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A spinal pathway between synergists can modulate activity in human elbow flexor muscles

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Abstract

Electrical stimulation of the brachioradialis branch of the radial nerve has been shown to inhibit the discharge of voluntarily activated motor units in biceps brachii during weak contractions with the elbow flexor muscles. The purpose of the present study was to characterise the inhibitory reflex by comparing its strength in the short and long heads of the biceps brachii and examining the influence of forearm position on the strength of the reflex. Spike-triggered stimulation was used to assess the influence of radial nerve stimulation on the discharge of single motor units in the biceps brachii of 15 subjects. Stimulation of the radial nerve prolonged the interspike interval ($P < 0.001$) of motor units in the long ($n = 31$, 4.8 ± 5.6 ms) and short heads ($n = 26$, 8.1 ± 12.3 ms) of biceps brachii with no difference between the two heads ($P = 0.11$). The strength of inhibition varied with forearm position for motor units in both heads ($n = 18$, $P < 0.05$). The amount of inhibition was greatest in pronation (7.9 ± 8.9 ms), intermediate in neutral (5.8 ± 7.1 ms), and least in supination (2.8 ± 3.4 ms). These findings indicate that the inhibition evoked by afferent feedback from brachioradialis to low-threshold motor units (mean force 3–5% MVC) in biceps brachii varied with forearm posture yet was similar for the two heads of biceps brachii. This reflex pathway provides a mechanism to adjust the activation of biceps brachii with changes in forearm position, and represents a spinal basis for a muscle synergy in humans.

Keywords

Motor unit; Inhibition; Biceps brachii; Brachioradialis; Synergy

Introduction

An elbow flexion torque is produced by the activation of a number of muscles that cross the elbow joint and insert onto the radius or ulna. Due to these attachment locations, most of the muscles that contribute to an elbow flexor torque also produce actions about other axes of rotation. As a consequence of this anatomical organisation, some muscles are synergists for an elbow flexor torque but are antagonists for other actions. One example of this arrangement is between the biceps brachii and brachioradialis muscles. Both contribute to an elbow flexor torque but biceps brachii can also generate a supination torque whereas brachioradialis can produce both supination and pronation torques depending on the orientation of the forearm (Gielen and van Zuylen 1986; Buchanan et al. 1989; Jamison and Caldwell 1993; Murray et al. 1995; Zhang et al. 1998). The opposing pronation–supination capabilities of these two muscles modifies the amount of activity that each generates during an elbow flexor task

according to the concurrent demands about the long axis of the forearm (Buchanan et al. 1989; Jamison and Caldwell 1993). For example, the EMG activity of biceps brachii is greater when the task involves concurrent flexion and supination torques compared with flexion and pronation torques (Barry and Carson 2004; Shemmell et al. 2005).

The relative activation of the long and short heads of biceps brachii has also been shown to vary with the pronation or supination torque that accompanies elbow flexion (Basmajian and Latif 1957; Buchanan et al. 1986; Jamison and Caldwell 1993). Experiments with single motor unit recordings have shown that some motor units in the long head of biceps brachii and all motor units in the short head are recruited only when the task requires both flexion and supination torques (ter Haar Romeny et al. 1982; ter Haar Romeny et al. 1984; van Zuylen et al. 1988). It has been proposed that spinal reflex pathways (Windhorst et al. 1989), in particular inhibitory pathways between antagonist muscles (Jongen et al. 1989), may underlie the differential recruitment of motor units within a population. Accordingly, the inhomogeneous activation of the biceps brachii motor neurone pool might be controlled by such a mechanism (van Zuylen et al. 1988; Jongen et al. 1989). It has also been suggested that biceps brachii is reflexively inhibited when the forearm is prone (Basmajian and Latif 1957) and that the recruitment of some biceps brachii motor units might be gated by inhibitory pathways that are active during pronation (ter Haar Romeny et al. 1984).

Naito et al. (1996) described an inhibitory reflex pathway from brachioradialis radial nerve afferents to biceps brachii that may contribute to the recruitment profiles of motor units in biceps brachii. When randomly stimulating the radial nerve below motor threshold, they found that the discharge of 52% of the recorded single motor units was delayed. The 21 motor units studied by Naito et al. (1996) were located in the medial portion of biceps brachii and the forearm was placed in a supinated position. Given the differential recruitment profiles of motor units in the short and long heads of biceps brachii and the influence of forearm position on biceps brachii EMG activity, we hypothesised that the strength of the inhibitory reflex would differ between the two heads and vary with forearm posture so that it is greatest when the forearm is pronated and biceps brachii activation is typically reduced. The purpose of this study was to characterise the inhibitory reflex by comparing its strength in the short and long heads of the biceps brachii and examining the influence of forearm position on the strength of the reflex. Some of these data have been presented in abstract form (Pascoe et al. 2006; Riley et al. 2006).

Methods

A series of experiments were conducted with 15 healthy adults (13 men, 2 women; 27.2 ± 4.8 years; range, 21–39 years). The Human Research Committee at the University of Colorado in Boulder approved the procedures and the experiments were performed in accordance with the declaration of Helsinki. All subjects gave written informed consent prior to participating in the study.

Experimental setup

Subjects were seated upright in a chair with the left upper arm vertical and slightly abducted from the trunk and the elbow resting on a support. The elbow was flexed to 1.57 rad with the forearm horizontal. The hand and forearm were secured with a modified wrist-hand orthosis (Orthomerica; Newport Beach, CA, USA) and the force exerted by the elbow flexor muscles was measured with a force-moment sensor (JR-3, 900-N range, 89.4 N/V; JR-3, Woodland, CA, USA). The transducer was attached to the orthosis at the level of the wrist. Subjects were instructed to contract their elbow flexor muscles to pull upwards against the orthosis.

