

Control of motor units in human flexor digitorum profundus under different proprioceptive conditions

S. Jayne Garland* and Timothy S. Miles

Department of Physiology, The University of Adelaide, Adelaide, SA 5005, Australia

1. Changing the posture of the human fingers can functionally 'disengage' the deep finger flexor muscle from its normal action on the terminal phalanx of the fourth (or third) finger. This enables the activity of the muscle to be studied both with and without its normal proprioceptive inputs.
2. Spike trains of long duration from pairs of concurrently active motor units in this muscle were recorded in both the engaged and disengaged hand postures. Subjects voluntarily kept one of the motor units (the 'controlled' unit) discharging at the same target frequency in both postures. The strength of short-term synchrony, the strength of common drive, and the variability of discharge of these pairs of motor units were determined in both postures.
3. All subjects reported that the effort required to activate the motor units in the disengaged hand posture was substantially greater than in the normal engaged posture.
4. Short-term synchrony, which is a function of common corticospinal inputs to pairs of motor units, was similar in both hand postures. However, the strength of common drive was significantly decreased when the muscle was disengaged. Although the neural substrate for common drive is not known, this observation suggests that proprioceptive feedback is involved either directly or indirectly.
5. Although the discharge rate of the 'uncontrolled' motor units increased when the muscle was disengaged, the variability of discharge of these and the 'controlled' motor units increased significantly. This supports the idea that the precision with which fine motor tasks can be performed is improved when proprioceptive feedback is intact.

During a voluntary muscle contraction, some of the excitatory input to the motoneurons comes from the central nervous system and some from sensory receptors in the muscles, joints and skin that are activated by the contraction itself. There are comparatively few studies on the relative importance of the descending command and the peripheral feedback on shaping motoneurone output, but the data that are available suggest that muscle afferents contribute up to 30% of the drive to motoneurons in voluntary contractions (Macefield, Gandevia, Bigland-Ritchie, Gorman & Burke, 1993).

However, two consequences of the neural command that can be measured in humans are short-term synchrony of motoneurons and the strength of common drive to motoneurons. Short-term synchrony is the greater than chance tendency of motoneurons to discharge within a few milliseconds of each other (Sears & Stagg, 1976). This is thought to be the result of neurones that branch to give excitatory postsynaptic potentials to several motoneurons simultaneously, thereby slightly increasing the probability

that they will discharge synchronously (Kirkwood & Sears, 1978; Datta & Stephens, 1990). Although the pathways that contribute to short-term synchronization are not known with certainty, there is evidence that corticospinal inputs play a major role (Datta, Farmer & Stephens, 1991; Farmer, Swash, Ingram & Stephens, 1993). Common drive is the tendency of the fluctuations in firing rates of motoneurons innervating a given muscle to change in parallel (De Luca, LeFever, McCue & Xenakis, 1982). This clearly reflects a common excitatory (or inhibitory) input to the motoneuronal pool, although the identity of the neurones responsible for common drive are not known.

In this study, we sought to determine the effect on motoneurons of disturbing the balance between their central and peripheral inputs, by exploiting the unique anatomy of the human hand. *Gray's Anatomy* (Williams & Warwick, 1980) describes a hand posture in which one cannot voluntarily flex (or extend) the distal interphalangeal joint of the fourth (or alternatively the third) finger. In this posture, the tendon of the flexor digitorum profundus (FDP)

* Present address to which correspondence should be sent: the Department of Physical Therapy, Elborn College, University of Western Ontario, London, Ontario, Canada N6G 1H1.

muscle is functionally 'disengaged' from the terminal phalanx on which it normally exerts tension. The muscle can still shorten, but does not exert force on the distal phalanx. The effectiveness of this disengagement has been demonstrated by the abolition of the normal stretch reflexes when the hand is held in this posture (Matthews & Miles, 1988). We reasoned that the functional disengagement would result in a marked change in the afferent input to the nervous system, particularly from proprioceptive afferents (Gandevia & McCloskey, 1976). Cutaneous afferent activity will be modified also in the disengaged posture as contraction of FDP will not result in the same pressure on the skin and subcutaneous tissues as it does during a normal isometric contraction.

In the present study, motoneuronal behaviour was studied under conditions in which the net excitatory drive was kept constant by voluntarily discharging one motor unit at a constant rate, and the balance of peripheral and central inputs to the parent motoneurone was varied.

METHODS

Eight successful experiments were conducted with one female and two male subjects (aged 24–49 years) including the authors. All subjects gave their informed consent and the project was approved by the University of Adelaide Human Ethics Committee. Two surface electromyogram (EMG) electrodes were placed on the skin overlying FDP to record the EMG in the bandwidth 30–300 Hz. Two separate fine-wire electrodes were inserted into FDP to record motor unit activity (bandwidth, 0.1–6 kHz). All electrodes were placed 1–2 cm apart approximately 8 cm distal to the medial epicondyle on the medial aspect of the forearm. The accuracy of the

placement was confirmed by the activity of the muscle or its motor units during specific finger movements. Twenty-six of the thirty FDP motor units studied were recruited during voluntary flexion of the distal interphalangeal joint of the fourth finger. The remaining four motor units were activated during voluntary flexion of the distal joint of the third digit, which can also be disengaged from FDP with the appropriate hand posture (details below). FDP motor units were not activated by active flexion of the proximal interphalangeal joints or during wrist flexion and radial deviation. The protocol required that the action potentials of different FDP motor units in each of the two electrodes could be accurately discriminated in the two hand postures used. Data were excluded when action potentials from the same motor unit could be detected in both electrodes, as this would result in discrimination errors due to superimposition of spike waveforms. The motor unit whose action potentials could be most accurately discriminated without off-line processing was usually taken as the 'controlled' unit.

