Voluntary activation of human elbow flexor muscles during maximal concentric contractions

S. C. Gandevia, R. D. Herbert* and J. B. Leeper

*Prince of Wales Medical Research Institute, University of New South Wales and *School of Physiotherapy, University of Sydney, Sydney, Australia*

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1. To measure voluntary activation of human elbow flexor muscles during maximal concentric contractions, the twitch interpolation method was modified to enable detection of torque increments evoked by single stimuli during contractions of up to 300 deg s^{-1}. Subjects flexed the elbow to rotate a loaded beam 'as fast as possible' (load typically 23–58 N m) from 70 deg below to 70 deg above the horizontal. Electrical stimuli were delivered to biceps brachii when the beam passed through the horizontal. Voluntary activation was estimated from the amplitude of the interpolated twitch, which was expressed as a percentage of the twitch produced by relaxed muscles shortening at the same velocity.

2. In eleven subjects, the level of voluntary activation during repeated maximal concentric contractions (median 99·4%) did not differ significantly from that during maximal isometric contractions (98·0%). Voluntary activation during maximal contractions did not depend on shortening velocity and was the same when tested at two angles 30 deg apart.

3. To induce fatigue, five subjects repeatedly lifted and lowered a heavy load at about 30 deg s^{-1}, and continued for ten to twelve contractions after they needed assistance to continue lifting. All maintained the capacity to attain maximal levels of activation.

4. It is concluded that voluntary drive to elbow flexor muscles during maximal concentric contractions is usually maximal or near-maximal, and that this level of drive can be maintained during development of peripheral fatigue.

If a single electrical stimulus is delivered to contracting muscles during a voluntary isometric contraction, a twitch-like increase in force is often observed. The size of this 'interpolated twitch' can be used to estimate the level of neural drive to muscles: a large interpolated twitch indicates low levels of voluntary activation, whereas a small or non-existent interpolated twitch indicates near-maximal or truly maximal voluntary activation (Merton, 1954). This method has been used to show that it is possible to produce maximal or near-maximal voluntary activation during brief maximal isometric contractions of limb muscles (e.g. Merton, 1954; Belanger & McComas, 1981; Bigland-Ritchie *et al.* 1986; Gandevia & McKenzie, 1988; Herbert & Gandevia, 1996; for more references see Allen *et al.* 1995). With repeated or sustained isometric contractions of limb muscles, the level of voluntary drive diminishes as fatigue develops (e.g. Gandevia *et al.* 1995); this is termed central fatigue. In isometric exercise, central fatigue may reflect effective inhibition at a motoneuronal level (Garland & McComas, 1990) along with diminishing drive to the motor cortex (Gandevia *et al.* 1995).

Less direct methods have been used to make inferences about the level of voluntary activation in maximal dynamic (concentric and eccentric) contractions. Dudley and colleagues (1990) showed that the isokinetic torque–angular velocity relationship obtained with voluntary contractions appeared flatter (with torque on the ordinate axis) than that obtained with contractions evoked by submaximal electrical stimulation. They suggested that this indicated failure of voluntary drive at negative (eccentric) angular velocities. Westing *et al.* (1990) arrived at a similar conclusion by measuring voluntary muscle torque and the torque produced when trains of near-maximal stimuli were delivered throughout maximal voluntary efforts. Torque in voluntary eccentric contractions was no greater than in voluntary isometric contractions, but the torque produced when electrical stimuli were delivered during voluntary contractions was greater in eccentric contractions than isometric contractions. These data suggest that failure of voluntary activation occurs during maximal voluntary eccentric contractions, but they do not allow conclusions about voluntary activation during concentric contractions. Neither study provides a quantitative measure of voluntary activation of motoneurones in dynamic contractions.

Twitch interpolation could provide a direct measure of voluntary activation in concentric and eccentric contractions. However, to our knowledge, only two groups have used twitch interpolation in this way (Newham *et al.* 1991; Beelen *et al.* 1995; see also James *et al.* 1995). Both reported

that the method lacked sufficient sensitivity to detect small failures of voluntary drive. Beelen and colleagues (1995, p. 228) reported that measurable twitches in the quadriceps muscles disappeared at only 50 % of maximal dynamic force. Newham and colleagues (1991) increased the sensitivity of the technique by applying 250 ms trains of submaximal stimuli at 100 Hz, yet even with trains of stimuli the technique was probably insufficiently sensitive to detect moderate failures of voluntary drive (see their Fig. 3). Nonetheless, they reported activation failures in the quadriceps muscles of nearly 30 % at low speeds (20 deg s^{-1}) following fatiguing contractions performed at 85 deg s^{-1}.