Single motor unit recordings

Single motor unit potentials were recorded from the long and short heads of biceps brachii using stainless-steel wires (50- μ m diameter, California Fine Wire, Grover Beach, CA, USA) that were insulated with Formvar and glued together at the recording tips. The insulation was only absent from the recording tip of each wire, and two or three wires were included in each electrode. The wires were inserted into the muscle belly using a 27- or 30-gauge hypodermic needle that was removed after the wires were in place. Adjusting electrode depth and using alternate bipolar configurations of the wires improved the quality of the motor unit signal. A reference electrode was placed on the skin over the lateral epicondyle. The single motor unit recordings were amplified (1,000–5,000 times) and band-pass filtered between 0.3 and 8.5 kHz (Coulbourn Instruments, Allentown, PA, USA). The motor unit signal was sampled at 20 kHz with a Power 1401 (CED, Cambridge, UK), stored on a computer, and the single motor unit potentials were identified on-line and off-line using Spike2 software (v.5.16, CED).

Interference EMG recordings

Interference electromyograms (EMG) were recorded with bipolar surface electrodes (Ag–AgCl, 4 or 8-mm diameter, 20-mm interelectrode distance) placed over the long and short heads of biceps brachii, triceps brachii, brachioradialis, and extensor carpi radialis. Interference EMG was obtained from the brachialis muscle using intramuscular bipolar electrodes made from 75 μ m Formvar-insulated, stainless-steel wire with 1 mm of insulation removed at the recording tip. Two separate wires were inserted into the brachialis approximately 20 mm apart using 30-gauge, 2.54-cm hypodermic needles. Reference electrodes were placed on the lateral epicondyle of the humerus, on the head of the radius, and on the acromion process of the scapula. EMG signals were amplified (100–10,000 times; S-series, Coulbourn Instruments) and band-pass filtered at 13 Hz to 1 kHz. Interference EMGs were sampled at 2 or 4 kHz and stored as described for the intramuscular signals.

Nerve stimulation

A Grass S88 stimulator (Grass Technologies, West Warwick, RI, USA) was used in series with an SIU5 isolation unit and a CCU1 constant-current unit to deliver a 0.5-ms rectangular pulse to the brachioradialis branch of the radial nerve at $0.9 \times$ motor threshold (MT). The cathodal stimulation was delivered at the lateral side of the upper arm, over the humerus and 3–4 cm superior to the lateral epicondyle. After locating an appropriate stimulation site by using a bipolar metal probe electrode, adhesive electrodes (NDM Peripheral Nerve Stimulation electrodes, 10 mm Ag–AgCl disc with a 2.4×1.9 cm gel contact area, Conmed, Utica, NY, USA) were positioned to evoke a clear brachioradialis M-wave at a low stimulus intensity, without any activation of extensor carpi radialis at a stimulus intensity of at least $2 \times$ MT for brachioradialis (Naito et al. 1996). Although smaller stimulating electrodes would have allowed more focal stimulation, larger electrodes ensured more consistent activation of the afferent fibres when different forearm positions were examined and there was movement of the surface electrode relative to the underlying nerve.

Because the brachialis muscle can receive some innervation from the radial nerve in addition to its primary innervation from the musculocutaneous nerve (Mahakkanukrauh and Somsarp 2002; Vicente et al. 2005; Blackburn et al. 2007), a separate experiment was conducted to evaluate the origin of the afferents responsible for the inhibition from stimulating the radial nerve. The radial nerve branch to brachialis is relatively close to that innervating brachioradialis and near the electrodes that were used to evoke the response. To assess the possible involvement of afferents arising from brachialis, the stimulation was optimised to elicit an M-wave in either brachialis or brachioradialis while ensuring that there was no activation of extensor carpi radialis at intensities up to $2.0 \times$ MT. The responses to ~100 stimuli were recorded for the same motor unit in biceps brachii to the stimulation first optimised for one of the two muscles and

then optimised for the other muscle. The motor threshold for both brachialis and brachioradialis was identified for each stimulation location to determine the effective stimulation intensity for the non-target nerve branch when the target nerve branch was activated at $0.9 \times \text{MT}$.

Tendon stimulation

Brief mechanical pulses (3 pulses at 200 Hz, 15 ms) were applied to the distal tendon or belly of brachioradialis using a mechanical vibrator (LDS V203 vibrator and PA25E power amplifier, Ling Dynamic Systems, Herts, UK). An 8-mm-diameter aluminium probe was mounted on the vibrator to interface with the skin. The reaction force against the skin was measured with an MLP-10 force transducer (Transducer Techniques, Temecula, CA) and maintained at a background level of 1–2 N. The location and force of the mechanical taps to elicit brachioradialis T-reflexes was determined by averaging the EMG response to 24 mechanical pulses (~ 0.5 Hz) as the subject maintained a small background contraction. The intensity during spike-triggered stimulation was set at approximately $0.5\text{--}0.8\times$ the threshold for a motor response and the stimulus was delivered at a 25 ms delay after each trigger motor unit discharge. Careful positioning of the vibrator was required to avoid eliciting monosynaptic Ia excitation of the biceps brachii by activation of muscle spindles in extensor carpi radialis (Cavallari and Katz 1989). It was necessary to locate the vibrator over the brachioradialis belly rather than the distal tendon for some subjects.

Maximal voluntary contractions

Maximal voluntary contractions (MVCs) were performed with the elbow flexor muscles with the forearm in a neutral position. Participants were instructed to increase the torque during the isometric contraction to maximum in ~ 3 s and then to exert as much torque as possible for an additional 3 s. After several practice attempts, MVCs were performed 3 times with successive attempts separated by 2–3 min of rest. The maximal torque achieved in the 3 attempts was taken as the MVC torque.

