (1984); Makropoulou (2009). Compare our theoretical

results in Table 3. with those of Table 2.

Table 3

The results for normalized stress ,force, length and volume of sarcomer derived from our model for $a = 0.17 \times 10^9$, $\theta = 37^\circ$; $C_{33} = 2.47 \times 10^9$, $a_{zz} = 0.143 \times 10^9$

P/ P _o	F/ F _o	L/ L _o	V/ V _o	t
1.262	1.262	0.946	0.946	t ₁ =0.02
1.006	1.006	0.846	0.846	t ₂ =0.057s
0.896	0.896	0.803	0.803	t ₃ =0.073s
0.834	0.834	0.778	0.778	t ₄ =0.082s
0.779	0.779	0.757	0.757	t ₅ =0.09s
0.723	0.723	0.735	0.735	t ₆ =0.098s
0.661	0.661	0.711	0.711	t ₇ =0.107s
0.606	0.606	0.689	0.689	t ₈ =0.115s
0.551	0.551	0.668	0.668	t ₉ =0.123s
0.489	0.489	0.643	0.643	t ₁₀ =0.132s
0.433	0.433	0.622	0.622	t ₁₁ =0.14s
0.378	0.378	0.6	0.6	t ₁₂ =0.148 s
0.316	0.316	0.576	0.576	t ₁₃ =0.157s
0.261	0.261	0.554	0.554	t ₁₄ =0.165s
0.205	0.205	0.532	0.532	t ₁₅ =0.173s
0.171	0.171	0.519	0.519	t ₁₆ =0.178s

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Author Information

M.B. Tsili

Department of Civil Engineering, Democritus University of Thrace

Xanthi, Greece

martsili@otenet.gr