Given the uncertainty about the maximal level of voluntary drive during concentric contractions, the main aim of this study was to develop a technique for making high-resolution measurements of voluntary activation with a single interpolated stimulus during concentric contractions. We then used the technique to compare the levels of voluntary activation attained during maximal isometric and concentric contractions, and during concentric contractions at different speeds and joint angles. Finally, we determined if declining voluntary activation contributes to the fatigue produced by repeated concentric and eccentric contractions. We used single stimuli, as originally applied by Merton (1954), to minimize the complications introduced by antidromic activation of motor axons and reflex effects due to activation of afferent axons. Subjects could usually attain maximal or near-maximal levels of voluntary drive during both maximal isometric and concentric contractions of the elbow flexor muscles. Fatigue produced by dynamic contractions was not accompanied by an appreciable decline in voluntary activation. A preliminary account of this work has been published (Herbert *et al.* 1997).

METHODS

Eleven subjects, eight men and three women aged between 25 and 43 years, participated in the study. All gave informed consent. The procedures conformed to the guidelines laid out in the Declaration of Helsinki and were approved by the local ethics committee.

Subjects sat in a rigid chair with the forearm firmly strapped to a rigid plate at the wrist (Fig. 1*A*). The upper arm remained approximately vertical. The plate was attached to an aluminium beam which rotated on low-friction bearings about the axis of the elbow, and could be loaded with weights that were firmly screwed into place to prevent movement. The plate also rotated about the elbow axis, but was attached at its distal end to the beam with a strain-gauge type load cell (XTran 2 KN, Applied Measurement, VIC, Australia).

For measurement of voluntary activation during maximal concentric contractions, subjects were asked to lift the weights 'as fast as possible'. To encourage maximal effort throughout, the subjects were instructed to keep pulling as fast as possible from a starting position with the bar about 70 deg below horizontal until the beam was stopped by a brake at about 70 deg above the horizontal. A light switch embedded in the device's axle triggered as the beam passed through the horizontal. After a delay of 25 ms, the switch triggered a constant-current stimulator which delivered a single, supramaximal stimulus to the elbow flexor muscles (0·1 ms duration; typically 100–300 mA) through 2 cm diameter electrodes firmly adhered to the skin over the mid-belly and distal tendon of the biceps muscle. The same switch triggered a purpose-built amplifier which subtracted the voltage of the amplified force signal at the time of the stimulus from the subsequent signal, before amplifying the signal a further 10 times (Hales & Gandevia, 1988; Allen *et al.* 1995). This permitted a high level of amplification of the analog force signal prior to sampling. The angular velocity of the beam (and hence also of the arm, plate and weights) was measured with an optical encoder built into the axle. The digital signal from the encoder was converted to an analog signal which was then integrated to give angular displacement and smoothed with a ten point running average and differentiated to give angular acceleration. Force and angular velocity signals were sampled at 1000 Hz with 12-bit resolution.

Force measured with the load cell was multiplied by the load cell's lever arm to give torque produced by the plate on the load cell (T_{lc}). The force seen by the load cell reflects the torque produced by muscles (and perhaps other soft tissues) at the elbow, as well as torques due to the weight and inertia of the plate and arm. Muscle torque (T_{mm}; positive when the torque acts to flex the arm) was thus calculated from the relation:

$$T_{mm} = T_{lc} - T_{w} + I\alpha,$$

where T_w is the weight torque of the plate and the arm (the value of this parameter is always negative because the weight always acts in the extension direction), I is the moment of inertia of the plate and arm, and α is the angular acceleration of the plate and arm (which are assumed to be equal). The weight torque of the plate was measured directly with the centre of mass of the plate horizontal to its axis, and thereafter was calculated by multiplying by the cosine of the angular displacement from that position. The moment of inertia of the plate was determined from its measured weight torque when horizontal and its period of oscillation (Resnick & Halliday, 1977). Weight torque and moment of inertia of the arm were estimated from body mass and height using the tables of Zatskiorsky *et al.* (1990) as modified by de Leva (1996), taking into account the flexed position of the fingers. The weight torque of the arm was subsequently multiplied by the cosine of the angle the beam made with the horizontal.

