

# 1. Force-Velocity Relation for Skeletal Muscle

## OBJECTIVES

- Use the Hill equation to model the force-velocity and power-velocity relations for a muscle fibre.
- Compare the force-velocity and power-velocity relations for a fast-twitch muscle fibre with those for a slow-twitch muscle fibre.

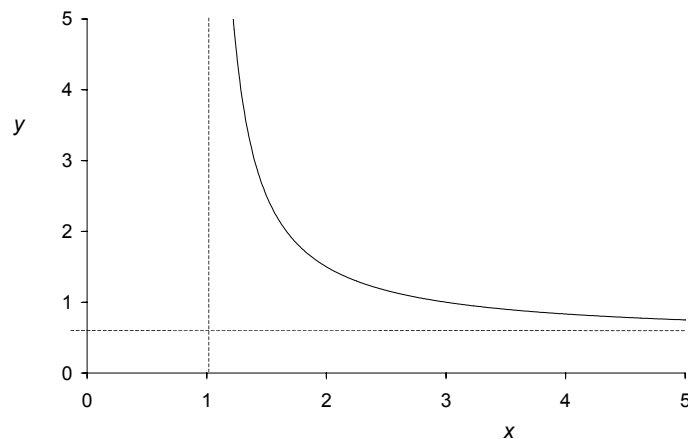
## INTRODUCTION

### *Rectangular Hyperbola*

The equation of a rectangular hyperbola is

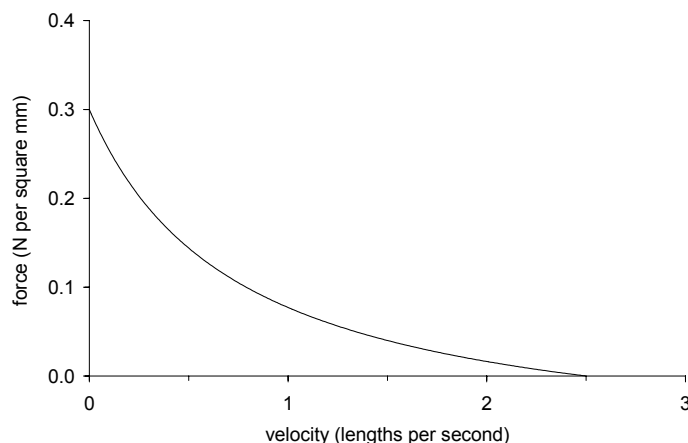
$$(x - x_0)(y - y_0) = \text{constant} . \quad (1)$$

A rectangular hyperbola has asymptotes  $y \rightarrow \infty$  at  $x = x_0$ , and  $x \rightarrow \infty$  at  $y = y_0$ . (A line is an asymptote to a curve if the curve approaches the line but never reaches it.) The graph below shows a rectangular hyperbola with asymptotes at  $x = 1.0$  and  $y = 0.5$ .



### *The Hill Equation*

Experiments have shown that the force a muscle or muscle fibre can produce decreases as the speed of contraction is increased. A typical curve is shown below.



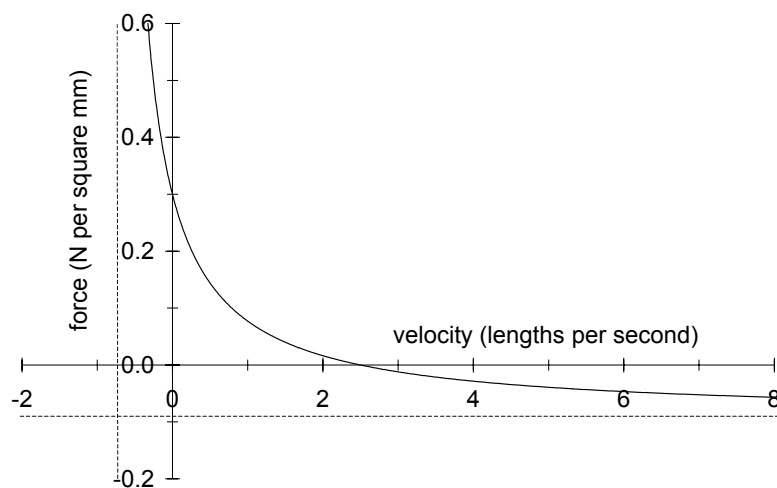
The force-velocity curve for a contracting muscle has the shape of a rectangular hyperbola, and may be written as

$$(F + a)(v + b) = (F_0 + a)b, \quad (2)$$

where  $F$  is the force generated by the muscle,  $v$  is the velocity of shortening,  $F_0$  is the maximum (isometric) force exerted by the muscle, and  $a$  and  $b$  are constants. The above equation is known as the Hill equation for muscle contraction, in honour of the British physiologist and biophysicist, A.V. Hill (1886–1977).

