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The Steadiness of Lengthening Contractions

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When a muscle is used to displace a load, the change in length experienced by the muscle depends on the relative magnitudes of the muscle torque and the opposing load torque about the joint. When the muscle and load torques are equal, for example, the net torque about the joint is zero and the muscle performs an isometric contraction. When the magnitude of the muscle torque is greater than the load torque, the load will be lifted as the muscle performs a shortening contraction. In contrast, when the magnitude of the load torque is greater than the muscle torque, the load will be lowered as the muscle performs a lengthening contraction. If the task is to lower a load with a prescribed trajectory, the muscle torque must be controlled precisely so that it is slightly less than the load torque throughout the entire movement.

Historically, research on differences between shortening and lengthening contractions has focused on the mechanical properties of muscle and on the adaptive capabilities of the neuromuscular system (Enoka, 1996). The classic force-velocity relation of muscle, for example, indicates that the maximum force a muscle can exert at a given contraction velocity is quite different for shortening and lengthening contractions (Flitney & Hirst, 1978; Hill, 1938; Katz, 1939) and that EMG amplitude is lower during lengthening contractions at comparable forces (Bigland & Lippold, 1954). Similarly, the strength gain achieved after several weeks of physical training is specific to the type of contraction performed in the training program (Higbie et al., 1996; Hortobagyi et al., 1996; Hortobagyi et al., 1997). Furthermore, the use of lengthening contractions appears to result in greater muscle damage and soreness compared with other types of contractions (Chleboun et al., 1998; Malm et al., 1999; McHugh et al., 1999; Proske & Morgan, 2001; Whitehead et al., 1998).

Accumulating evidence suggests that control strategies used by the nervous system differ across the contraction types. Such findings include the inability of subjects to maximally activate a muscle during a voluntary lengthening contraction (Aagaard et al., 2000; Webber & Kriellaars, 1997; Westing et al., 1990) and differences in the magnitude of evoked potentials between shortening and lengthening contractions (Abbruzzese et al., 1994; Nardone & Schieppati, 1988; Sekiguchi et al., 2001). Furthermore, there is an apparent greater resistance to fatigue during voluntary but not during artificially evoked lengthening contractions (Binder-Macleod & Lee, 1996; Tesch et al., 1990), greater synchronization of motor unit discharge during lengthening contractions (Semmler et al., 2001), and increased cortical potentials as measured by electroencephalography during lengthening contractions (Fang et al., 2001). The most controversial of these observations, however, has been reports of differences in the recruitment order of motor units during lengthening compared with shortening contractions (Howell et al., 1995; Nakazawa et al., 1993; Nardone et al., 1989; Nardone & Schieppati, 1988; c.f. Bawa & Jones, 1999; Christova & Kossev, 2000; Kossev & Christova, 1998; Sogaard et al., 1996).

Because the ability to perform a steady contraction can be influenced by the discharge behavior of motor units (Laidlaw et al., 2000; Taylor et al., 2000), we have compared the steadiness of shortening and lengthening contractions. Steadiness is measured as the fluctuations of force or acceleration in the time domain but can also be expressed in the frequency domain; selected bandwidths within the frequency domain are quantified as tremor (McAuley & Marsden, 2000). The functional significance of steadiness is that it influences the ability of an individual to exert a precise force and to perform consistent movement trajectories. Although the steadiness of isometric and shortening contractions has been studied for over a century (Fullerton & Cattell, 1892), the steadiness of lengthening contractions has received much less attention. The purpose of this chapter is to examine factors that contribute to differences in steadiness between shortening and lengthening contractions.

Lengthening Contractions Are Less Steady Within and Across Trials

Several different experimental tasks have been used to compare steadiness of shortening and lengthening contractions (Figure 1). Such tasks have included matching velocity or force templates, movements at various speeds, and movements with different types of loads (e.g., inertial, isokinetic).

The findings of experiments with inertial loads indicate that when subjects attempt to match a constant-velocity template with light loads, the performance is less steady during lengthening contractions compared with shortening contractions (Burnett et al., 2000; Graves et al., 2000; Laidlaw et al., 2000; Tracy et al., 2002). In these studies, the shortening contractions typically preceded the lengthening contractions and the movement speed was slow (<0.5 rad/s). When the order of the contractions was reversed, however, no differences in steadiness were found between shortening and lengthening contractions (Laidlaw et al., 2001). To eliminate the potential order effect and examine the influence of movement speed on steadiness, we compared the steadiness of shortening and lengthening contractions that were performed at various speeds in a random order. Each contraction was performed separately and was always preceded by an isometric contraction (Christou et al., 2001). We found that the steadiness of a contraction decreased with movement speed and that lengthening contractions produced greater fluctuations in acceleration compared with shortening contractions. Furthermore, the declines in steadiness with movement speed were greater for the lengthening contractions compared with shortening contractions.

