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Does the speed of shortening affect steady-state force depression in cat soleus muscle?

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Abstract

It has been stated repeatedly for the past 50 years that the steady-state force depression following shortening of an activated muscle depends on the speed of shortening. However, these statements were based on results from experiments in which muscles were shortened at different speeds but identical activation levels. Therefore, the force during shortening was changed in accordance with the force–velocity relationship of muscles: that is, increasing speeds of shortening were associated with decreasing forces, and vice versa. Consequently, it is not possible at present to distinguish whether force depression is caused by the changes in speed, as frequently stated, or the associated changes in force, or both. The purpose of this study was to test if force depression depends on the speed of shortening. We hypothesized that force depression was dependent on the force but not the speed of contraction. Our prediction is that the amount of force depression after shortening contractions at different speeds could be similar if the force during contraction was controlled at a similar level. Cat soleus muscles ($n = 7$) were shortened by 9 or 12 mm at speeds of 3, 9, and 27 mm/s, first with a constant activation during shortening (30 Hz), then with activation levels that were reduced (<30 Hz) for the slow speeds (3 and 9 mm/s) to approximate the shortening forces of the fast speed contractions (27 mm/s). If done properly, force depression could be precisely matched at the three different speeds, indicating that force depression was related to the force during the shortening contraction but not to the speed. However, in order to match force depression, the forces during shortening had to be systematically greater for the slow compared to the fast speeds of shortening, suggesting that force depression also depends on the level of activation, as force depression at constant activation levels can only be matched if the force during shortening, evaluated by the mechanical work, is identical. Therefore, we conclude that force depression depends on the force and activation level during shortening, but does not depend on the speed of shortening as has been assumed for half a century. These results support, but do not prove, the current hypothesis that force depression is caused by a stress-related cross-bridge inhibition in the actin–myosin overlap zone that is newly formed during muscle shortening.

Keywords: Muscle; Force depression; Cat; Soleus; History dependence

1. Introduction

It has been known for a long time, and is universally accepted, that the steady-state isometric force of a muscle is decreased if the isometric contraction is preceded by shortening of the activated muscle (e.g. Abbott and Aubert, 1952). This property is typically referred to as steady-state, or residual, force depression (Fig. 1). Force depression is known to increase with increasing magnitudes of shortening (Abbott and Aubert, 1952; Maréchal and Plaghki, 1979; Meijer et al., 1998; Josephson and Stokes, 1999). Furthermore, force depression is long lasting (i.e., in excess of 20 s; (Abbott and Aubert, 1952; Herzog et al., 1998)) and is associated with a decrease in the stiffness of the muscle or single fibre in the force-depressed compared to the isometric reference state (Sugi and Tsuchiya, 1988; Lee and Herzog, 2003). Also, force depression following

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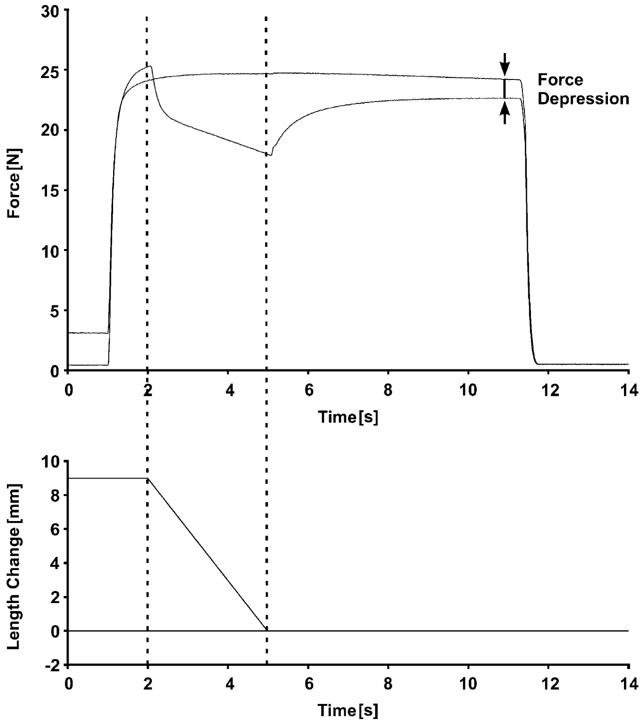

Fig. 1. An isometric-shortening-isometric contraction and a purely isometric reference contraction at the same final muscle length. The difference in force after the test contraction has reached steady-state force following shortening is defined as the steady-state force depression.