Protocol

The strength of the reflex was assessed by recording the discharge of single motor units from biceps brachii with a fine wire electrode that was inserted into either the long or short head of biceps brachii. The subject produced low flexion forces until a single motor unit was isolated that could be clearly discriminated using a threshold window discriminator (S-series, Coulbourn Instruments). Spike-triggered stimulation (Stephens et al. 1976; Fournier et al. 1986) was then delivered every 2–3 s as subjects maintained a steady discharge rate of ~ 11 pulses per second (pps). Each of the 100 stimuli was given at a set delay after a selected discharge.

In addition to threshold discrimination, online template matching of the motor unit action potential was performed with Spike2 software (CED) to verify that the same single motor unit was monitored throughout the experiment. Audio feedback of the motor unit discharge and visual feedback of elbow flexion force and motor unit discharge rate were provided to the subject to aid in maintaining the steady discharge rate. To measure the stability of the background discharge rate, control pulses were interspersed between successive stimuli at a random interval at least 1 s after a stimulation trigger and 0.7 s before the next stimulation trigger.

Naito et al. (1996) did not report the stimulation delay used in their investigation, so the first experiment tested the effect of three stimulation delays on the same single motor unit. The results (Fig. 1) indicated that there was no difference in the prolongation of the interspike interval with delays of 30, 40 or 50 ms, so a delay of 30 ms was used in all subsequent experiments. The 30 ms delay minimised contamination of the subsequent motor unit recording

by the stimulus artefact and maximised the influence of the stimulation on the entire interspike interval distribution.

The possible influence of cutaneous afferents on the reflex inhibition was also investigated. Electrical stimuli were delivered either to the side of the upper arm adjacent to the site of radial nerve stimulation or to the skin overlying the bony prominences of the elbow. These sites were selected because subjects typically experienced only a local sensation when the radial nerve was stimulated and not a paraesthesia that radiated down the arm (Burke et al. 1992). The intensity of the cutaneous sensation was $\sim 2 \times$ perceptual threshold to resemble either the current delivered or the perceived intensity associated with stimulating the radial nerve at $0.9 \times$ MT. The response of the same motor unit in biceps brachii was recorded for 100 stimuli delivered separately to the radial nerve and cutaneous sites, or from a random combination of stimuli from the two locations.

To assess the electrical threshold for the response, the strength of the reflex inhibition in the same motor unit was assessed for eight stimulation intensities (0.5, 0.6, 0.7, 0.75, 0.8, 0.9, 1.0, and $1.1 \times$ MT) applied to the brachioradialis branch of the radial nerve. As a further test for the involvement of Ia-afferents from the brachioradialis muscle, responses for the same single motor unit were compared for stimulation of the brachioradialis branch of the radial nerve and mechanical taps to brachioradialis. Both these and the cutaneous stimulation experiments were performed with the forearm in a neutral position. To compare the strength of the reflex between the long and short heads, the sample for motor units recorded from both heads was expanded and stimulation was applied to the brachioradialis branch of the radial nerve with the forearm in a neutral position. In a subset of experiments, motor units were sampled from both heads in the same experimental session to ensure consistency of the nerve stimulation.

To examine the influence of forearm position on the strength of the reflex, the same single motor unit in either head of biceps brachii was tracked as the forearm was held in three different positions: pronation (~ 0.79 rad), supination (~ 0.79 rad) or neutral (~ 0 rad). The responses to approximately 100 stimuli were recorded for each posture, but trials were only conducted when the amplitude, width, and shape of a motor unit action potential were sufficiently consistent across positions to indicate that the recording was from the same motor unit. The arm was moved minimally between the different positions to avoid disrupting the single motor unit recording. As an index of stimulus consistency, brachioradialis M-waves were measured either prior to or after each sequence in the different forearm positions.

Data analysis

Mean force, mean discharge rate, and the coefficient of variation (CV) for interspike interval (ISI) were calculated around the times when the stimuli were delivered. Template matching with Spike2 software was repeated offline to discriminate individual motor unit action potentials. The accuracy of this discrimination was verified by visual inspection of each discriminated action potential and by reviewing the distribution of interspike intervals. The offline analysis also verified that no motor unit discharges occurred in the time period between a stimulation or control event and the preceding trigger discharge of the motor unit. Post-stimulus time histograms (PSTH) were constructed with 0.5-ms bins for the 100-ms period after the delivery of a stimulus and for control conditions when no stimulus was provided. Cumulative sums were calculated from the stimulation and control histograms (Ellaway 1978).

The degree of inhibition across the motor unit sample was quantified by measuring the prolongation of the interspike interval induced by the radial nerve stimulation (Datta and Stephens 1981; Nafati et al. 2005). The three ISIs prior to stimulation were averaged (ISI-pre) and the ISI that included the stimulation (ISI-0) was measured. The difference between the two

values (ms) was used to indicate the strength of the reflex inhibition. A positive value for either index corresponded to inhibition, whereas a negative value indicated facilitation. These intervals were extracted for every stimulation and control trigger and the average values for each motor unit were calculated.

The selectivity of radial nerve stimulation was measured by averaging the EMG from the brachioradialis and extensor carpi radialis muscles following stimulation at or above motor threshold for both muscles. The peak-to-peak amplitude of the brachioradialis M-wave in response to stimulation at $1-2 \times MT$ was recorded before and at the end of each experimental session or during each change in forearm position to ensure that stimulation conditions did not change. The waveform was also averaged during the motor unit trials to ensure there was no motor response to the stimulation during the low-force contractions.