The focus of the above studies was the fluctuations of acceleration within each trial. However, motor output also varies across trials. Trial-to-trial variability is often assessed from rapid contractions (~200 ms) that are performed repetitively, in which the subjects attempt to match a prescribed force-time parabola (Carlton & Newell, 1993; Christou & Carlton, 2001). Two such studies have examined trial-to-trial variability of the knee extensor muscles during shortening and lengthening contractions performed on an isokinetic dynamometer (Christou & Carlton, 1999; Christou & Carlton, 2002). The first study examined the trial-to-trial variability of shortening and lengthening contractions performed by young individuals over a range of absolute target forces (50-250 N), whereas the second study compared the performance of young and old individuals to relative target forces (20-90% MVC). The two studies found that the trial-to-trial variability in peak force, force-time integral, and temporal characteristics of the movement was greater during lengthening contractions compared with shortening contractions (Figure 1C). A similar result was observed when subjects performed constant-velocity contractions while lifting and lowering an inertial load with the first dorsal interosseus muscle (Christou et al., 2001).

With the exception of one study, current evidence indicates that lengthening contractions are not only less steady than shortening contractions within a trial but also are more variable across trials. Although these findings are consistent across various experimental tasks, the differences between shortening and lengthening contractions appear to be greater with light loads and during rapid tasks.

Old Adults Are Less Steady During Lengthening Contractions

Several studies indicate that the ability of old adults to perform a steady isometric contraction is impaired (Burnett et al., 2000; Keen et al., 1994; Laidlaw et al., 2000; Laidlaw et al., 1999; Semmler et al., 2000b; Tracy and Enoka, 2002). Some of these studies have examined the effect of age on the steadiness of shortening and lengthening contractions. Findings from these studies suggest that the ability of old individuals to perform steady lengthening contractions declines to a greater extent than that for shortening contractions. For example, old adults exhibit greater fluctuations in displacement (Laidlaw et al., 2000) and acceleration (Burnett et al., 2000) of the index finger than young adults when lowering light inertial loads with the first dorsal interosseus muscle (Figure 2A). Similarly, fluctuations in acceleration while lowering light loads with the elbow flexor muscles were greater for old adults compared with young adults, especially during lengthening contractions (Graves et al., 2000) (Figure 2B).

Not all studies, however, have found that the steadiness of lengthening contractions is reduced in old adults. For example, similar fluctuations were observed in acceleration and displacement for the elbow flexor (Tracy et al., 2002) and knee extensor (Tracy & Enoka, 2002; Tracy et al., 2002) muscles of young and old adults. Although old adults produce less steady movements while lifting and lowering light loads (<15% maximum) with the first dorsal interosseus and elbow flexor muscles (Burnett et al., 2000; Graves et al., 2000; Laidlaw et al., 2000), old adults are at least as steady as young adults when lifting heavier loads (Burnett et al., 2000; Graves et al., 2000) (Figure 2). Furthermore, when the lengthening contractions preceded shortening contractions, steadiness was similar for the young and old subjects (Laidlaw et al., 2001). In addition, when active old adults are compared with young adults at various movement speeds during separate lengthening and shortening contractions that are preceded by an isometric contraction, the fluctuations in acceleration are less in old adults (Christou et al., 2001). Nonetheless, the relative increase in the standard deviation of acceleration with speed is greater for old adults during lengthening contractions. These findings indicate that differences in the steadiness of lengthening contractions between young and old adults vary with the muscle group used, the type of task performed, and the speed of the movement.

When old adults are asked to perform the same contraction repetitively, however, their performance is consistently more variable, especially during lengthening contractions. For example, when active old adults perform constant-velocity contractions while lifting or lowering loads with the first dorsal interosseus muscle, they exhibit greater trial-to-trial variability compared with young adults during lengthening contractions (Christou et al., 2001). Similarly, old adults demonstrate greater trial-to-trial variability than young adults when they reproduce a force-time parabola (20-90% MVC) with the knee extensor muscles (Christou & Carlton, 2002). This variability, which is most evident during lengthening contractions, is the result of an impaired ability to reproduce the timing characteristics of the contraction (Figure 3).