Subjects sat with the shoulder and elbow flexed to about 90 deg and the forearm vertical with the wrist extended. Where possible, the activity of the same pair of motor units was recorded in two hand postures. In the 'FDP-engaged' posture, all fingers were extended and supported by a vertical surface. In the 'FDP-disengaged' posture (shown schematically in Fig. 1), the fourth finger was passively held in the fully flexed position with the other digits in full extension as before. Strong efforts to flex the distal joint of the fourth finger produced large EMG signals in FDP but did not move the joint in this posture. The distal phalanx of the third finger was disengaged when required by fully flexing the third finger while keeping the other digits in full extension.

Subjects were first taught to activate FDP in both the extended and flexed (disengaged) postures by observing its EMG on an oscilloscope screen. The feedback was then changed to a visual display of the controlled motor unit's firing rate, plus the sound of its spike train. Subjects were instructed to keep this unit firing

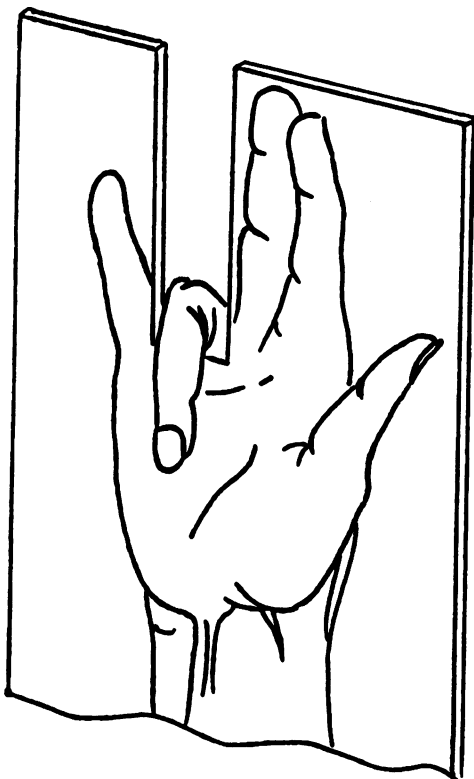


Figure 1. Schematic diagram of the apparatus for holding the hand in the engaged and disengaged postures

The forearm was vertical with the elbow resting on a cushion (not shown) and the palm of the hand held against a vertical board that was rigidly fixed to the bench. This board, drawn here as though it were transparent, had a vertical slot through which the fourth (or third) finger could be fully flexed, as shown, while the other fingers remained extended and pressing against the board: this is the FDP-disengaged posture. In some experiments, the finger was held in this fully flexed position by straps. In the FDP-engaged posture, the slot was covered by a plate (not shown): all of the fingers were extended, and the subject flexed the distal interphalangeal joint of the fourth (or third) finger isometrically against this plate.

steadily at a comfortable mean rate (usually 10–12 Hz) for about 3 min while the fingers were held in one posture, then in the other. The sequence in which the two postures were adopted was random from one experiment to the next. In each posture, the subject flexed or attempted to flex the distal interphalangeal joint isometrically for about 3 min in a manner that kept the controlled motor unit firing at a constant rate. The motor unit was then kept discharging constantly as the finger was moved slowly to the second posture. The waveforms of both units were watched carefully on a digital oscilloscope throughout this repositioning. It was often not possible to identify both units in both postures, in which case the data were not used for cross-correlogram and common-drive analysis. The spike train data from both intramuscular electrodes and the surface EMG were recorded on digital tape (sampling rate, 22 kHz per channel), together with a regular timing pulse that was used in the subsequent off-line analysis.

The spike trains from both intramuscular electrodes were discriminated off-line. When more than one motor unit was present in the recorded spike train signal, a graphic equalizer was used to maximize the difference in the shapes of their spikes before the signal was discriminated. The computer-based discriminator sampled the spike train at 90 kHz and used a template-matching algorithm to sort the spikes (SPS-8701 waveform discriminator, Signal Processing Systems, Malvern, Australia). For the cross-correlogram analyses used to assess short-term synchrony, the accuracy of discrimination was always >90% for both motor unit spike trains. However, for the common-drive analysis, it is essential to have >99% accuracy of spike identification, although the spike trains need not be so long. For this analysis, waveforms that did not match the spike template, usually because they consisted of two motor unit potentials that occurred simultaneously, were subjected to a further analysis in which they were decomposed into the constituent motor unit potentials by a subtraction algorithm using an in-built function of the SPS-8701 waveform discriminator.

