Voluntary activation. A muscle is activated voluntarily when force is produced by the recruitment of motoneurons through increased descending drive from the motor cortex. This activation is usually deliberate and is accompanied by a sense of effort. There are many other influences on motoneurons at rest and during voluntary contractions that may alter the response of motoneurons to descending drive. Such influences include excitatory and inhibitory sensory feedback, as well as alterations in motoneuron properties that may make them more or less responsive to synaptic input (21). However, descending drive from the motor cortex is the major determinant of the timing and strength of voluntary contractions.

Qualitatively, voluntary activation of a muscle is the recruitment of its motor units by increased descending drive. As a quantity, voluntary activation has been defined as the level of voluntary drive during an effort (12). What twitch interpolation measures is the drive by the motoneurons to the muscle and how this translates into force. Thus measured voluntary activation is the proportion of maximal possible muscle force that is produced during a voluntary contraction. It does not quantify the descending drive reaching the motoneurons or whether motoneuron firing rates are maximal and does not take into account the source of drive to the motoneurons.

Principle of twitch interpolation. During increasing strengths of voluntary muscle contraction, motor units are recruited progressively and increase their firing rates. The principle of twitch interpolation is to stimulate the peripheral nerve during a voluntary contraction to add, in most motor axons, an additional action potential to those produced voluntarily (7, 19). If any individual motor unit is not firing fast enough to produce its maximal force then this additional action potential will evoke an increment in force from the muscle fibers of the motor unit. The sum of increments from different motor units produces a twitchlike increment in force from the whole muscle. The more motor units recruited in a contraction and the faster they are firing, the smaller the superimposed twitch. During a contraction that produces maximal muscle force, all motor units in the muscle should be recruited and all firing fast enough to produce fused contractions of their muscle fibers.

The principle of twitch interpolation is supported by an inverse relationship between the amplitude of the twitch evoked by an interpolated stimulus and voluntary force output at the moment of stimulation. Such a relationship has been reported for adductor pollicis, biceps brachii, quadriceps, ankle plantarflexors, tibialis anterior, masseter, trapezius, and the diaphragm (e.g., 1, 6, 7, 10, 13, 18, 19, 23). Thus twitch interpolation does give a measure of voluntary activation in many muscle groups. However, easy quantification of voluntary activation, using the formula, Voluntary activation = 100 × [1 - (superimposed twitch/potentiated resting twitch)], relies on near linearity of the inverse relationship, so that calculated voluntary activation equals the percentage of maximal force that the subject is generating with the tested muscle(s).

Model of twitch interpolation. A computer model of a hand muscle with a pool of motor units with realistic motor unit numbers, recruitment, firing rates, and twitch and tetanus properties was developed (15). In the model, superimposed twitches were generated by twitch interpolation, which consisted of addition of an extra action potential to each motor axon that was not refractory at the moment of stimulation. As peripheral nerve stimulation produces antidromic as well as orthodromic potentials, collision with subsequent “voluntary” potentials was incorporated. Although the relationship between input to the motoneurons and force output was sigmoidal so that large increases in “excitation” to the motoneurons were needed to produce small falls in twitch amplitude in near-maximal contractions, the model predicted a linear inverse relationship between the superimposed twitch and contraction strength. Thus modeling supports the proposal that twitch interpolation can measure the proportion of muscle force recruited voluntarily, i.e., “voluntary activation.”

Practical twitch interpolation. In contrast to the model, most published graphs of the amplitude of the superimposed twitch against the force of voluntary contraction show nonlinearities. Belanger and McComas (7) described the curve as S-shaped with a convex up portion at low contraction strengths and a concave up portion at high contraction strengths. Often curves fitted to the relationship approach the x-axis at a very shallow
angle or even asymptotically. Thus extrapolation of these curves can predict maximal muscle forces that are impossible. Both methodological and physiological issues contribute to nonlinearities (see Fig. 1 and Refs. 3, 12, 22). Problems that influence the whole relationship include shortening of the muscle fibers during contraction through compliance of the tendon, myograph, and/or coupling to the myograph (Fig. 1, a–c; Refs. 3, 4, 17), and lack of potentiation of the muscle recruited into the twitch (Fig. 1d; Ref. 11). Reduction of the superimposed twitch by antidromic collision is likely to be most prominent in medium to strong contractions (Fig. 1e; Ref. 15). Most commonly, voluntary activation is of interest during maximal efforts and it is here that it is most variable. Factors that can lead to a reduced or absent superimposed twitch at high but submaximal forces include poor resolution and frequency response of the myograph (Fig. 1f; Ref. 14) and stimulation of antagonists (Fig. 1g) by stimulus spread (e.g., to triceps with biceps stimulation) or innervation through the stimulated nerve (e.g., femoral nerve innervates the knee flexor sartorius as well as the knee extensors). Variability is also introduced by factors that can alter voluntary force output without altering voluntary activation of the target muscle (Fig. 1h). These include the actions of other muscles such as differential voluntary activation of synergists (3, cf. Ref. 25) and varying voluntary activity in antagonists, as well as lengthening of muscle fibers during contraction (5, 8). Many, although not all, of these sources of error can be minimized by careful experimental technique.

Despite possible errors and inherent variability in measuring voluntary activation with twitch interpolation, the technique shows changes in maximal activation with interventions within subjects (e.g., with fatigue, altered muscle length, and hyperthermia; Refs. 12, 20, 24) and between control and patient groups (e.g., Refs. 2, 9, 16). Thus it is a useful technique that gives a practical measure of voluntary drive to the muscle.

Conclusion. Does twitch interpolation provide a valid measure of voluntary activation of muscle? If we consider that voluntary activation of muscle is a measure of how much of the muscle’s possible force is produced by a voluntary contraction, then twitch interpolation does provide a valid measure. Twitch interpolation does not measure descending drive to the motoneurons or take into account the nonlinear input-output relationship of the motoneuron pool (15). However, it does give a measure of drive to the muscle. Its underlying principle is sound, although there are numerous practical pitfalls. Ideal twitch interpolation requires a muscle that has very short tendons, which is the only muscle acting about its joint, and that has no source of compliance between the muscle and the force transducer. Thus measurement of voluntary activation is never ideal in the human body but it is sufficiently good to reveal changes with physiological interventions and with pathology.

REFERENCES

Janet L. Taylor
Prince of Wales Medical Research Institute
University of New South Wales
Randwick, New South Wales, Australia
e-mail: jl.taylor@powmri.edu.au

COUNTERPOINT: THE INTERPOLATED TWITCH DOES NOT PROVIDE A VALID MEASURE OF THE VOLUNTARY ACTIVATION OF MUSCLE

The interpolated twitch technique (ITT) was first used by Merton (17) who superimposed an evoked stimulation on a twitch of one muscle in the extensor digitorum longus (EDL) and recorded the sum of the twitch and the evoked twitch. The evoked twitch was then assumed to represent the maximum possible twitch of the muscle. This assumption is incorrect because the evoked twitch is not a maximum twitch but a twitch at the maximum possible level of activation. This is because the maximum possible level of activation is not the same as the maximum possible twitch. The maximum possible level of activation is the level of activation that occurs when the muscle is activated to its maximum level of force, whereas the maximum possible twitch is the twitch that occurs when the muscle is activated to its maximum level of force, but with no other forces acting on the muscle. The maximum possible level of activation is therefore always less than the maximum possible twitch.