Statistical analysis

Discharge rate characteristics, force, and EMG for each muscle were compared with repeated-measures ANOVAs for each stimulation trial. Peak-to-peak amplitudes of the M waves were compared between forearm positions with repeated-measures ANOVA. Chi-square statistics were used to examine the influence of stimulation on the PSTHs for the stimulation and control triggers. PSTHs were compared for 25–95 ms after the stimulation. The observed and expected counts for calculation of the Chi-square statistic were drawn from groups of 10 bins of the PSTHs to ensure a mean bin count of ≥ 5 to satisfy the assumptions of the Chi-square test. Repeated-measures ANOVAs were used to contrast the mean interspike intervals recorded prior to (ISI-pre) and during (ISI-0) the motor unit discharges selected to generate the triggers (stimulation and control) and to assess the difference between the two heads of biceps brachii and the different forearm positions. All motor units were included in the analysis of the mean interspike intervals. An alpha level of $P < 0.05$ was used to identify significant differences. All statistical analyses were performed in SPSS (Chicago, IL). Data are presented in the text and tables as mean $\pm$ standard deviation (SD).

Results

Prolongation of the interspike intervals was similar ($P = 0.59$; Fig. 1b) for all three stimulus delays (30, 40, and 50 ms) in 16 motor units; 8 each from the short and long heads of biceps brachii (3 subjects). Significant inhibition was evident in 14 of 16 PSTHs for the 30-ms delay and in 13 of 16 PSTHs for the 40- and 50-ms delays. The peak negative values for the cumulative sums were -28.3 ± 19.3 impulses/stimulus for the 30-ms delay, -29.8 ± 17.6 impulses/stimulus for the 40-ms delay, and -22.0 ± 8.5 impulses/stimulus for the 50-ms delay ($P = 0.13$). The latency of the inhibition relative to the trigger motor unit discharge was 64.2 ± 8.8 ms for the 30-ms delay (34.2 ms following stimulation), 69.0 ± 6.1 ms for the 40-ms delay (29.0 ms following stimulation) and 72.1 ± 8.1 ms for the 50-ms delay (22.1 ms following stimulation) ($P < 0.05$). The duration of the trough in the cumulative sum did not differ ($P = 0.96$) for the 3 stimulation delays (30 ms: 19.3 ± 13.0 ms; 40 ms: 18.0 ± 11.7 ms; 50 ms: 18.3 ± 20.9 ms).

The time course of reflex input was examined further in 66 motor units from 13 subjects by assessing the influence of radial nerve stimulation (30-ms delay) on several interspike intervals after the selected motor unit trigger (Fig. 2). There was a significant effect of the stimulation ($P < 0.001$) that varied across the interspike intervals ($P < 0.01$). Independent *t* tests indicated significant differences at each ISI following stimulation ($P < 0.05$), with the most consistent effect occurring during ISI-0 and ISI + 1. After the initial prolongation of the interspike interval (ISI-0), the duration of the next interspike interval (ISI + 1) was shorter, but then increased again for the second interspike interval after stimulation (ISI + 2). By the fourth interspike

interval after stimulation (ISI + 4), the duration of the interspike interval was similar to control levels.

Responses were obtained for nine motor units (six subjects) with the stimulation optimised for the brachioradialis branch of the radial nerve in one sequence, and for the brachialis branch in another sequence (Table 1). The two nerve branches could only be stimulated with limited selectivity. Stimulation of the brachioradialis branch at $0.9 \times \text{MT}$ corresponded to an intensity of $0.78 \pm 0.15 \times \text{MT}$ for the brachialis branch of the radial nerve. Similarly, stimulation of the brachialis branch at $0.9 \times \text{MT}$ was associated with an intensity of $0.69 \pm 0.13 \times \text{MT}$ for the brachioradialis branch. Stimulation at each location elicited significant inhibition of motor unit discharge ($P < 0.001$), and although the percentage change in ISI was greater for stimulation of the brachioradialis nerve branch (6.1%) than for the brachialis branch (2.2%), the difference was not significant for the two locations ($P = 0.197$).

Additional measurements verified the specificity of the stimulation used to evoke reflex inhibition of biceps brachii motor unit discharge. The influence of stimulating the brachioradialis branch of the radial nerve was compared to electrical stimulation of the skin for 14 motor units (seven subjects). Significant inhibition was only observed after stimulation of the brachioradialis branch of the radial nerve ($P < 0.05$). The interspike interval was prolonged by 3.68 ± 3.31 ms with radial nerve stimulation compared with 0.52 ± 2.01 ms for cutaneous stimulation (Fig. 3). The strength of the reflex inhibition in the same motor unit ($n = 4$) increased significantly ($P < 0.05$) with an increase in stimulation intensity from 0.5 to $1.1 \times \text{MT}$ (Fig. 4). The interspike interval was significantly prolonged by the mechanical activation of brachioradialis afferents ($P < 0.05$) and by electrical stimulation of the brachioradialis branch of the radial nerve ($P < 0.05$) for six single motor units from six subjects (Fig. 5).

The strength of the inhibition in motor units from the long and short heads of biceps brachii was compared to spike-triggered stimulation for 57 motor units (31 long head, 26 short head) from 11 subjects. On average, the responses to 99 ± 22 stimuli were recorded over a period of 271 ± 64 s. Subjects exerted a mean force of $3.6 \pm 2.2\%$ MVC force to maintain a steady motor unit discharge rate of 11.2 ± 0.8 pps (Table 2). There were no differences in trial duration, number of stimuli, or discharge characteristics ($P > 0.3$) between the long and short heads, with the exception of a slightly higher mean force for the short head ($P < 0.05$). Chi-square analyses of the PSTH revealed significant inhibition for 40 of the 57 histograms, with no difference between the long (22/31, 71%) and short (18/26, 69%) heads of biceps brachii. There was also no statistically significant difference ($P = 0.20$) in the peak negative value of the cumulative sum for motor units from the long (-18.4 ± 13.2 impulses/stimulus) and short head (-24.4 ± 19.7 impulses/stimulus) of biceps brachii.