Measurement of interpolated twitch amplitude

During maximal concentric contractions, muscle torque was changing at the time the stimulus was delivered, presumably because the force-generating capacity of muscles is length and velocity dependent. This was readily observed in trials in which the muscle was not stimulated; muscle torque was then usually decreasing (or occasionally increasing) even though no twitch was evoked. The decrease or increase in torque was almost always monotonic for several hundred milliseconds and could not be mistaken for the twitch response to a single stimulus. Nevertheless, estimates of interpolated twitch amplitude obtained by subtracting torque immediately preceding the twitch from the peak torque of the twitch would have been biased if they did not take account of the changes in torque that occur throughout the twitch. We estimated the muscle torque that would have occurred in the absence of an interpolated twitch by assuming that the rate of change in torque over 25 ms preceding the stimulus was sustained for the brief duration of the twitch. Interpolated twitch amplitude was determined by subtracting the torque predicted in this way from the measured torque. To enable comparison of voluntary activation during concentric and isometric contractions, the amplitude of interpolated twitches obtained under isometric

conditions was obtained in the same way. This method, based on extrapolation, has previously been used for isometric contractions and does not alter the level of voluntary activation measured from a series of contractions in individual subjects (Allen *et al.* 1995).

Measurement of resting twitch amplitude

To calculate voluntary activation, the amplitude of interpolated twitches was normalized to the amplitude of twitches evoked from resting muscle ('control' twitches). Control twitches for dynamic contractions were obtained in the following way. First, the beam was fixed in the horizontal position and the subject performed a maximal isometric contraction (to potentiate the muscle). Five seconds later, with the subject completely relaxed, the beam was swung through the horizontal at a range of angular velocities, triggering the stimulator to evoke a control twitch. The EMG obtained from surface electrodes placed over the belly of the triceps and brachioradialis muscles was displayed on an oscilloscope at high gain to confirm that subjects were relaxed at the time the stimulus