The mean interspike interval (ISI), its standard deviation (s.d.) and the coefficient of variation (c.v.) of the ISIs (i.e. s.d./mean ISI) were calculated in each of the two positions. ISIs that were more than twice the mean were excluded from these calculations on the grounds that they probably represented missed spikes (Andreassen & Rosenfalck, 1980; Nordstrom, Fuglevand & Enoka, 1992). To determine the strength of short-term synchronization of pairs of motor units whose spike trains were recorded from different electrodes, cross-correlograms (bin-width, 1 ms) were constructed for a period of ± 100 ms around the discharge of the reference motor unit. The width of the peak (n bins) was measured from the cusum of the cross-correlogram. The strength of short-term synchrony for each pair was estimated with the k' value ($k' = x/nm$, where x is the sum of the counts in the n bins of the peak, and m is the mean count expected to fall into any bin by chance, which was calculated from fifty bins in flat parts of the histogram on each side of the peak; Ellaway & Murthy, 1985).

The strength of common drive of motor unit pairs was determined for 20–50 s of the 3 min contraction in 3–5 s epochs distributed throughout the trial, using the method of De Luca *et al.* (1982): the algorithm is given in the Appendix. Briefly, the instantaneous discharge frequency of both units in each pair of simultaneously active motor units was smoothed with a 400 ms symmetrical Hanning-window digital filter. The smoothed firing rates were then high-pass filtered at 0.75 Hz to remove the DC offset so that only fluctuations in smoothed firing rate were analysed. The fluctuations were cross-correlated to reveal common variations in discharge rate. Coefficients for common drive can range from +1, indicating perfect correlation of the fluctuations of the discharge rates of the two motor units, to -1, indicating a perfect negative correlation. The coefficient for common drive was determined as the mean value from five to ten epochs. The statistical analyses were performed using Student's paired t test and linear regression with a significance level set at $P = 0.05$.

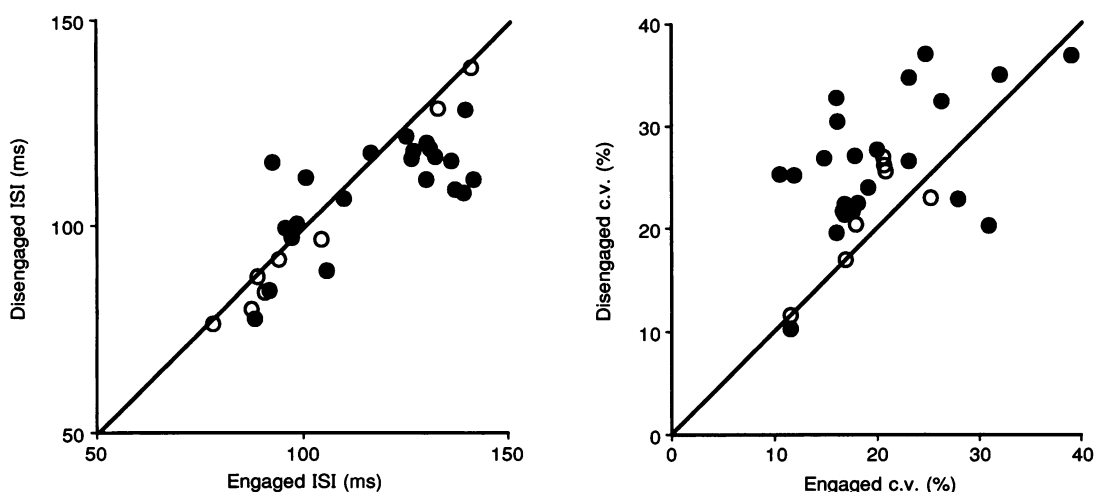


Figure 2. Analysis of pooled spike train data for thirty FDP motor units for which spike trains were recorded in both the extended (engaged) and flexed (disengaged) hand postures

Open circles show data for the eight controlled motor units, and filled circles the data for the twenty-two concurrently active motor units, whose firing rates were not controlled. The spike trains of all the uncontrolled motor units were recorded while a controlled unit was discharging concurrently. Five of the uncontrolled motor units were discriminated from the same electrode as the control channel, and seventeen from the second electrode. The diagonal line is the line of identity. Left panel, mean ISIs in the two hand postures; right panel, coefficients of variation (c.v.) for the same motor units.

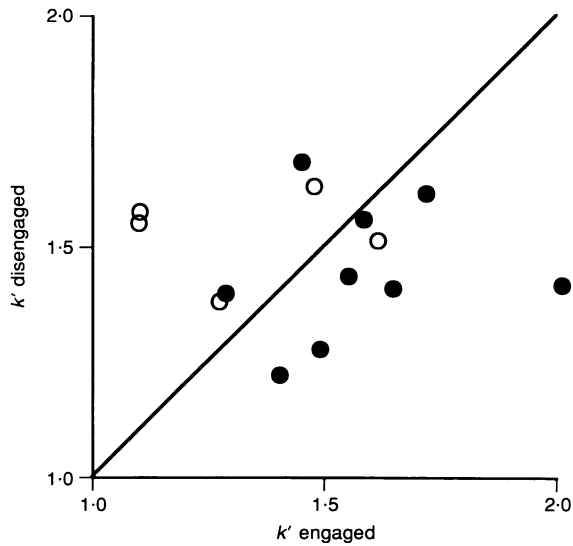


Figure 3. Strength of short-term synchrony between fourteen pairs of concurrently active FDP motor units in the extended (engaged) and flexed (disengaged) hand postures

Each pair consists of one controlled and one uncontrolled motor unit. The k' values show that there is no consistent difference in the strength of synchrony between the two positions. Open circles show the k' values for the pairs of motor units that were also analysed for common drive in the two hand postures.