Findings from the various studies presented suggest that the ability of old adults to perform steady lengthening contractions declines only with light loads. The variability in force from trial-to-trial, furthermore, is impaired especially during lengthening contractions. Clearly, the steadiness of lengthening contractions performed by old adults is influenced by such factors as physical activity, experimental task, and the load lifted.

Steadiness of lengthening contractions varies with muscle group

A series of studies in different muscle groups suggest that the difference in steadiness between shortening and lengthening contractions is dependent on the muscle group studied. For example, fluctuations in displacement during contractions of the first dorsal interosseus muscle were greater while lowering loads compared with lifting loads that ranged from 2.5 to 10% of maximum (Laidlaw et al., 2000). A similar finding was observed for the fluctuations in acceleration while lowering loads with the first dorsal interosseus muscle (Burnett et al., 2000). In these two studies, the differences in steadiness between shortening and lengthening contractions were attributable to the greater fluctuations during lengthening contractions in old adults compared with young adults. Nevertheless, subsequent findings suggest that the lengthening contractions with the first dorsal interosseus also appear to be less steady in young adults compared with their shortening contractions (Christou et al., 2001; Semmler et al., 2001). Comparable results were also found while lifting and lowering loads (10 and 15% of maximum) with the elbow flexor muscles (Graves et al., 2000). In contrast, fluctuations in displacement were similar during shortening and lengthening contractions of the knee extensor muscles with loads that ranged from 5 to 50% of maximum (Tracy & Enoka, 2002).

Although the experimental design and methods were similar in these separate studies on hand, arm, and leg muscles, the studies used different subject cohorts. Accordingly, subtle differences in the characteristics of the subject samples might at least partially explain differences observed between the studies. To minimize this confounding influence, we have measured fluctuations in acceleration during shortening and lengthening contractions of the first dorsal interosseus, elbow flexor, and knee extensor muscles in the same individuals (Tracy et al., 2002). A preliminary analysis of these data provides further evidence of differences among muscle groups.

Lengthening contractions with light loads (5-10% of maximum) were less steady compared with shortening contractions for the first dorsal interosseus and the knee extensor muscles, but not with the elbow flexor muscles (Tracy et al., 2002) (Figure 4). Furthermore, it appears that the first dorsal interosseus exhibits a greater difference between shortening and lengthening contractions with the lightest load (5% of maximum) compared with the elbow flexor and knee extensor muscles (Figure 4).

Taken together, these findings suggest that differences in steadiness between shortening and lengthening contractions vary across muscle groups. The differences between studies, therefore, appear to be confounded by differences in experimental design and the muscle examined.

Neural Mechanisms

Several features of the activation signal generated by the nervous system can influence the steadiness of lengthening contractions. These include details of the motor output from the spinal cord, the organization of the descending command, and the integration of feedback from sensory receptors.

Recent interest in the neural control of lengthening contractions was heightened by the observation (Nardone et al., 1989) that the recruitment order of motor units may deviate from that prescribed by the Size Principle (Henneman, 1957). Nardone et al. (1989) found that high-threshold motor units were selectively activated during lengthening contractions with the triceps surae muscles. Furthermore, when motor unit activity was recorded from the first dorsal interosseus while lifting and lowering a load, Howell et al. (1995) found that three high threshold motor units out of 21 recorded were selectively recruited during lengthening contractions. In contrast, a number of studies have failed to find evidence of selective activation of high-threshold motor units during lengthening contractions (Bawa & Jones, 1999; Christova & Kossev, 2000; Kossev & Christova, 1998; Laidlaw et al., 2000; Sogaard et al., 1996). These results suggest that although recruitment order may be disrupted during lengthening contractions, the most common strategy is not to alter the recruitment order (Enoka & Fuglevand, 2001).

Nonetheless, muscle activity can shift from slow to fast muscles during lengthening contractions. Such findings were observed in the triceps surae muscles when shortening contractions involved greater activation of the soleus muscle (80% type I muscle fibers) and lengthening contractions involved greater activation of the gastrocnemius muscle (50 % type II muscle fibers) (Nardone & Schieppati, 1988). Selective activation of muscles during lengthening contractions has also been observed during movements produced by the elbow flexor muscles (Nakazawa et al., 1993). The relative activation of the brachioradialis muscle changed through the range of motion during lengthening contractions but not during shortening contractions. Altered distribution among synergist muscles during lengthening contractions, therefore, may potentially influence the steadiness of a movement.