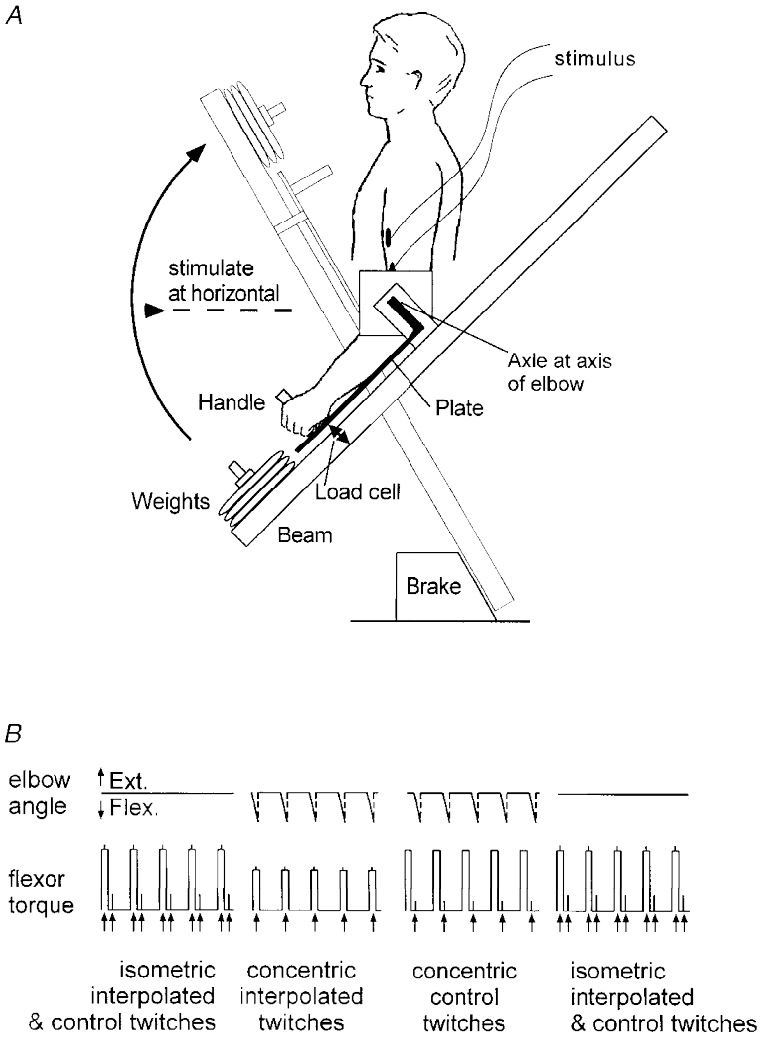

Figure 1. Experimental apparatus and protocol

A, device shown as positioned at the start of a lift (thick lines) and at the end of a lift (fine lines, background). The subject sat with the upper arm approximately vertical, the elbow axis aligned with the axis of the device, the forearm strapped to the plate, and the hand grasping the handle. *B*, schematic diagram of the protocol. Vertical bars indicate maximal voluntary contractions, and arrows indicate stimuli. The protocol is depicted in four sections. In the first, subjects performed maximal voluntary isometric contractions and stimuli were delivered during and 5 s after each contraction. In the second, subjects performed maximal concentric contractions and stimuli were delivered during contractions. In the third, subjects performed maximal voluntary isometric contractions (to potentiate the muscle) and then the arm was passively flexed. Stimuli were delivered during the passive flexion. Finally, a repeat series of maximal isometric contractions was performed and stimuli were delivered during and 5 s after each contraction. Stimuli superimposed on maximal voluntary contractions sometimes evoked interpolated twitches (small spikes), and stimuli delivered to the resting muscle evoked larger, 'control' twitches (larger spikes). The process of obtaining interpolated twitches and control twitches under concentric conditions was performed first with a moderate load on the bar and then repeated with a larger and a smaller load. See text for more details.

was delivered. Resting twitches were evoked at a range of angular velocities and the relationship between control twitch amplitude and angular velocity was determined for each subject.

Calculation of voluntary activation

Voluntary activation was calculated as $100 \times (1 - a/b)$ where a is interpolated twitch amplitude and b is the amplitude of the control twitch (e.g. Bigland-Ritchie *et al.* 1983; Allen *et al.* 1995). When calculated in this way, voluntary activation is relatively insensitive to the amplitude of the resting twitch. For example, underestimation of resting twitch amplitude by 20% would produce an error in voluntary activation of only 1·2% if voluntary activation was truly 95%. To calculate voluntary activation for a particular concentric contraction, the amplitude of the control twitch at the velocity of that contraction was estimated from the regression of control twitch amplitude on angular velocity (see above). Voluntary activation was not calculated for trials in which angular velocity exceeded 300 deg s^{-1}, because the resolution of the method was limited at high velocities (see Discussion).

Protocol

First, interpolated twitches and control twitches were evoked during and after five maximal voluntary isometric contractions (Fig. 1*B*). Then the beam was unclamped and loaded with a moderate weight, typically to a torque of 36 N m with the beam horizontal. This compares with a median maximal isometric torque for the present group of subjects of 81·4 N m. Subjects performed five maximal lifts with this weight, during which interpolated twitches were obtained, and after which control twitches were obtained as described above. The procedure was repeated with a heavy weight (typically 58 N m) and a light weight (typically 23 N m), before five final isometric contractions. Subjects were asked to perform 'maximal' efforts regardless of the weight being lifted, so the effect of varying the weight was to vary the velocity of contraction. At least 1 min of rest was allowed between contractions. For three subjects, the stimulus was sometimes delivered at angles 30 deg above the horizontal to see if there was any effect of joint angle on voluntary activation.

Effect of fatigue

To investigate the level of voluntary drive during fatiguing dynamic contractions, five subjects repeatedly lifted and lowered a near-maximal weight and a stimulus was delivered to the contracting muscles during each lift. Subjects were asked to perform the lifts at a regular cadence (rather than at the maximal possible speed as for other measurements reported here), so initially the lifts involved submaximal efforts. The weights lifted were set so that between the sixth and twelfth concentric contractions subjects became unable to continue lifting without assistance. At that stage, one of the investigators supplied as little assistance as was necessary to help the subject complete the lift, and the subject continued lifting in this way, with increasing levels of assistance, for another ten to twelve repetitions. No assistance was provided as the load was lowered. The cadence and angular velocity of the lifts was kept