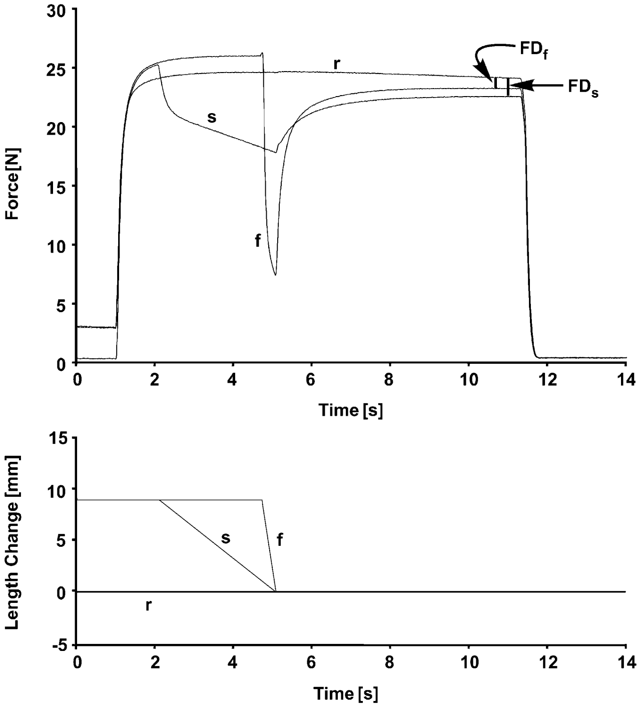

Fig. 2. Force time histories of an isometric reference contraction (*r*) and two isometric-shortening-isometric test contractions performed at a slow (*s*—3 mm/s) and a fast (*f*—27 mm/s) shortening speed. Note how the fast shortening contraction (*f*) is associated with much lower forces than the slow shortening contraction (*s*), a result that is perfectly explained with the force–velocity properties of muscle (Hill, 1938). However, because of the force–velocity relationship, it is not clear if it is the speed, the force or both the speed and force that produce the difference in force depression for the two test contractions. FD_s = force depression for the slow contraction. FD_f = force depression for the fast contraction. $FD_s > FD_f$.

shortening can be abolished instantaneously by deactivating the muscle just long enough for force to drop to zero (Abbott and Aubert, 1952; Herzog and Leonard, 1997).

It has also been argued that force depression is directly influenced by the speed of shortening (Abbott and Aubert, 1952; Maréchal and Plaghki, 1979; Sugi and Tsuchiya, 1988; Meijer et al., 1997; Herzog and Leonard, 1997; Morgan et al., 2000; De Ruiter et al., 2000; Lee and Herzog, 2003). This argument has been based on experiments in which a muscle was shortened by a given magnitude and with a given activation, but at different speeds, and the force depression was observed to consistently increase with decreasing speeds of shortening. However, for these experimental conditions, the changes in speed of shortening would also be associated with changes in the force during shortening, in accordance with the force–velocity properties of skeletal muscles ((Hill, 1938); Fig. 2). Maréchal and Plaghki (1979) used a modified form of the Hill force–velocity relationship to relate the observed force deficit to the shortening speed of the muscle. They suggested that the force deficit was related to the force during release. Their experiments were performed on the sartorius muscle of the frog at 0 °C. Morgan et al. (2000) reported that given the shape of the force–velocity curve, faster shortening would reduce the force deficit and that this was most likely due to differences in shortening speed between strong and weak sarcomeres being reduced at high compared to slow speeds of shortening. The experiments by Morgan et al. (2000) were performed on cat soleus muscle.

However, in both sets of experiments, muscle activation was held constant during the contraction, and so the force during shortening changed as a function of the speed of shortening. Therefore, it was not possible to determine whether the observed changes in force depression were associated with the changes in speed or the changes in force during shortening, or both.

Recently, we performed experiments in which the cat soleus muscle was shortened by a given amount and a fixed speed, but force was changed, either by altering the voltage or the frequency of nerve stimulation (Herzog and Leonard, 1997). Force depression for these conditions was directly proportional to the force produced during the shortening phase, providing direct evidence that the force during shortening influences force depression (Fig. 3). However, these results gave no information about the possible effect of the speed of