Comparing the Hill equation to the equation for a rectangular hyperbola, we see that the  $x$ -axis is the contraction velocity  $v$ , the  $y$ -axis is the muscle force  $F$ , and the *constant* is  $(F_0 + a)b$ . The asymptotes for the hyperbola are  $v \rightarrow \infty$  at  $F = -a$  and  $F \rightarrow \infty$  at  $v = -b$ . Note that in the Hill equation the asymptotes have negative values.

Shown below is a plot of the Hill equation for a muscle with  $F_0 = 0.3 \text{ N/mm}^2$ ,  $a = 0.09 \text{ N/mm}^2$  and  $b = 0.75 \text{ lengths/s}$ . The asymptotes are therefore  $F = -0.09 \text{ N/mm}^2$  and  $v = -0.75 \text{ lengths/s}$ . In a muscle contraction we are only interested in the part of the rectangular hyperbola that is in the region of positive values for  $F$  and  $v$ .



Starting from the Hill equation, one may show that the maximum speed of contraction of the muscle (where  $F = 0$ ) is given by

$$v_{\max} = \frac{bF_0}{a}. \quad (3)$$

The derivation of equation (3) is left as an exercise.

### **About Formulas in Microsoft Excel**

Formulas can help you analyse data on a worksheet. An *Excel* formula always begins with an equal sign (=). A simple formula contains constant values with operators to produce a new value. The Arithmetic Operators available in *Excel* are:

- + addition
- subtraction
- / division
- \* multiplication
- % percent
- ^ exponentiation

As an example, entering the formula  $=B4/25+100$  will divide the contents of cell **B4** by 25 and then add 100 to the result. *Excel* evaluates the operators from left to right. Use parentheses to group expressions in your formula if you wish to alter the order of evaluation.

A formula may be entered directly in the active cell, or by clicking on the formula bar and entering the formula there. A cell containing a formula normally displays the formula's resulting value in the worksheet. When you select a cell containing a formula, the formula is always displayed in the formula bar.

*Excel* has a large number of functions (some of which are relatively complex) to use in formulas. You can use the **Insert Function** command to help you select a function, assemble the arguments correctly, and insert the function into your formula. (To access the **Insert Function** command you may need to click the **Formulas** tab in the **Office Fluent Ribbon** at the top of the screen.) To find out more about formulas, see **Function reference** in the Microsoft Excel Help.

## PROCEDURE

Go to one of the University computers and log on to the computer in the usual way. To start the software running, go to the **Windows** toolbar, click on **Start**, select **Programs**, then **Microsoft Office Excel 2007**. *Microsoft Office Excel 2007* will start up and you will be presented with a blank worksheet (*Sheet1*) within a workbook (*Book1*). Give your worksheet a suitable name (e.g. *Muscle Force Data*) by double clicking on the **Sheet 1** tab and typing in the desired name. Now save your workbook to the computer hard disk. To do this, click the **Save** icon in the toolbar at the top of the screen. You will need to give your workbook with an appropriate name (e.g. *Muscle Force*). As usual, take care to save your file in an appropriate place and remember where you have put it.

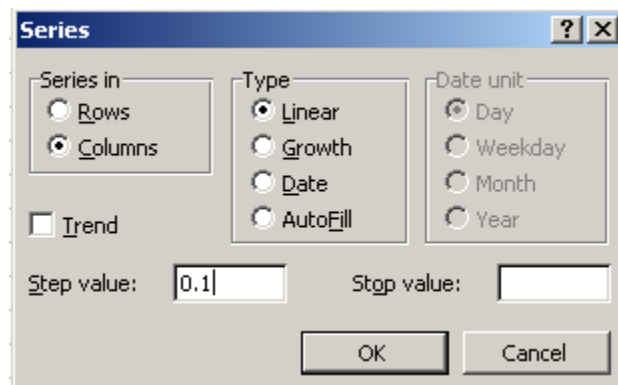
### **Force-Velocity Relation**

Here we will compare the force-velocity relation for a fast-twitch muscle fibre with that for a slow-twitch fibre. The force per cross-sectional area of a fast-twitch and a slow-twitch muscle fibre are about the same. That is, both types of fibre have the same value of  $F_0$  in the Hill equation. However, a fast-twitch fibre has a greater maximum speed of contraction (and hence has a higher value of  $b$ ).

Representative values for fast-twitch and slow-twitch muscle fibres are given below.