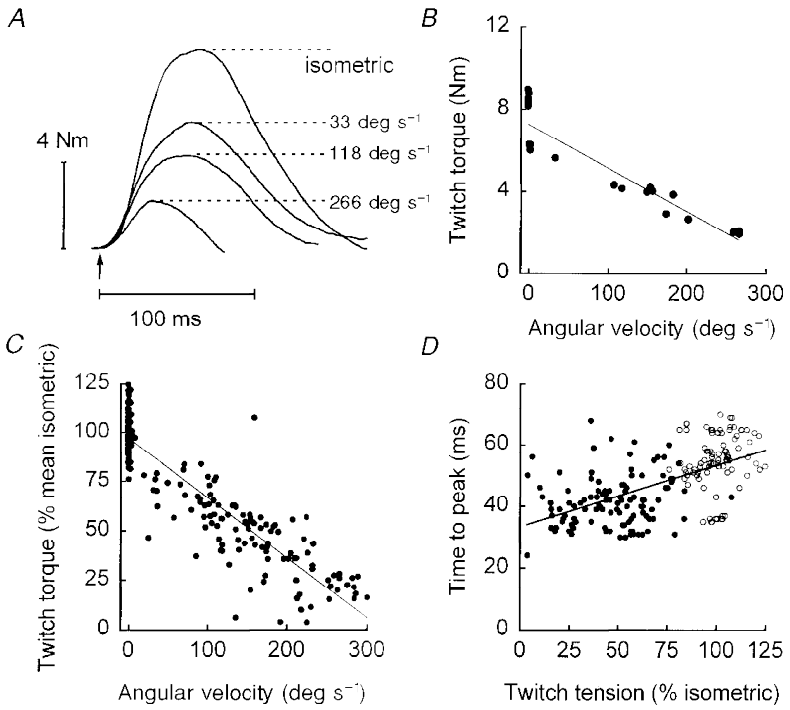

Figure 2. Effect of angular velocity on control twitch amplitude

A, torque-time profiles of typical control twitches evoked from resting muscles at increasing angular velocities of 0–266 deg s^{-1} in one subject. Arrow indicates time of delivery of stimulus. *B*, relationship between control twitch amplitude and velocity. Data are all control twitches from the same subject as in panel *A*. *C*, relationship between control twitch amplitude and velocity for all subjects. *D*, relationship between time-to-peak tension (measured from the onset of the twitch) and twitch tension. Data from isometric control twitches and concentric control twitches are shown with open and filled symbols, respectively. Linear regressions are drawn in panels *B*–*D* (all $P < 0{\cdot}001$). Data are all control twitches from all subjects. In *C* and *D*, torque has been expressed as a percentage of the mean maximal isometric torque for each subject.

as constant as possible across repetitions. As it was not possible to determine resting twitch amplitude for each level of fatigue, voluntary activation scores were not formally calculated for fatigue experiments.

Statistics

Because levels of voluntary activation are not normally distributed, non-parametric statistical tests were used and details are given in the Results. Some correlations were examined with linear regression. Statistical significance was set at the 5% level.

RESULTS

Twitches obtained from relaxed, shortening muscles

For all subjects, the amplitude of the control twitch evoked from the resting muscle declined approximately linearly with increasing angular velocity (Fig. 2; median r^2 of 0·88, range 0·66–0·97). Small control twitches (those evoked at higher angular velocities) had briefer contraction times than large twitches, but even the smallest control twitches had contraction times greater than about 30 ms (measured from the onset of the twitch; Fig. 2*D*).

Voluntary activation during maximal contractions

Small interpolated twitches were sometimes observed during maximal contractions in all subjects (Fig. 3*A*). However, all subjects were able to attain maximal or near-maximal voluntary activation during most contractions (Fig. 3*B*). Under isometric conditions subjects appeared to attain truly maximal voluntary activation in 23% of contractions (median of all contractions 98·2%, median of subject medians 98·0%, interquartile range of medians 95·6–99·1%), compared with 44% of concentric contractions (median activation of all contractions 99·4%, median of subject medians 99·4%, interquartile range 96·1–100%). This small difference was not statistically significant (comparison of all contractions, Mann–Whitney test, $P = 0{\cdot}10$; comparison of subject medians, Wilcoxon test, $P = 0{\cdot}07$). A small proportion of concentric contractions was