RESULTS

All subjects reported that the effort required to keep a single motor unit discharging at a constant rate was much higher in the FDP-disengaged posture than in the more physiological posture in which all of the fingers were extended and FDP was able to move the distal phalanx. However, after familiarization with the task, all subjects could keep the controlled unit firing without discomfort for

several minutes, although this exercise was reported to be tiring. It was difficult to record well-discriminated spike trains from the same pair of motor units in the two hand postures. On many occasions, it was possible to discriminate pairs of motor units accurately in one hand posture, but one or both units could not then be discriminated when the finger was moved, presumably because of a change in the electrode-to-muscle fibre geometry.

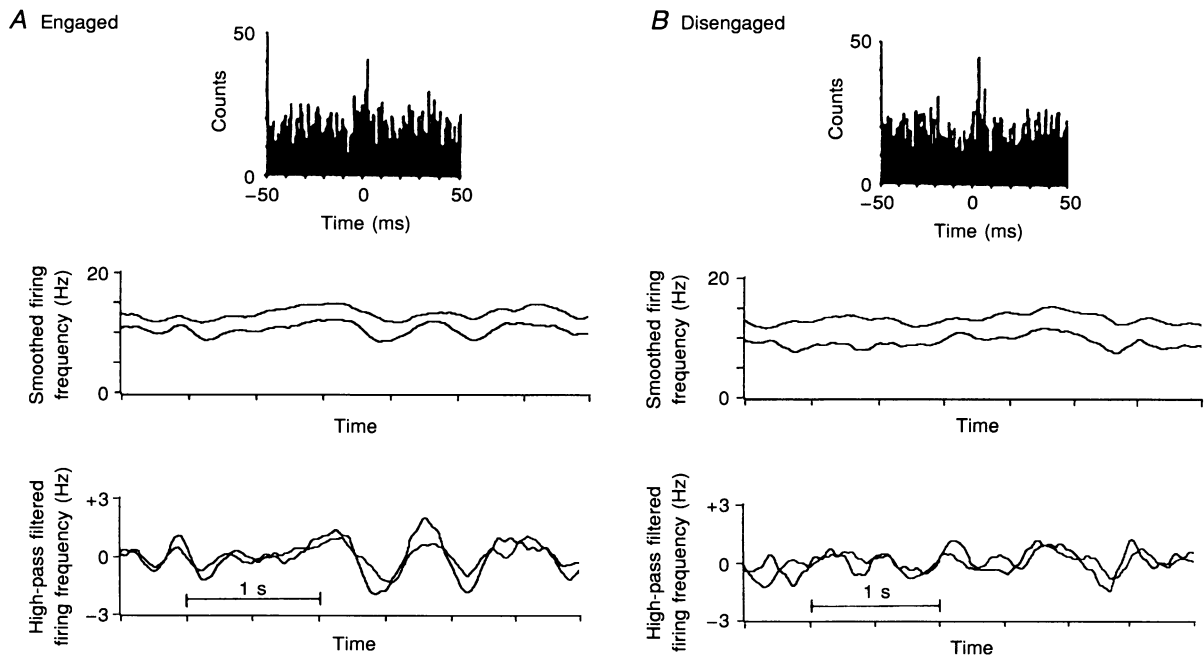


Figure 4. Common drive in a pair of concurrently active FDP motor units in extension (engaged) and flexion (disengaged)

In each panel, the inset shows the cross-correlogram of the spike trains of the two motor units. The k' value is 1.27 and 1.38 when the finger is engaged and disengaged, respectively. Below this is a record of the firing rates of the two units, smoothed with a 400 ms Hanning-window filter. The lowermost records show the fluctuations in smoothed firing rates during the same 3.5 s epoch. In this epoch, the CD coefficient was 0.86 and 0.73 in extension and flexion, respectively.

Table 1. Short-term synchrony indices and mean common drive cross-correlation coefficients for five pairs of FDP motor units in the engaged posture (extension) and the disengaged posture (flexion)

Motor unit pair no.	k'		Common drive index	
	Engaged	Disengaged	Engaged	Disengaged
1	1.27	1.38	0.72	0.71
2	1.48	1.63	0.59	0.53
3	1.61	1.51	0.57	0.44
4	1.10 *	1.58	0.53	0.47
5	1.10 *	1.55	0.49	0.38

* Not significant.

The mean ISI and c.v. of ISIs for the thirty motor units from which useful data were obtained in both hand postures are plotted for both postures in Fig. 2. Note that the mean ISI was controlled by the subject in eight of these motor units in both hand postures (Fig. 2, open circles), with the help of auditory and visual feedback. Hence, the mean ISIs for these eight controlled units fell close to the line of identity (mean ISI \pm s.d. was 102 ± 23 ms when engaged, 98 ± 23 ms when disengaged). The discharge rates of the other twenty-two motor units were not under feedback control. Their mean ISI was 118 ± 19 ms when engaged with the fingers-extended hand posture. However, Fig. 2 shows that they usually discharged at higher mean rates when FDP was disengaged (mean ISI, 109 ± 13 ms).