A significant interspike interval $\times$ trigger effect ($P < 0.001$) indicated that the interspike intervals were prolonged by stimulating the brachioradialis branch of the radial nerve. The ISI during stimulation (ISI-0) was significantly longer than the average of the three preceding ISIs (ISI-pre) for both the long (94.3 ± 6.9 and 89.5 ± 5.4 ms, respectively) and short heads (98.9 ± 14.5 and 90.8 ± 5.7 ms, respectively). There was no significant difference ($P = 0.11$) in the prolongation of ISI-0 between the 31 motor units from the long head and the 26 motor units from the short head of biceps brachii. On 13 occasions, motor units were sampled from both the long ($n = 13$) and short heads ($n = 13$) of biceps brachii in the same experiment session, which permitted comparison with a common stimulation site. These data also displayed a significant effect of stimulation ($P < 0.05$), with no significant difference between the long and short heads of biceps brachii (ISI difference: 4.9 ± 5.2 and 9.8 ± 15.9 ms, respectively; $P = 0.22$). There was considerable variability in the influence of the stimulation on single motor unit discharge, both between and within subjects, especially for the short head of biceps brachii (Fig. 6).

For the second part of the purpose, the response to stimulating the brachioradialis branch of the radial nerve was recorded for 18 single motor units (9 long head, 9 short head) in 3 different forearm positions from 8 subjects. Subjects exerted low forces ($4.0 \pm 1.8\%$ MVC forces) with the elbow flexor muscles and maintained an average discharge rate of 11.4 ± 0.8 pps for the active motor unit (Table 3). There were no significant differences in trial duration, number of stimuli, elbow flexion force, or discharge characteristics ($P > 0.14$) across the three forearm positions.

Chi-squared statistics of the PSTH revealed significant inhibition in 12/18 histograms when the forearm was pronated, 11/18 when it was in a neutral position, and 11/18 when it was supinated; the peak negative values for the cumulative sums were -21.9 ± 18.6 impulses/stimulus in pronation, -23.1 ± 20.0 impulses/stimulus in neutral, and -17.4 ± 13.7 impulses/stimulus in supination. Example PSTHs, cumulative sums, and associated motor unit action potentials are shown in Fig. 7 for the three forearm positions. Prolongation of the interspike intervals after radial nerve stimulation was apparent in all three arm positions, with the greatest inhibitory effect in pronation (7.9 ± 8.2 ms), intermediate in neutral (5.8 ± 7.1 ms), and least in supination (2.8 ± 3.4 ms; $P < 0.05$; Fig. 8a). There was considerable variability between individual motor units, and this variability was less in the supination position than in the neutral and pronated positions (Fig. 8b). There was no difference in the response to stimulation across the three positions between motor units from the short ($n = 9$) and long ($n = 9$) heads of biceps brachii ($P = 0.75$).

As an index of stimulus consistency, the brachioradialis M-wave amplitude did not change (Fig. 8c) across the three positions (expressed as a proportion of the control M-wave: pronation 0.94 ± 0.15 ; neutral 0.95 ± 0.14 ; supination 1.05 ± 0.19 ; $P = 0.9$). Furthermore, background levels of muscle activity were quantified for each of the three arm positions by averaging the root mean square of the EMG amplitude over multiple 0.5-s intervals starting 1 s prior to each stimulation or control event. There was a significant task $\times$ muscle interaction ($P < 0.05$) for the normalised EMG data. Similar levels of normalised EMG were recorded for brachioradialis (1.41 ± 0.94 , 1.42 ± 0.86 , $1.40 \pm 0.90\%$ for pronation, neutral, and supination, respectively), brachialis (8.44 ± 11.20 , 7.93 ± 10.38 , $7.97 \pm 10.41\%$), and triceps brachii (3.49 ± 2.89 , 3.41 ± 2.86 , $3.45 \pm 3.00\%$) across the three arm positions although brachialis activity was higher than all of the other muscles in the three tasks. EMG amplitude was lower when the forearm was in the pronated position for the long head (3.08 ± 2.10 , 5.29 ± 5.85 , $5.05 \pm 3.79\%$ MVC for the three positions, respectively) and short head (2.01 ± 1.53 , $2.55 \pm 1.90\%$, $2.54 \pm 2.07\%$ MVC) of biceps brachii.

Discussion

The main findings of this study were the presence of reflex inhibition in both heads of biceps brachii, with no difference in the level of inhibition of motor unit discharge between the two heads, and modulation of the strength of reflex inhibition with changes in forearm position. These results confirm the original findings of Naito et al. (1996) that a spinal reflex pathway from the brachioradialis, a synergist muscle for elbow flexion, can slow the ongoing discharge of a voluntarily activated motor unit in biceps brachii. The results on the influence of forearm position are consistent with the hypothesis, but the similarity of the strength of the reflex in the two heads of biceps brachii contrasts with the expected results.

Identifying the source of inhibition

Inhibition was quantified by examining the influence of stimulation on the mean duration of the interspike interval (Datta and Stephens 1981; Nafati et al. 2005). Post-stimulus time histograms were also calculated to permit comparison with previous data (Naito et al. (1996). The mean interspike interval analysis indicated a progressive increase in inhibition as forearm

position was adjusted from supination to pronation. The reliability of the mean interspike interval analysis was verified with the control interspike interval analysis by also assessing the mean interspike intervals before and after control triggers interspersed with stimulation triggers throughout the spike trains.