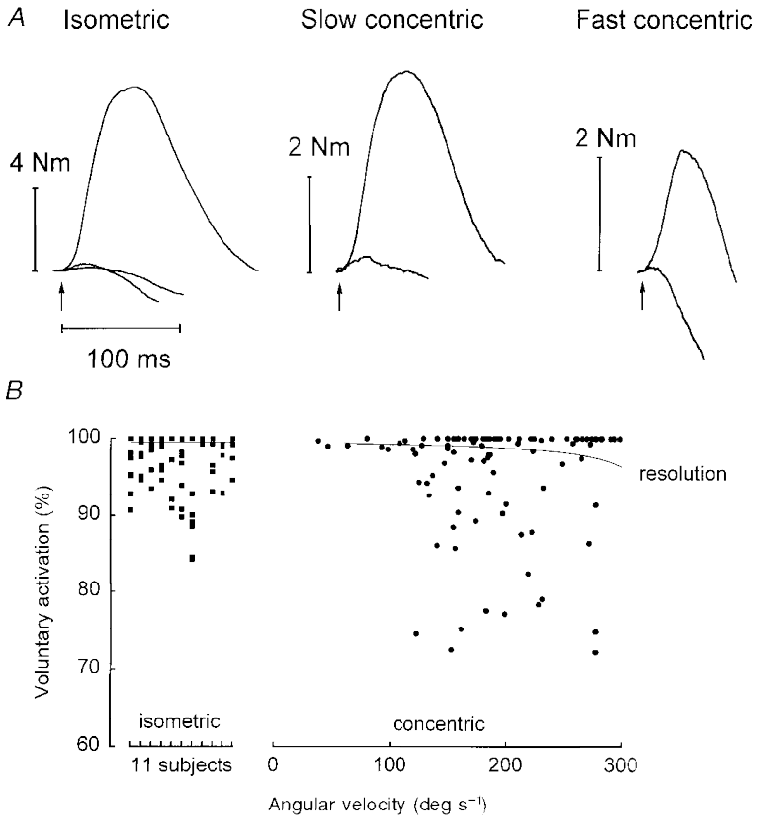

Figure 3. Interpolated twitches, control twitches and voluntary activation during maximal voluntary efforts

A, control twitches (large amplitude twitch) and interpolated twitches (small amplitude twitches) evoked from same subject as in Fig. 2 under 'isometric', 'slow concentric' and 'fast concentric' conditions. Arrows indicate when the stimulus was delivered. To enable comparison of control and interpolated twitches, torque at the time of the stimulus has been subtracted from interpolated twitches and the records are superimposed. Voluntary activation was calculated as 100 × (1 − interpolated twitch amplitude/control twitch amplitude). Note the different vertical calibrations. *B*, voluntary activation in maximal isometric efforts (left panel). Each column shows all data from one subject (median of subject medians 98·0%). Right panel, voluntary activation in maximal concentric efforts plotted against angular velocity. All contractions from all subjects are shown (median of subject medians 99·4%). Not all data points can be seen, as many are superimposed. The estimated resolution of the technique is shown (see text).

associated with very low voluntary activation (activation $< 80\%$). In these contractions, subjects probably did not continue to pull with a maximal effort throughout the lift. There was no effect of angular velocity (to 300 deg s^{-1}) on voluntary activation (Spearman's test, $\rho = 0{\cdot}13$, $P = 0{\cdot}18$). Delivery of the stimulus at the horizontal or 30 deg above the horizontal had no detectable effect on voluntary drive (medians of 99·1 and 99·0% for all contractions at horizontal and 30 deg above horizontal, respectively; Mann–Whitney test, $P = 0{\cdot}77$).

Fatigue

Figure 4 shows the results from a series of fatiguing contractions performed by one subject. In the first seven contractions, which involved submaximal efforts, large interpolated twitches were observed, indicating that the subject was able to lift the weight with submaximal levels of voluntary drive (Fig. 4*A* and *D*). The angular velocity declined during these initially submaximal contractions (Fig. 4*C*). By the eighth contraction the subject's capacity to produce force had declined to below that required to lift the weight, and the investigator provided assistance to complete that and subsequent lifts. Lowering was not assisted. Thereafter voluntary torque during the lift declined (Fig. 4*B*); by the nineteenth contraction it was about half that required to lift the weight. In all twelve lifts requiring maximal efforts, interpolated twitch amplitude was small indicating that voluntary activation was maximal or near-maximal (median amplitude 0·4% of the unfatigued control twitch at that velocity; range 0–5·6%). There was no evidence of a progressive increase in interpolated twitch amplitude. Similar results were observed in four other subjects tested in this way.

DISCUSSION

The main finding of the present study is that healthy subjects are capable of maximal or near-maximal voluntary activation of the biceps brachii during maximal concentric contractions of the elbow flexor muscles. Levels of voluntary activation attained in maximal concentric contractions are similar to those attained in maximal isometric contractions, and can be generated repeatedly even when the muscle is substantially fatigued by repeated dynamic contractions.