The most consistent difference in motor output between shortening and lengthening contractions is the amplitude of muscle activation. A number of studies have found that the EMG amplitude is significantly less during lengthening contractions compared with shortening contractions with similar muscle torques (Bawa & Jones, 1999; Burnett et al., 2000; Christou et al., 2001; Howell et al., 1995; Kossev &

Christova, 1998; Laidlaw et al., 2000; Nardone & Schieppati, 1988; Sogaard et al., 1996). The differences in EMG activity during voluntary movements become greater with movement speed (Christou et al., 2001; Kossev & Christova, 1998; Westing et al., 1991). Similarly, reduced levels of activation are observed in experiments where motor evoked potentials and H-reflexes are elicited during shortening and lengthening contractions (Abbruzzese et al., 1994; Nardone et al., 1989; Sekiguchi et al., 2001). This reduction in EMG amplitude during lengthening contractions is at least partially due to a decrease in discharge rate of the motor units (Kossev & Christova, 1998; Laidlaw et al., 2000; Sogaard et al., 1996). For example, motor units discharge at lower frequencies during lengthening contractions with low loads (<10% of maximum) in the first dorsal interosseus and biceps brachii muscles (Howell et al., 1995; Sogaard et al., 1996) and with moderate loads (50% of maximum) in the triceps brachii (Kossev & Christova, 1998). At lower discharge rates, the contractions of individual motor units will be less fused and will cause greater fluctuations in muscle force during low-force contractions (Fuglevand et al., 1993). Furthermore, the discharge rate of motor units is more variable during eccentric contractions (Laidlaw et al., 2000), which computer simulations indicate can cause greater fluctuations in force (Taylor et al., 2000).

The discharge of action potentials by motor units may also become more correlated during lengthening contractions. The summation of twitch forces that result from this synchronous discharge of motor units can potentially contribute to the observed differences in steadiness between shortening and lengthening contractions (Semmler, 2002). For example, when the level of motor unit synchronization was varied while keeping all other factors constant, the steadiness of a computer-simulated contraction declined with increases in the level of synchronous discharge (Yao et al., 2000). Experimental evidence also provides support for this finding. Synchronous discharge was quantified in pairs of motor units during isometric, shortening, and lengthening contractions with the first dorsal interosseus muscle (Semmler et al., 2001; Semmler et al., 2000a). Lengthening contractions were less steady and exhibited higher levels of synchronization compared with shortening contractions. Furthermore, the synchronization of motor unit discharge was correlated with the steadiness of isometric and anisometric contractions.

Because motor unit synchronization is an index of the strength of common input to motor neurons (Semmler, 2002), the descending command may differ during lengthening contractions. Several studies support this possibility. For example, responses evoked in the biceps brachii by magnetic and electrical stimulation of the motor cortex were reduced while lowering compared with lifting a load (Abbruzzese et al., 1994). Furthermore, differences in motor evoked potentials between shortening and lengthening contractions have been observed during various intensities of electrical stimulation of the motor cortex (Sekiguchi et al., 2001). Specifically, the plateau value and maximum slope of the sigmoidal curve that characterizes the relation of evoked potential size with intensity of stimulation were lower for lengthening contractions. In addition, movement-related cortical potentials, as measured by electroencephalography, were greater during lengthening contractions compared with shortening contractions (Fang et al., 2001). These findings indicate that a constant excitatory input to the motor cortex during the two types of contractions results in a reduced output for lengthening contractions, whereas when the output is the same between the two contractions the cortical input is greater for lengthening contractions.

In addition to differences in the motor output from the spinal cord and the descending command, lengthening contractions appear to involve qualitative differences in the integrations of sensory feedback. For example, data from both primates (Schieber & Thatch, 1985) and humans (Burke et al., 1978) show that muscle spindle afferents discharge at a higher rate and for a longer duration during lengthening contractions. Furthermore, the sign of the short-latency response to a cutaneous stimulus is reversed during lengthening contractions compared with shortening contractions (Haridas et al., 2000). One potential explanation for these differences in reflex responses is that the role of sensory feedback is more critical during lengthening compared with shortening contractions. Experimental evidence suggests, for example, that when the contribution of sensory feedback to the control of a movement is limited, such as occurs in rapid movements, there is a further reduction in the steadiness of lengthening contractions (Christou et al., 2001).