The latency of the inhibition in the current study was similar to that reported by Naito et al. (1996). When the brachioradialis branch of the radial nerve was stimulated at a delay of 50 ms after the trigger motor unit discharge, the decline in the cumulative sum occurred 22 ms after stimulation. The apparent latency of the inhibition was longer when stimulation was delivered at 30 and 40 ms, but the resolution to accurately identify the onset of inhibition is reduced when relatively few discharges occurred at the shorter interspike intervals influenced by earlier stimulation. The 18.5 ms average duration of the trough in the PSTH was longer than the 8–15 ms reported by Naito et al. (1996), but their stimulation intensity was $1.0\text{--}1.3 \times \text{MT}$ compared with $0.9 \times \text{MT}$ in the current study. The discrepancy in the duration of the PSTH troughs could be influenced by the fewer triggers that were used in the present study, but there are limits in the accuracy of measuring the duration of an inhibitory synaptic potential from PSTHs (Turker and Powers 2003, 2005).

The current study suggests that the inhibition lasts longer than the duration estimated from the PSTH troughs. The prolongation of the interspike interval did not differ for stimulus delays of 30, 40, or 50 ms (Fig. 1b), despite evidence that brief (~20 ms) inhibitory postsynaptic potentials (IPSPs) elicit larger increases in the interspike interval when the IPSP occurs later in the interspike interval (Turker and Powers 1999). Analysis of several interspike intervals after stimulation (Miles et al. 1989; Mattei et al. 2003) suggested a long-lasting inhibition for 150–300 ms after stimulation (Fig. 2). However, these data must be interpreted cautiously, due to the influence of lengthening a preceding interspike interval (e.g. ISI-0) on subsequent discharges (i.e. ISI + 1 to ISI + 4) independent of any continuing inhibition (Turker and Powers 1999).

Naito et al. (1996) estimated the central delay of the inhibition to be 0.7–1.2 ms later than monosynaptic Ia homonymous facilitation, which indicates that the pathway involves more than one synapse. Because the reflex involves muscles that are not strict antagonists, it may comprise a form of type I non-reciprocal inhibition involving Ia and Ib afferents and interneurons (Naito et al. 1996; Pierrot-Deseilligny and Burke 2005). However, the inhibition lasts longer than the typical duration (≤ 10 ms) of type I non-reciprocal inhibition (Pierrot-Deseilligny and Burke 2005). The long-lasting inhibition may be presynaptic in origin (Hultborn et al. 1987; Pierrot-Deseilligny and Burke 2005) and involve disfacilitation of motor neurone discharge due to a brief reduction in the Ia-afferent input to the motor neurone pool (Priori et al. 1998). Such an action might be superimposed on type I non-reciprocal inhibition, which would suggest that stimulation of the radial nerve influences biceps brachii motor neurones in the spinal cord through pre- and post-synaptic mechanisms.

The current study produced limited evidence of the muscle from which the afferent volleys originated. Motor units that were inhibited by electrical stimulation of the brachioradialis branch of the radial nerve were similarly inhibited by mechanical impulses delivered to the tendon or belly of brachioradialis. This contrasts with the excitatory effect of mechanically activating afferents from the adjacent extensor carpi radialis muscle (Cavallari and Katz 1989) and supports a role for Ia-afferents from brachioradialis in the inhibition evoked by electrical stimulation of the radial nerve. The low electrical threshold of the inhibition ($\sim 0.5 \times \text{MT}$) was consistent with the involvement of group 1 afferents. The current results also dismiss a role for cutaneous afferents in the inhibition; the discharge of motor units in biceps brachii was not influenced by stimulation of the skin at two different sites on the upper arm.

It was not possible to stimulate with sufficient selectivity the branches of the radial nerve to brachialis and brachioradialis with surface electrodes. The strength of inhibition with brachialis stimulation (2.2%) tended to be less than with brachioradialis stimulation (6.1%), but optimising the stimulation to the brachialis branch was still $\sim 0.7 \times$ MT for the brachioradialis branch. Because an intensity of $0.7 \times$ MT was sufficient to delay the discharge of a biceps brachii motor unit (Fig. 4), this might explain the observed inhibition with brachialis nerve branch stimulation. However, it was not possible to exclude the involvement of afferents from the brachialis muscle.

Inhibition in the two heads of biceps brachii

Motor unit recruitment and discharge characteristics in the two heads of biceps brachii can differ (ter Haar Romeny et al. 1984; van Zuylen et al. 1988; Herrmann and Flanders 1998). For example, some motor units in the medial portion of the long head of biceps brachii had lower recruitment thresholds when supination torques were performed concurrently with an elbow flexor torque, whereas motor units in the lateral portion could only be recruited when a flexor torque was exerted by itself (ter Haar Romeny et al. 1984). In contrast, motor units in the short head of biceps brachii could only be recruited when the task involved a combination of flexion and supination torques (van Zuylen et al. 1988). Few motor units were recorded in these studies, however, and more recent evidence indicates that motor units with different recruitment patterns are distributed continuously across biceps brachii rather than being clustered into discrete muscle regions (Herrmann and Flanders 1998). Nonetheless, the activation patterns of motor units from the long and short heads of biceps brachii does appear to differ (Herrmann and Flanders 1998).

Consistent with a possible functional distinction between motor units in the short and long heads of biceps brachii, a cadaveric study found that the distal tendon attachment had two distinct parts in 10 of 17 specimens and was interdigitated in the other 7 specimens (Eames et al. 2007). The tendon for the short head inserted distally on the radial tuberosity, which places it in a more advantageous position to produce flexion torques. The tendon for the long head inserted proximally on the radial tuberosity, and based on its origin at the supraglenoid tubercle, appears to be positioned for a stronger contribution to a supination torque (Athwal et al. 2007; Eames et al. 2007).