These findings are surprising as there is evidence that voluntary activation is less than maximal during eccentric contractions (Westing *et al.* 1990; Dudley *et al.* 1990; see Introduction). Moreover, reflex facilitation, presumably from

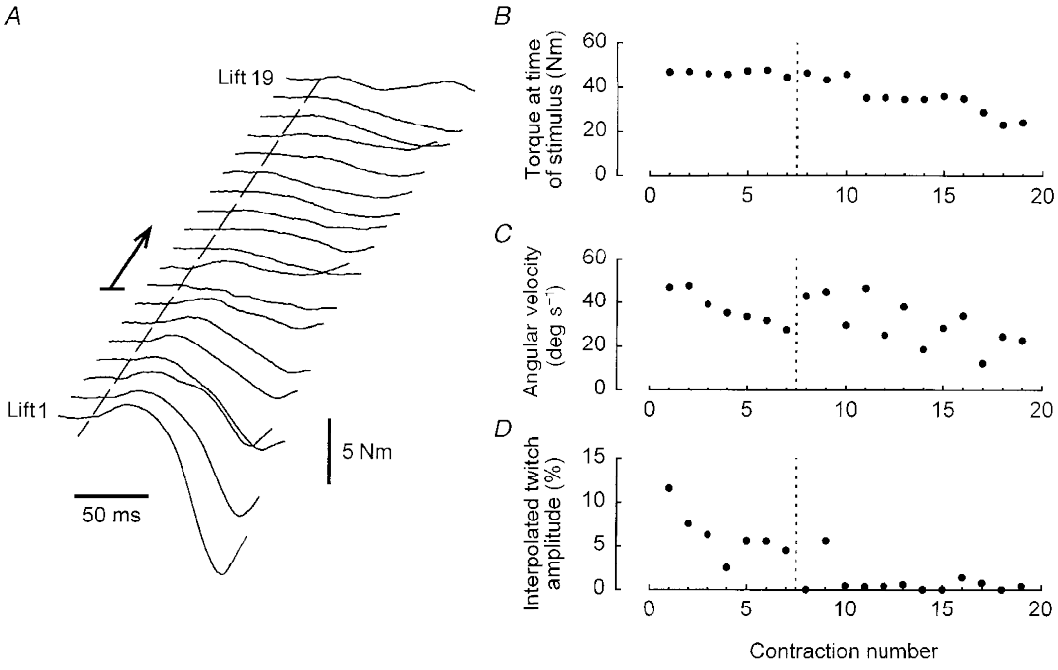

Figure 4. Effect of fatigue on voluntary activation during repeated concentric contractions

A, interpolated twitches evoked during nineteen consecutive concentric lifts by one subject with subtraction of the torque at time of stimulus. The lowest trace is the first lift, and progressively higher traces represent successive lifts. The dashed line indicates the time at which the stimulus was delivered. The arrow indicates when the subject first required assistance to continue the concentric contractions. The experimenter gave the minimal amount of assistance needed for the subject to complete the lift. *B*, voluntary torque at the time of the stimulus for each lift. After the seventh lift (dotted vertical line in this and subsequent panels) the subject could not continue lifting without assistance. *C*, angular velocity at the time of the stimulus. *D*, interpolated twitch amplitude for each lift expressed as a percentage of the unfatigued control twitch at the same velocity.

muscle spindle afferents, may contribute up to 30% of the excitation to motoneurones during sustained isometric contractions (Gandevia *et al.* 1990, 1993; Garland & Miles, 1997). This reflex support is probably not available in rapid concentric contractions, as we estimate that angular velocities of 300 deg s^{-1} would be associated with shortening velocities of muscle fibres in the main elbow flexor muscles of 1–2 fibre lengths s^{-1}. At these velocities, fusimotor drive would probably be insufficient to maintain high levels of muscle spindle discharge (Burke *et al.* 1978; Prochazka *et al.* 1979). The present study indicates that complete activation of the relevant motoneurone pool can be obtained during brief maximal concentric contractions when muscle spindle input is absent or reduced.