When the data for all FDP motor units were pooled, the mean c.v. was significantly greater in the disengaged position than in the engaged position. The increase was significant in both the controlled and uncontrolled motor units: when the muscle was disengaged, the mean increase in c.v. was 2.8% ($t = 2.5$; 7 degrees of freedom (d.f.); $P = 0.04$) for the controlled units, and 6.1% ($t = 3.53$; 21 d.f.; $P = 0.002$) for the uncontrolled units.

The spike trains of fourteen pairs of motor units active in both hand postures were cross-correlated. The k' values indicating the strength of short-term synchrony in the FDP-disengaged posture are plotted against the k' values for the FDP-engaged posture in Fig. 3. Twelve pairs of motor units showed significant short-term synchrony in both hand postures. Two pairs had significant short-term synchrony in the disengaged but not in the engaged position. The mean k' for engaged and disengaged postures was 1.48 ± 0.25 and 1.48 ± 0.14 , respectively. The width of the cross-correlogram peak was 12 ± 3 and 12 ± 4 ms in the engaged and disengaged positions, respectively. Overall, there was no significant difference in the amount of short-term synchrony (k' or width of peak) between the engaged and disengaged postures. Five pairs of motor units (shown as open circles in Fig. 3) were analysed for common drive both when FDP was engaged and disengaged (Table 1). Strong common drive was found for all five pairs. Figure 4 illustrates the strong tendency for the smoothed firing

frequency and the high-pass filtered firing frequency of one pair of motor units to covary in both the engaged and disengaged postures (motor unit pair no. 1 in Table 1). When the finger was moved from the FDP-engaged to the FDP-disengaged posture, the mean firing rate of the controlled unit (about 12.5 Hz) did not change, however, the mean firing rate of the second motor unit decreased from a mean of about 10 Hz to about 8 Hz. The strength of common drive also declined when the muscle was disengaged. The cross-correlograms show that the strength of short-term synchrony between the two motor units was unchanged when the muscle was disengaged. The strength of common drive was lower in all five pairs when FDP was disengaged than when engaged (mean, 0.51 ± 0.13 vs. 0.58 ± 0.09 ; $P = 0.03$).

DISCUSSION

Muscle afferents normally provide a net facilitation to the motoneurons which reflexly increases the motor output at all levels of voluntary drive. For example, Macefield *et al.* (1993) have shown that, when proprioceptive afferent signals were blocked with local anaesthetic, the maximal voluntary firing rates of the motoneurons fell significantly. The present study is based on the premise that changing the hand posture so that FDP is either engaged in the normal way or is disengaged will decrease the afferent feedback primarily from muscle receptors. Steady-state muscle spindle primary afferent discharge from the finger flexor muscles has been shown to decline with increasing flexion of the metacarpophalangeal joint in the non-contracting muscle (Vallbo, 1974). In contracting muscle, the steady state muscle spindle afferent discharge from finger extensor muscles was found not to change between two joint angles that differed by 20 deg (Hulliger, Nordh & Vallbo, 1982).

It is not clear whether the above observations can be extrapolated to the present experiment, since the change in the joint angle between the engaged and disengaged postures was about 100 deg, and this resulted in functional disengagement of the muscle tendon. There is no direct evidence on the effect of disengagement on the spindle afferent activity when the muscle is active. However, the

anatomy of this muscle suggests that the extrafusal fibres which exert force on the terminal phalanx during an isometric contraction will shorten with less resistance when the muscle is disengaged than when it is engaged. If this is so, the intrafusal fibres in the active, disengaged muscle should also contract without resistance, which would result in diminished afferent discharge at comparable levels of muscle activity (for a related reference, see Proske, Morgan & Gregory, 1992).

While it is not possible from the present experiments alone to know precisely how the proprioceptive input from FDP changes in the disengaged position, there are other lines of evidence that support our contention that it is markedly decreased in this posture. Firstly, we have shown elsewhere that the activity of the motor cortex is greater when FDP motor units are made to discharge at the same rate in the disengaged compared with the engaged posture (Garland & Miles, 1997). In this earlier study, we compared the response of single FDP motor units to transcranial magnetic brain stimulation in both hand postures. Although the subjects kept the motor units discharging tonically at the same rate in both postures, the response evoked by motor cortical stimulation at corticospinal latency was significantly greater when the muscle was disengaged. The net drive to the motoneurons was similar in both hand postures (as in the present experiments), therefore, the increased response to the magnetic stimulus indicates that the level of tonic corticofugal activity is increased in the disengaged posture, presumably to compensate for a decrease in the proprioceptive input. This is consistent with the observations of Macefield *et al.* (1993) who estimated that the proprioceptive drive to motoneurons was as much as 30% of the total excitatory input.