In summary, the motor output from the spinal cord to muscle differs during lengthening compared with shortening contractions. These differences, which include the recruitment of fewer motor units, a lower and more variable discharge rate, and a greater amount of motor unit synchronization, likely contribute to the differences in steadiness between shortening and lengthening contractions. Variation in the motor output is a consequence of differences in the net input received by the motor neurons, due to changes in both the descending drive and the integration of sensory feedback.

Figure Legends

Figure 1. Representative data for shortening and lengthening contractions as performed in three different tasks. Panels A and B show position (top trace) and acceleration (bottom trace) during shortening and lengthening contractions performed in a fixed (A) or a randomized order (B). Panel C shows representative force data (top) from a single trial in which a subject attempted to match a force-time parabola during repetitive rapid contractions on an isokinetic dynamometer. The variability of impulse (force-time integral) around the mean for 40 separate contractions is shown at the bottom of Panel C.

Figure 2. Standard deviation (SD) of acceleration was greater for old individuals during slow lengthening contractions with light loads for the first dorsal interosseus (A) and elbow flexor muscles (B).

Figure 3. Between-trial variability (coefficient of variation, CV) for the force-time curve integral (impulse, A) and the time to peak force (B) during shortening and lengthening contractions with the knee extensor muscles. Old adults exhibited greater variability for impulse and time to peak force during lengthening contractions.

Figure 4. Standard deviation (SD) of acceleration during lengthening contractions expressed as a percentage of the value obtained for the shortening contractions performed with the first dorsal interosseus (FDI), elbow flexor, and knee extensor muscles. Values greater than 100% indicate a less steady performance during the lengthening contractions. The difference between lengthening and

shortening contractions appears to be greater for the first dorsal interosseus and knee extensor muscles compared with the elbow flexor muscles. For all three muscles, lengthening contractions appear to be less steady with light loads and steadier with heavy loads, compared with shortening contractions.

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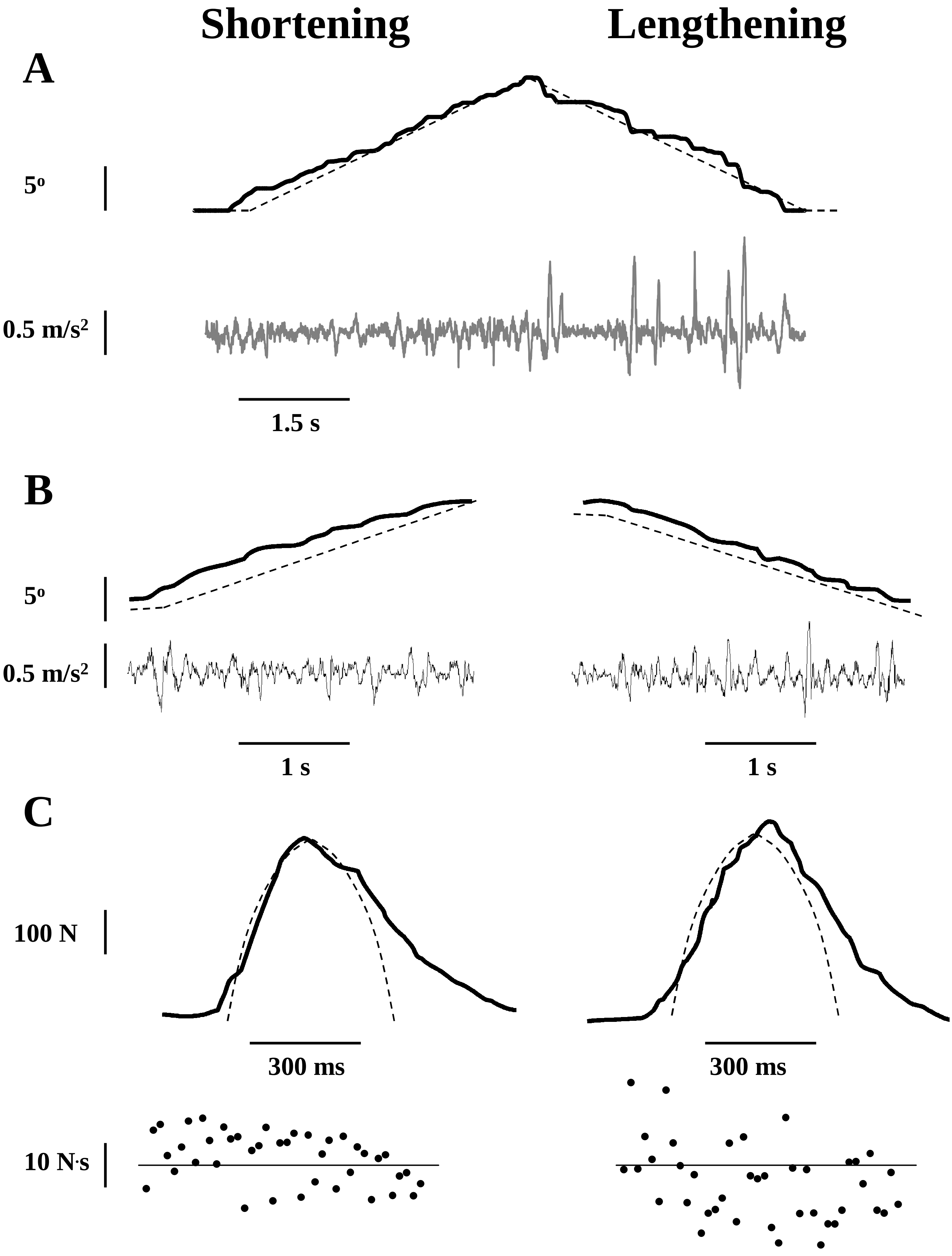
Figure 1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300 ms
10 N·s