During maximal isometric contractions it was possible to resolve interpolated twitches with a characteristic twitch profile as small as 0·5% of the isometric twitch (see Fig. 4*A*; Gandevia *et al.* 1995). Thus, assuming the same amplitude twitches could be detected during dynamic contractions, the resolution of voluntary activation at any angular velocity was $100 \times 0{\cdot}5/[c\omega + d]$, where $c\omega + d$ is the linear regression of control twitch amplitude (percentage of isometric twitch) on angular velocity. Measured in this way, the resolution of the method was 0·5% for isometric contractions, and it declined non-linearly to 3% for measurements made at 300 deg s^{-1} because of the decline in the size of control twitches with increasing angular velocity (Fig. 3*B*). An independent estimate of resolution was obtained by pooling the data from the nineteen contractions from one fatigue run (see Fig. 4) with a median angular velocity of 34 deg s^{-1}. A linear regression was performed on the 25 ms of the force preceding the stimulus. The 95% prediction interval about the regression line (i.e. the range within which individual data points are expected to fall, not the confidence interval for the regression line) was used to estimate how large a force might be expected in the absence of a stimulus. The prediction interval was 0·1 N m, or between 1·2 and 1·5% of the dynamic control twitch at comparable velocities, slightly larger than the estimate given above (which gives 0·5–0·6% at the same velocities). These data suggest that the method is capable of detecting physiologically meaningful failures of voluntary drive.

The amplitude of interpolated twitches was determined by extrapolation of the linear trend of the voluntary torque immediately preceding the stimulus and subtracting this from the measured torque. To estimate the bias produced by assuming a linear trend in baseline torque, we analysed torque traces from thirty trials in which no stimulus was delivered. Subjects were unaware that a stimulus would not be delivered, so these trials indicated the true baseline from which interpolated twitch amplitude should be measured. They included trials in which subjects were relaxed and trials in which they attempted to contract maximally, at the full range of angular velocities. In these trials, extrapolation of the linear trend of voluntary torque slightly overestimated the measured torque over the period in which interpolated twitches would normally be seen, and the degree of overestimation increased with time. Consequently, our measures of interpolated twitch amplitude tended to underestimate true values. The bias in measures of interpolated twitch amplitude (mean percentage of the control twitch at that velocity) was 0·1% at 5 ms, 2·4% at 20 ms, and 31·2% at 70 ms. However, as the amplitudes of both the interpolated twitch and the control twitch were underestimated, measures of voluntary activation were relatively unbiased. For example, the bias in voluntary activation of a typical contraction (interpolated twitch of 0·6% control twitch, time to peak of 11 ms, control twitch time to peak of 42 ms) was less than 0·2%.

When subjects repeatedly lifted a heavy load with their elbow flexor muscles, all were able to extinguish, or nearly extinguish, interpolated twitches. This suggests that, in our test protocol, the primary site of fatigue during repeated high-intensity maximal dynamic contractions is in the muscle, and that the decline in force is not due in any significant way to a failure of voluntary drive. These findings are consistent with the earlier findings of Beelen *et al.* (1995) and James *et al.* (1995). They found that peak voluntary knee extensor forces and knee extensor forces evoked by trains of stimuli declined similarly over brief periods of maximal dynamic exercise, and they interpreted this as indicating that declines in force were primarily due to a decline in the intrinsic force-generating capacity of muscle. In contrast, Newham *et al.* (1991) used isokinetic twitch interpolation of the quadriceps to demonstrate significant reductions in voluntary activation with fatigue. Beelen and colleagues speculated that the difference between their results and those of Newham *et al.* might be because Newham *et al.* used contractions at low velocities ($\approx$ 20 deg s^{-1}), and failures of voluntary activation might be more evident at the high forces associated with low velocity contractions. However, in the present study there was little evidence of progressive failure of voluntary drive, even though the fatiguing contractions were performed at low angular velocities ($\approx$ 30 deg s^{-1}). Another explanation might lie in the observation that the mechanisms which mediate fatigue are task dependent (e.g. McKenzie *et al.* 1992; for review see Enoka & Stuart, 1992), as the subjects used by Newham *et al.* performed seated isokinetic contractions of the knee extensors, whereas the subjects in the present study used their elbow flexors to lift a load that was free to accelerate, and subjects used by Beelen *et al.* (1995) performed isokinetic cycling. In addition, voluntary activation during maximal isometric contractions differs significantly among muscles (Belanger & McComas, 1981; McKenzie *et al.* 1992; Herbert & Gandevia, 1996).

It is concluded that maximal or near-maximal levels of voluntary activation can be attained in concentric contractions, even when the muscles have been fatigued by repeated dynamic contractions.

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Corresponding author

S. C. Gandevia: Prince of Wales Medical Research Institute, High Street, Randwick NSW 2031, Australia.

Email: S.Gandevia@unsw.edu.au