There is less direct, but still compelling evidence from the observation in both the present and our earlier study that all of the subjects, who were familiar with adopting the two hand postures, reported that far more effort was required to make a motor unit discharge at the same rate when the muscle was disengaged, and that this effort was tiring. The sense of effort is thought to be mediated by a copy of the descending motor command to the motoneurone pool (e.g. Gandevia & McCloskey, 1977). Thus, the increased effort required to keep the controlled motoneurone discharging at the same rate during disengagement indicates an increase in the level of descending excitatory activity to FDP motoneurons in this hand posture.

Short-term synchrony

There is considerable evidence that the substrate for short-term synchrony in pairs of motor units is corticospinal fibres that branch to facilitate both parent motoneurons (Datta *et al.* 1991; Farmer *et al.* 1993). The k' is usually accepted as an index of the strength of these common synaptic inputs to pairs of motoneurons. The strength of short-term synchronization that we observed in FDP lies within the range of values reported for other hand muscles. Our values

of k' (from 1.1 to 2.01) for FDP are somewhat less than those for extensor digitorum communis, for which k' values of 1.2 to 3.49 have been reported (Schmied, Ivarsson & Fetz, 1993), and for first dorsal interosseous (FDI) in which Nordstrom *et al.* (1992) found k' values of 0.79–3.44.

Earlier studies have shown that the strength of short-term synchrony can change with different motor tasks. Adams, Datta & Guz (1989) compared synchronization in the same pairs of sternocleidomastoid motor units in conscious humans during reflex hypercapnic breathing, obstructed voluntary breathing, and unresisted isometric neck rotation. The strength of synchronization was strongest during voluntary breathing, suggesting that different pathways to motoneurons are utilized for reflexly driven compared with voluntary breathing. Bremner, Baker & Stephens (1991) compared the synchronization of FDI motor units during index finger flexion, extension, and abduction. They found that synchronization was greatest during finger extension and least during finger flexion. Thus, different motor commands appear to utilize different common presynaptic inputs to the same motoneurons. These previous studies demonstrated differences in motor command signal organization during different tasks. However, in the present study, the task was nominally the same in two hand postures, i.e. to flex or attempt to flex the distal joint of the fourth finger. In the extended position, the tendon was engaged and exerted forces on the distal phalanx in the normal way. In the flexed position, the tendon did not transmit force across the joint. Although the sensory feedback associated with the contraction was different in the flexed compared with the extended position, Fig. 3 shows that this did not result in a significant difference in the strength of short-term synchrony. This is consistent with observations made on pairs of FDI motor units in a deafferented subject, in which the strength of synchrony was apparently unchanged (Baker, Bremner, Cole & Stephens, 1988), and with the earlier conclusion that short-term synchrony is primarily the result of corticospinal rather than peripheral inputs to pairs of motoneurons (Datta *et al.* 1991; Farmer *et al.* 1993).

Hence, the present observation that the k' did not change significantly when the finger was moved between the engaged and disengaged postures shows that, even when the overall descending drive to the motoneurons increases, the relative contribution of branched inputs to different motoneurons from corticospinal neurons controlling finger flexion remains the same.

Common drive

The present study demonstrates the presence of common drive in pairs of motor units in FDP. Because the common drive cross-correlations increase with increasing widths of the Hanning-window filter, our values for common drive are compared only with those from studies utilizing the same 400 ms window. In our task, which was essentially a steady isometric contraction of FDP, the common drive correlation

ranged from 0.37 to 0.74. These are similar to those found in other hand muscles. De Luca & Mambrito (1987) reported common drive cross-correlations of 0.58 ± 0.14 for pairs of flexor pollicis longus motor units during an isometric co-contraction task, and 0.83 ± 0.08 during isometric random-force tracking experiments. Semmler, Wallace & Nordstrom (1996) found mean common drive cross-correlations of 0.44 (range, 0.03–0.74) in FDI muscle during a sustained low-force isometric task.

The neural substrate for common drive is not known, although De Luca & Mambrito (1987) concluded that it must be mediated at least in part by central sources because it is present in motoneurons in co-active antagonistic muscles. Later, Kamen & De Luca (1992) found that levels of common drive in facial muscles that lack muscle spindles (although they do have stretch reflexes), were comparable with those in limb muscles. In the present study, the strength of common drive to all motor unit pairs decreased when the hand posture was changed from FDP-engaged to FDP-disengaged, indicating that common drive is sensitive to changes in proprioceptive feedback or, less probably, to the level of descending drive. This could be the result of a direct contribution of proprioceptive feedback to common drive. Alternatively, the decreased strength of common drive in the disengaged muscle could be secondary to a change in the balance of the descending inputs from several sources that must increase in order to maintain the same rate of discharge in the controlled motoneuron during disengagement.