Figure 2

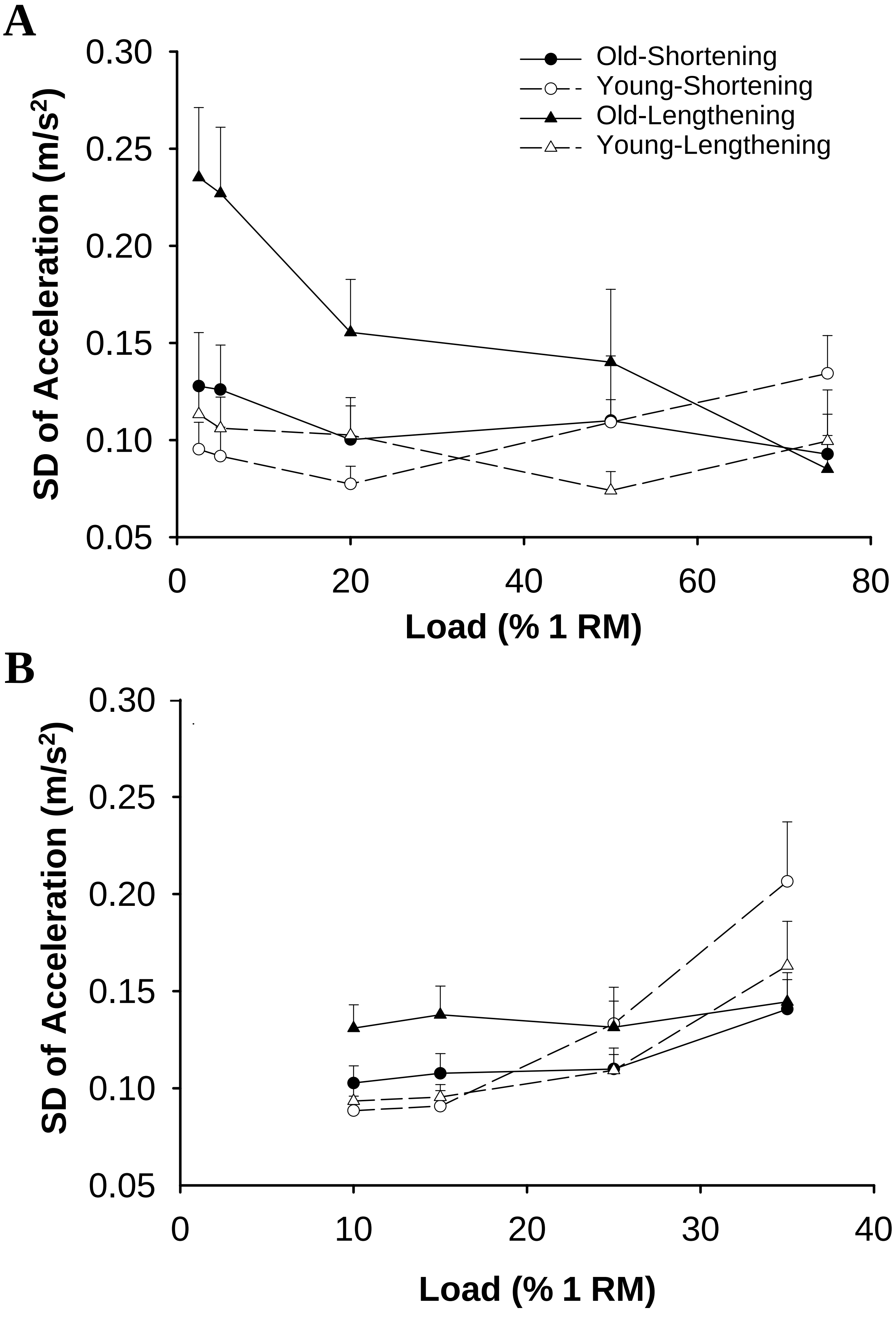

A
SD of Acceleration (m/s²)
0.30
0.25
0.20
0.15
0.10
0.05
Old-Shortening
Young-Shortening
Old-Lengthening
Young-Lengthening
0
20
40
60
80
Load (% 1 RM)
B
SD of Acceleration (m/s²)
0.30
0.25
0.20
0.15
0.10
0.05
0
10
20
30
40
Load (% 1 RM)