It has been proposed that spinal reflex pathways are responsible for the difference in activation of the motor unit populations in the two heads of biceps brachii (Jongen et al. 1989). Results obtained in the present study, however, suggest that reflex inhibition from brachioradialis to biceps brachii is not one of the pathways that contribute to the selective activation of motor units from the two heads of biceps brachii, at least not for low-threshold motor units. Ter Haar Romeny et al. (1984) found that the variation in activation was observed in motor units with recruitment thresholds up to 45% MVC force in the long head of biceps brachii, and it could be that the results in the current study are limited by only having recorded low-threshold motor units. Furthermore, the current experiment focused on motor unit activity when the task was to exert an elbow flexion torque and actions about the pronation–supination axis were not measured.

Alternatively, inhibitory reflex pathways from other upper arm muscles could be responsible for controlling the differential recruitment profiles of motor units in the two heads of biceps brachii (Cavallari and Katz 1989; Jongen et al. 1989; Naito 2004). Reciprocal inhibition has been demonstrated between the biceps brachii and triceps brachii (Katz et al. 1991), and coactivation of these muscles during elbow flexion tasks results in different patterns of muscle activation within and between the two heads of biceps brachii (Jongen et al. 1989).

Forearm position

Biceps brachii and brachioradialis act as synergists when producing an elbow flexion torque, but can be synergists or antagonists when exerting a torque about the pronation–supination axis of the forearm (Gielen and van Zuylen 1986; Buchanan et al. 1989; Jamison and Caldwell 1993; Murray et al. 1995; Zhang et al. 1998). Biceps brachii always has a supination moment regardless of forearm position, whereas brachioradialis has a pronation moment when the forearm is supinated and a supination moment when the forearm is pronated (Zhang et al. 1998). Biceps brachii EMG activity is greater when the task involves concurrent flexion and supination torques compared to flexion and pronation torques, but brachioradialis EMG remains relatively constant with variation in forearm position (Buchanan et al. 1989). Motor units located medially in the long head of biceps brachii that contribute to flexion and supination torques have also been shown to become silent when even minimal pronation is produced (ter Haar Romeny et al. 1984). It was suggested that the discharge of these motor units was “gated” by pronation, which could explain the reduced muscle activity observed in biceps brachii when producing pronation torques or when the forearm is in a pronated position (Buchanan et al. 1986; van Zuylen et al. 1988; Buchanan et al. 1989; Jongen et al. 1989; Jamison and Caldwell 1993).

Consistent with these observations, results in the current study included the greatest overall strength of inhibition to the biceps brachii when the forearm was in pronation coupled with the least amount of EMG activity. This finding establishes a spinal reflex basis for the reduced activation of biceps brachii when the forearm is pronated, and is consistent with the reported modulation of the flexor carpi radialis H-reflex between pronated and supinated forearm positions (Baldissera et al. 2000). Because the reflex inhibition of biceps brachii was least when the forearm was supinated, it seems likely that the reduced inhibition enables greater activation of the biceps brachii with the forearm in this position. Furthermore, Naito et al. (1996) only reported inhibition in 11 of the 21 motor units in the biceps brachii, and this may have been a result of the supinated position of the forearm used in that study. Although the task in the current study required subjects to produce low flexion forces, similar patterns of EMG activity between the elbow flexor muscles have been observed during stronger contractions in the flexion and pronation or supination directions (Jamison and Caldwell 1993).

While the modulation of this inhibitory reflex corresponded closely with the typical activation patterns for the elbow flexor muscles, it is paradoxical that the inhibitory feedback from brachioradialis to biceps brachii was actually greatest when the forearm was pronated and both muscles contributed to supination torque, and was least over the small segment of the range of motion when the forearm was supinated and biceps brachii and brachioradialis acted as antagonists about the pronation–supination axis (Zhang et al. 1998). An understanding of the functional significance of this pathway, however, requires information about the opposing inhibitory pathway from biceps brachii to brachioradialis (Naito 2004) and an assessment of the reflex actions when the task involves actions about the pronation–supination axis in addition to a torque in the flexion direction.

In summary, there was no difference in the strength of inhibition observed in the discharge of single motor units located in the two heads of biceps brachii, although the amount of inhibition varied with forearm position. Because the strength of inhibition depended on forearm position, the results suggest that this reflex has a role in modulating the activation of biceps brachii. The inhibition was greatest when the forearm was in a pronated position and biceps brachii activation was reduced, but in this position both muscles can contribute to a supination torque.

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Fig. 1. **a** Schematic representation of the timing of inhibition evoked at 3 different delays (30, 40 and 50 ms following the trigger motor unit discharge at time 0 ms) and a normally distributed interspike interval histogram for a motor unit discharging at approximately 11 pps. These simulated data display the typical variability of the interspike intervals for a “regularly” discharging motor unit with a mean interspike interval of 90 ms (11.1 pps) and a coefficient of variation for the interspike interval of 18% (Matthews 1996; Moritz et al. 2005; Barry et al. 2007), which was similar to the coefficient of variation for the interspike interval for the experimental data. The anticipated arrival of the inhibitory volley 22 ms after stimulation is indicated by the right hand edge of the *horizontal line* beside each numeric label and the *left hand edge* indicates the time at which stimulation was delivered. **b** The mean data for the difference in the interspike intervals for 16 motor units tested with the 3 stimulus delays. This index is the difference between the interspike interval that included the stimulus (ISI-0) and the three interspike intervals that preceded the stimulation (ISI-pre) for the stimulus and control conditions. Positive values for the ISI difference denote inhibition of the motor unit discharge, which was similar for all three delays ($P = 0.59$). The slightly smaller ISI difference for the 50-ms delay presumably arose because the earliest motor unit discharges would have occurred

prior to the arrival of the inhibitory volley at the motor neuron. The ISI difference for the control condition was close to 0 ms, which indicated that the target background discharge rate was maintained consistently throughout each trial. The stimuli were delivered to the brachioradialis branch of the radial nerve with the forearm in a neutral position

Fig. 2.