Coefficient of variation

The clearest finding in the present study was the increased variability in the discharge of FDP motoneurons when the muscle was disengaged. This was particularly prominent for the motor units whose firing rates were not being directly controlled by voluntary effort. There is normally a clear relationship between mean motor unit firing rate and discharge variability in which discharge variability decreases with increases in discharge rate (Person & Kudina, 1972; Warren, Miles & Türker, 1993). Figure 2 shows that although the uncontrolled units (filled circles) tended to fire at higher rates when the muscle was disengaged, the faster discharges were associated with more variability, not less as is normally the case. This increase in discharge variability can be accommodated within our hypothesis of a relative increase in the corticospinal input to FDP motoneurons to replace the reduced proprioceptive input in the disengaged posture. One important source of discharge variability in a tonically discharging motor unit is the level of synaptic noise on the membrane potential of the parent motoneuron (Warren *et al.* 1993). Temporal facilitation of corticospinal excitatory postsynaptic potentials (EPSPs) in motoneurons is known to be strong (Porter & Muir, 1973). Hence, when FDP is disengaged, the relative increase in the corticospinal input to FDP motoneurons would produce more, larger EPSPs that would increase the synaptic noise on FDP motoneurons and contribute to the increased discharge variability.

In their classical study on the motor performance of a deafferented subject, Rothwell, Traub, Day, Obeso, Thomas & Marsden (1982) found that their subject had particular difficulty with complex fine motor tasks requiring hand dexterity such as handwriting, and picking up small objects. The deficit in performing these tasks suggests that proprioceptive feedback normally contributes to the process by which fine voluntary control is exerted over muscles. Thus, the diminished accuracy with which the discharge rate of FDP motoneurons was controlled when it was disengaged could also be explained by a more general deficit in the mechanism of motor control due to the decrease of proprioceptive information.

Finally, it is possible that the increased discharge variability in the disengaged posture is due in some way to the unusual sensation experienced when one strives to contract the disengaged muscle. However, given that the subjects were very familiar with this exercise, and that increased variability was observed in all subjects, we believe that this is a less likely explanation.

In the present study, disengaging the muscle led to an increase in the variability of motor unit discharge but no change in the strength of synchrony. This suggests that these two phenomena are the result of different underlying processes. A similar disassociation between short-term synchrony and common drive has recently been observed in FDI where only 6% of the variation in common drive could be accounted for by differences in the strength of short-term synchrony (Semmler *et al.* 1996).

In summary, changing the hand posture so that FDP is functionally disengaged from exerting force across the terminal interphalangeal joint increases the sense of effort required to discharge motor units at the same rate, increases the mean firing rate of the uncontrolled motor unit while also increasing its variability of discharge, and decreases the common drive to pairs of motor units without changing the short-term synchrony of those pairs. These observations support the idea that disengaging the muscle changes the balance between tonic descending and proprioceptive inputs to voluntarily activated motoneurons in favour of the descending, principally corticospinal input. They also suggest that proprioceptive feedback does not contribute noticeably to short-term synchrony between motoneurons but may directly or indirectly contribute to the in-phase variation of motoneurons innervating a muscle that is known as common drive.

APPENDIX

Common drive correlation analysis

The method of De Luca *et al.* (1982) for determining the strength of common drive of pairs of motor units was followed, using an implementation developed by Mr Christopher Wallace. It involved the following three steps.

Construction of a continuous firing rate for the discharges of both motor units. The impulse train representation of the motor unit discharges was passed through a time-symmetric, non-causal Hanning-window digital filter with a sample interval of 0.25 ms, based on the spike discriminator's resolution. This is equivalent to finding the sum of the set of functions in which each discharge time is the centre of a unit area, full-period cosine 'hump' rising from a zero baseline. The standard width of 400 ms was used for smoothing.

High-pass filtering so as to consider the fluctuations in each of the firing rates. To remove DC bias another (digital time-symmetric, non-causal) zero-phase filter was used, with its low-frequency -3 dB point at 0.75 Hz:

$$H(f) = 1 - \sin(\pi f)/\pi f = 1 - \text{sinc}(f),$$

where $H(f)$ is the Fourier transform function and f is frequency. This was implemented in the frequency domain by multiplication with the Fourier-transformed firing rate records. The problem of this circular convolution is avoided by buffering the analysis epoch by 500 ms on each side, then dispensing with the buffer.

Cross-correlating the firing rates to determine a coefficient that measures their covariation. To investigate common firing rate behaviour, a correlation function was evaluated over a range of lead/lag intervals extending beyond the ± 50 ms range in which appreciable common drive occurs:

$$r_{xy}(i) = \frac{\sum_{j=0}^{n-i-1} x(j+i)y(j)}{\sqrt{\left(\sum_{k=0}^{n-1} x(k)^2\right)\left(\sum_{k=0}^{n-1} y(k)^2\right)}},$$

$$0 \leq i < N < n; r_{xy}(-i) = r_{yx}(i).$$

The maximum positive correlation in this range was taken to be the common drive correlation coefficient for each motor unit pair. N , \pm number of samples over which to calculate correlation function; n , length of constructed firing rate functions in samples.

- ADAMS, L., DATTA, A. K. & GUZ, A. (1989). Synchronization of motor unit firing during different respiratory and postural tasks in human sternocleidomastoid muscle. *Journal of Physiology* **413**, 213–231.
- ANDREASSEN, S. & ROSENFALCK, A. (1980). Regulation of the firing pattern of single motor units. *Journal of Neurology, Neurosurgery and Psychiatry* **43**, 897–906.
- BAKER, J. R., BREMNER, F. D., COLE, J. D. & STEPHENS, J. A. (1988). Short-term synchronization of intrinsic hand muscle motor units in a 'Deafferented' man. *Journal of Physiology* **396**, 155P.
- BREMNER, F. D., BAKER, J. R. & STEPHENS, J. A. (1991). Effect of task on the degree of synchronization of intrinsic hand muscle motor units in man. *Journal of Neurophysiology* **66**, 2072–2083.