	Fast-twitch	Slow-twitch
$F_0$ (N/mm <sup>2</sup> )	0.25	0.25
$v_{\max}$ (lengths/s)	2.5	1.0
<i>constant</i>	0.3	0.3
$a$ (N/mm <sup>2</sup> )	0.075	0.075
$b$ (lengths/s)	0.75	0.30

In the first five columns in your worksheet, create headings called *Velocity*, *Fast-twitch*, *Value*, *Force*, and *Power*. In the *Velocity* column, make a list of velocity values from 0 to 5.0 lengths/s. To do this, type 0 in the first data cell (i.e. cell **A2**). Now use the mouse to select cells **A2** to **A52**. Select **Fill**, then **Series**, from the **Editing** group on the **Home** tab. The **Series** dialog box will appear.



Select **Columns** and **Linear**, then enter *0.1* in the **Step value** window. Click the **OK** button. This will create a series of values, 0.0, 0.1, 0.2, 0.3, 0.4, etc, down to 5.0.

Now enter the values of  $F_o$ ,  $v_{\max}$ , *constant*, *a*, and *b* for the *Fast-twitch* muscle fibre.

	A	B	C	D	E	F	G	H	I	J
				Force	Power					
1	Velocity	Fast-Twitch	Value							
2	0.0	$F_o$	0.25							
3	0.1	$v_{\max}$	2.5							
4	0.2	constant	0.3							
5	0.3	<i>a</i>	0.075							
6	0.4	<i>b</i>	0.75							
7	0.5									
8	0.6									
9	0.7									
10	0.8									

The muscle force may be calculated by re-arranging equation (2) to obtain

$$F = \frac{(F_o + a) b}{(v + b)} - a. \quad (4)$$

In cell **D2** we want to calculate the muscle force at a velocity of 0.0. In cell **D2** enter the formula `=(C2+C5)*C6/(A2+C6)-C5`. This is the *Excel* version of equation (4).

It may take you a while to work out what the *Excel* formula is doing. The `(C2+C5)*C6` part of the formula is adding the contents of cell **C2** and **C5**, and then multiplying by the contents of cell **C6**. That is, it is calculating the top half of the fraction in equation (4), i.e.  $(F_o + a) b$ . This calculation turns out to be  $(0.25 + 0.075) \times 0.75$ . By looking carefully at the *Excel* formula given above, you should be able to convince yourself that it is the *Excel* equivalent of equation (4).

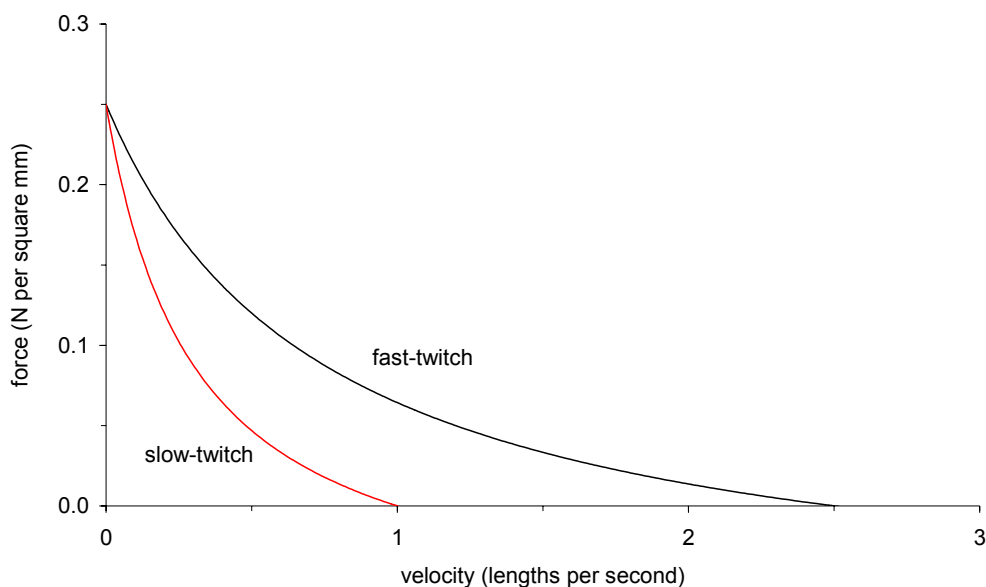
To do the calculations for cells **D3** to **D52**, select cells **D2** down to **D52**. From the **Editing** group on the **Home** tab, select **Fill**, then **Down**, then click the **OK** button. This is a lot faster than typing in the equation for every cell in the **D** column. However, you should always carefully check the contents of the cells to make sure that they are exactly as you want.