The influence of stimulating the brachioradialis branch of the radial nerve on successive interspike intervals. The stimulation was delivered during ISI-0. Data are shown for 66 motor units recorded with the forearm in a neutral position. The *error bars* indicate the 95% confidence intervals

Fig. 3.

Data for 14 single motor units showing the ISI difference evoked by stimulation of the brachioradialis branch of the radial nerve (**b**) and the combined effect of two different sites of cutaneous stimulation (**a**). These data were obtained with the forearm in a neutral position

Fig. 4.

The average response of 4 motor units in biceps brachii to increasing intensities of stimulation applied to the brachioradialis branch of the radial nerve. 87 ± 12 stimuli were delivered at each of the 8 stimulus intensities with the forearm in a neutral position. No responses were obtained from one motor unit to stimuli at 0.75 and $1.1 \times MT$

Fig. 5.

Mechanical tendon taps (200 Hz, 15 ms) were applied either to the distal tendon or belly of extensor carpi radialis and brachioradialis in two sequences while recording from the same single motor unit. **a** Sample PSTHs and cumulative sums from a single subject reveal the previously described excitatory effect of stimulating muscle spindles in the extensor carpi radialis, which contrasts with an inhibitory effect induced by mechanical taps applied to the brachioradialis. **b** Mean data for 6 single motor units in response to randomly intermingled electrical stimulation to the brachioradialis branch of the radial nerve and mechanical taps to the tendon or belly of the brachioradialis muscle. These data were obtained with the forearm in a neutral position

Fig. 6.

The ISI difference for the stimulus and control conditions for each of 31 motor units from the long head (**a**) and 26 motor units from the short head (**b**) of biceps brachii. The difference between the baseline ISIs and the ISI that included the stimulation was significant for both heads ($P < 0.001$) with no difference between the heads ($P = 0.11$). The data were obtained with the forearm in a neutral position and stimuli were delivered to the brachioradialis branch of the radial nerve. The 2 motor units from the short head of biceps brachii (**b**) that displayed the greatest inhibition were both recorded from the same subject and motor units recorded from this subject's long head also displayed some of the largest inhibition in the sample

Fig. 7.

Post-stimulus time histograms and overlaid motor unit action potentials for the same single motor unit recorded with the forearm in pronated, neutral, and supinated positions. The post-stimulus time histograms were constructed for the stimulation and control conditions, and the cumulative sum procedure was applied to the difference between the stimulation and control histograms; the negative deflection denotes an inhibitory effect of the stimulation that prolonged the time to the next discharge of an action potential by the motor neurone. The stimulation was delivered at time 0 ms, which corresponded to a delay of 30 ms after the preceding motor unit discharge

Fig. 8.

The difference between the interspike interval that included the stimulus (ISI-0) and the three interspike intervals that preceded the stimulus (ISI-pre) for stimulation and control conditions averaged for all motor units (**a**) and for each motor unit (**b**) when the forearm was in the pronated, neutral, and supinated positions. The strength of inhibition was significantly modulated with forearm position ($P < 0.05$). As an index of stimulus consistency, the peak-to-peak amplitudes of the M-wave responses (**c**), expressed as a proportion of a control M-wave, is shown for each motor unit when the forearm was in the pronated, neutral, and supinated positions ($P = 0.9$)

Table 1

Relative stimulus intensities for brachioradialis and brachialis when the stimulation was optimised for the other muscle

Motor unit	Brachioradialis 0.9 MT Proportion of brachialis MT	Brachialis 0.9 MT Proportion of brachioradialis MT
1	0.95	0.65
2	0.54	0.88
3	0.90	0.72
4	0.78	0.74
5	0.57	0.82
6	0.86	0.56
7	0.86	0.64
8	0.72	0.46
9	0.87	0.73
Mean (SD)	0.78 (0.15)	0.69 (0.13)

Table 2

Summary data for 57 motor unit recordings from the short and long heads of the biceps brachii during spike-triggered stimulation of the brachioradialis branch of the radial nerve

	Long head (<i>n</i> = 31)	Short head (<i>n</i> = 26)
Trial duration (s)	271 ± 53	270 ± 77
Number of stimuli	98 ± 20	100 ± 24
Mean force (% MVC)	3.0 ± 2.0	4.3 ± 2.2
Mean interspike interval (ms)	89.1 ± 5.7	90.9 ± 6.4
Coefficient of variation for ISI (%)	18.3 ± 5.0	17.7 ± 7.6

No significant differences between the heads ($P > 0.3$), except for mean force ($P < 0.05$)

Table 3

Force and discharge characteristics for 18 motor units recorded in each of the three forearm positions

	Pronated	Neutral	Supinated
Trial duration (s)	234 ± 58	275 ± 87	233 ± 62
Number of stimuli	90 ± 24	94 ± 23	88 ± 26
Mean force (% MVC)	4.1 ± 1.5	3.7 ± 1.9	4.3 ± 1.9
Mean interspike interval (ms)	88.3 ± 5.2	89.1 ± 5.8	86.7 ± 6.1
Coefficient of variation for ISI (%)	15.5 ± 5.2	17.1 ± 6.3	14.9 ± 4.4

No significant differences for force ($P > 0.45$) or interspike interval (ISI) data ($P > 0.14$). Data are combined for the nine motor units from each head of biceps brachii because there was no significant difference ($P \geq 0.20$) between these samples for the force or discharge rate characteristics