Figure 3

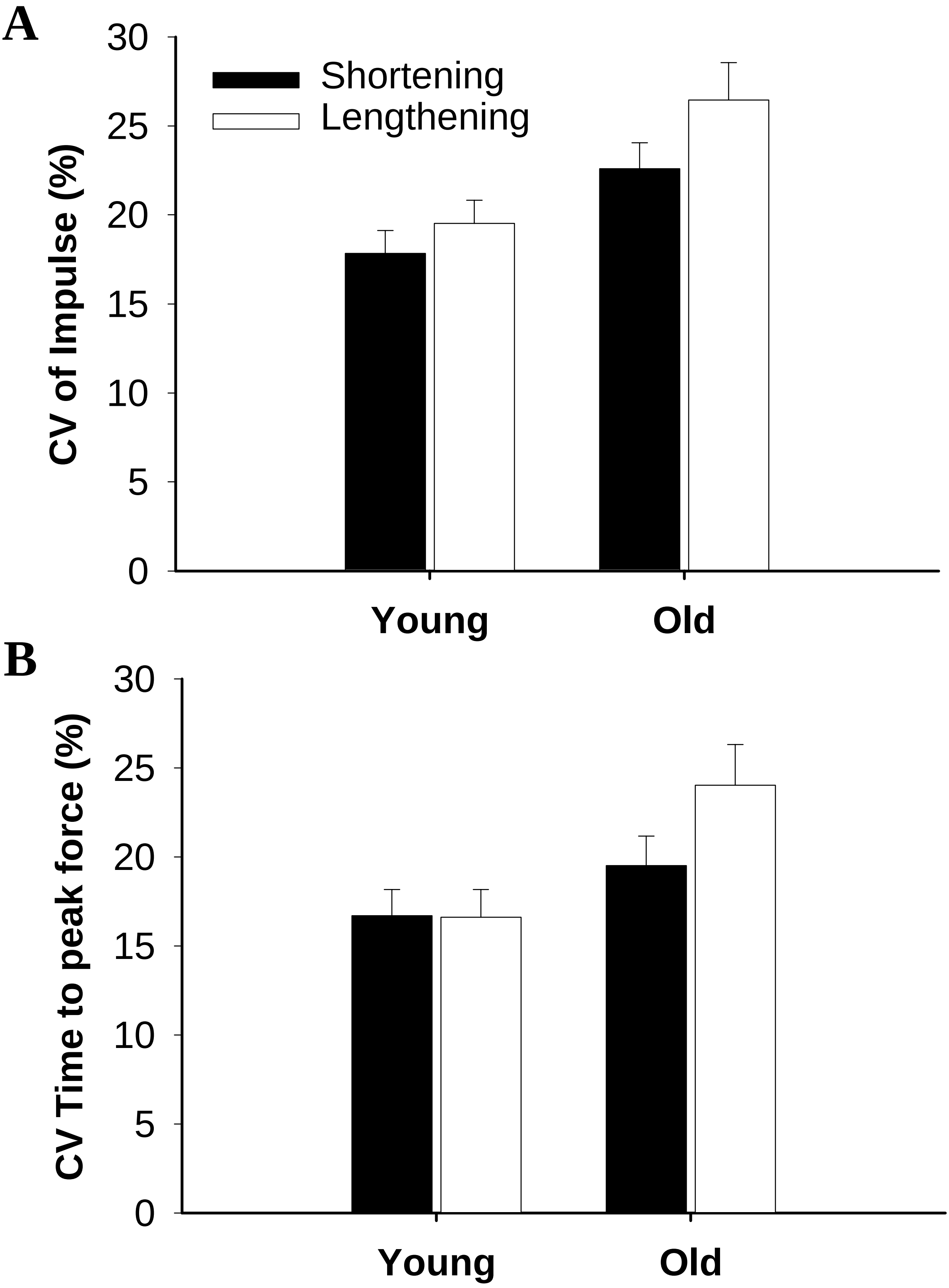
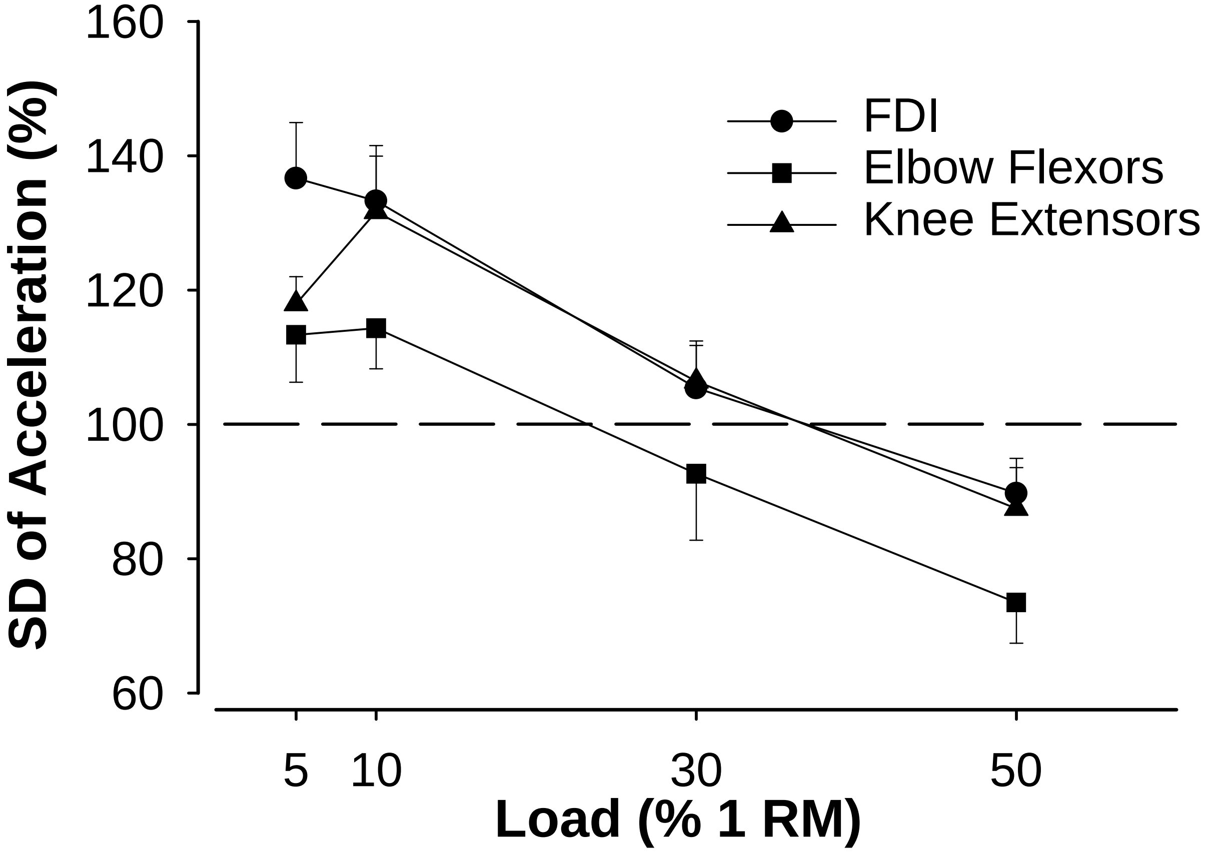

A
30
25
20
15
10
5
0
Shortening
Lengthening
CV of Impulse (%)
Young
Old
B
30
25
20
15
10
5
0
CV Time to peak force (%)
Young
Old

Figure 4



SD of Acceleration (%)
160
140
120
100
80
60
FDI
Elbow Flexors
Knee Extensors
5
10
30
50
Load (% 1 RM)