You may be wondering what the \$ symbols are in the *Excel* formula. You may have thought it OK to enter in cell **D2** the formula `=(C2+C5)*C6/(A2+C6)-C5`. This is, in fact, the correct formula for

equation (4), and will produce the correct force value for cell **D2**. However, when you come to use the **Fill Down** function, *Excel* will put the formula  $= (C3+C6)*C7/(A3+C7)-C6$  in cell **D3** and the formula  $= (C4+C7)*C7/(A4+C8)-C7$  in cell **D4**, etc. That is, *Excel* will assume that you want to use the next cells down in columns **A** and **C** when doing the calculations for column **D**. But in our situation, we do not want to do this. (Take some time to convince yourself that the above formulas are not correct.) Here we want to always use cells **C2**, **C5**, and **C6** because they contain the values of  $F_0$ ,  $a$ , and  $b$ . In *Excel*, these cells are referred to as “absolute references”. Cell references that change relative to where the formula is placed are referred to as “relative references”. Whenever we want *Excel* to use an absolute cell reference, we must put a “\$” symbol before the cell column and cell row. For example, we type,  $\$C\$2$ , rather than  $C2$ . Note that we write  $A2$  because we do want to use the next value down in the column (i.e. cell **A3**, then cell **A4**, then cell **A5**) when calculating the force values for column **D**.

	A	B	C	D	E	F	G	H	I	J
1	Velocity	Fast-Twitch	Value	Force	Power	Slow-Twitch	Value	Force	Power	
2	0.0	$F_0$	0.25	0.250	0.000	$F_0$	0.25	0.250	0.000	
3	0.1	$v_{max}$	2.5	0.212	0.021	$v_{max}$	1.0	0.169	0.017	
4	0.2	constant	0.3	0.182	0.036	constant	0.3	0.120	0.024	
5	0.3	$a$	0.075	0.157	0.047	$a$	0.075	0.088	0.026	
6	0.4	$b$	0.75	0.137	0.055	$b$	0.30	0.064	0.026	
7	0.5			0.120	0.060			0.047	0.023	
8	0.6			0.106	0.063			0.033	0.020	
9	0.7			0.093	0.065			0.023	0.016	
10	0.8			0.082	0.066			0.014	0.011	

Plot the curves of force versus velocity for the fast-twitch and slow-twitch fibres. The graph you should obtain is shown below. Note that at any given speed of shortening, the fast-twitch fibre can exert more force than the slow-twitch fibre, although their isometric forces are equal.

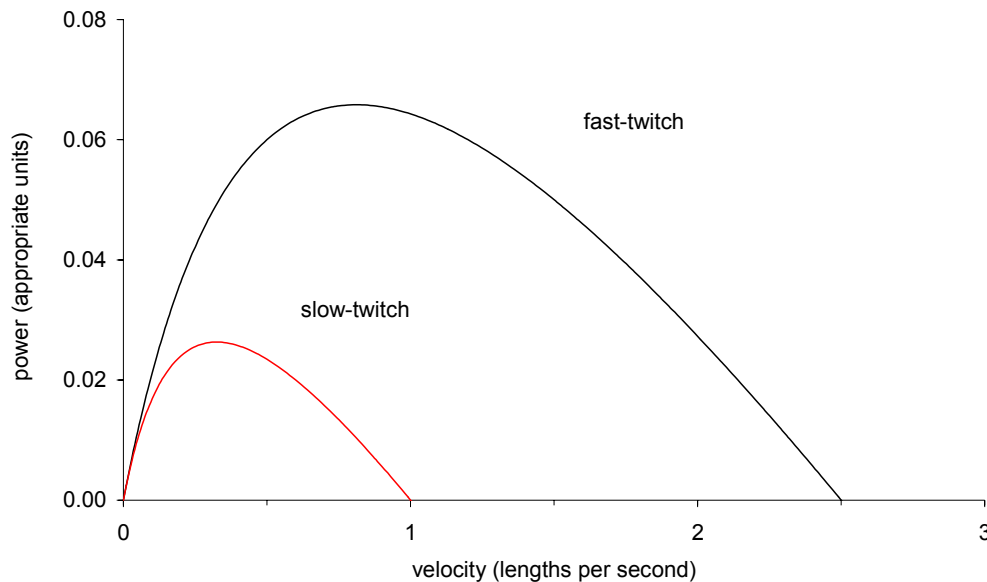


### Power-Velocity Relation

The power,  $P$ , produced by a muscle fibre is given by

$$P = Fv. \quad (5)$$

In your *Excel* spreadsheet, calculate the power for the fast-twitch and slow-twitch muscle fibres using equation (5). Plot the two curves of power versus velocity. The graph you should obtain is shown below. Note that the fast-twitch fibre produces more power and has a greater optimum contraction speed. (For this graph the units of power are  $\text{N}/\text{mm}^2 \cdot \text{lengths}/\text{s}$ .)



### Reference

MacIntosh, B. R., & Holash, R. J. (2000). Power output and force-velocity properties of muscle. In B. M. Nigg, B. R. MacIntosh, & J. Mester (Eds.), *Biomechanics and biology of movement* (pp. 193–210). Champaign, IL: Human Kinetics.

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