- DATTA, A. K., FARMER, S. F. & STEPHENS, J. A. (1991). Central nervous pathways underlying synchronization of human motor unit firing studied during voluntary contractions. *Journal of Physiology* **432**, 401–425.
- DATTA, A. K. & STEPHENS, J. A. (1990). Synchronization of motor unit activity during voluntary contraction in man. *Journal of Physiology* **422**, 397–419.
- DE LUCA, C. J., LEFEVER, R. S., MCCUE, M. P. & XENAKIS, A. P. (1982). Control scheme governing concurrently active human motor units during voluntary contractions. *Journal of Physiology* **329**, 129–142.
- DE LUCA, C. J. & MAMBRITO, B. (1987). Voluntary control of motor units in human antagonist muscles: coactivation and reciprocal activation. *Journal of Neurophysiology* **58**, 525–542.
- ELLAWAY, P. H. & MURTHY, K. S. K. (1985). The origins and characteristics of cross-correlated activity between gamma-motoneurons in the cat. *Quarterly Journal of Experimental Physiology* **70**, 219–232.
- FARMER, S. F., SWASH, M., INGRAM, D. A. & STEPHENS, J. A. (1993). Changes in motor unit synchronization following central nervous lesions in man. *Journal of Physiology* **463**, 83–105.
- GANDEVIA, S. C. & MCCLOSKEY, D. I. (1976). Joint sense, muscle sense, and their combination as position sense, measured at the distal interphalangeal joint of the middle finger. *Journal of Physiology* **260**, 387–407.
- GANDEVIA, S. C. & MCCLOSKEY, D. I. (1977). Sensations of heaviness. *Brain* **100**, 345–354.
- GARLAND, S. J. & MILES, T. S. (1997). Responses of human single motor units to transcranial magnetic stimulation. *Electroencephalography and Clinical Neurophysiology* **105**, 94–101.
- HULLIGER, M., NORDH, E. & VALLBO, A. B. (1982). The absence of position response in spindle afferent units from human finger muscles during accurate position holding. *Journal of Physiology* **322**, 167–179.
- KAMEN, G. & DE LUCA, C. J. (1992). Firing rate interactions among human orbicularis oris motor units. *International Journal of Neuroscience* **64**, 167–175.
- KIRKWOOD, P. A. & SEARS, T. A. (1978). The synaptic connexions to intercostal motoneurons as revealed by the average common excitation potential. *Journal of Physiology* **275**, 103–134.
- MACEFIELD, V. G., GANDEVIA, S. C., BIGLAND-RITCHIE, B., GORMAN, R. B. & BURKE, D. (1993). The firing rates of human motoneurons voluntarily activated in the absence of muscle afferent feedback. *Journal of Physiology* **471**, 429–443.
- MATTHEWS, P. B. C. & MILES, T. S. (1988). On the long-latency reflex responses of the human flexor digitorum profundus. *Journal of Physiology* **404**, 515–534.
- NORDSTROM, M. A., FUGLEVAND, A. J. & ENOKA, R. M. (1992). Estimating the strength of common input to human motoneurons from the cross-correlogram. *Journal of Physiology* **453**, 547–574.
- PERSON, R. S. & KUDINA, L. P. (1972). Discharge frequency and discharge pattern of human motor units during voluntary contraction of muscle. *Electroencephalography and Clinical Neurophysiology* **32**, 471–483.
- PORTER, R. & MUIR, R. B. (1973). The effect of a preceding stimulus on temporal facilitation at corticomotoneuronal synapses. *Journal of Physiology* **228**, 736–749.
- PROSKE, U., MORGAN, D. L. & GREGORY, J. E. (1992). Muscle history dependence of responses to stretch of primary and secondary endings of cat soleus muscle spindles. *Journal of Physiology* **445**, 81–95.

- ROTHWELL, J. C., TRAUB, M. M., DAY, B. L., OBESO, J. A., THOMAS, P. K. & MARSDEN, C. D. (1982). Manual motor performance in a deafferented man. *Brain* **105**, 515–542.
- SCHMIED, A., IVARSSON, C. & FETZ, E. E. (1993). Short-term synchronization of motor units in human extensor digitorum communis muscle: relation to contractile properties and voluntary control. *Experimental Brain Research* **97**, 159–172.
- SEARS, T. A. & STAGG, D. (1976). Short-term synchronization of intercostal motoneurone activity. *Journal of Physiology* **263**, 357–381.
- SEMMLER, J. G., WALLACE, C. J. & NORDSTROM, M. A. (1996). Short-term synchronization and common drive of firing rates are relatively independent properties of voluntary motor unit discharge. *Proceedings of the Australian Neuroscience Society* **7**, 196.
- VALLBO, A. B. (1974). Afferent discharge from human muscle spindles in non-contracting muscles. Steady state impulse frequency as a function of joint angle. *Acta Physiologica Scandinavica* **90**, 303–318.
- WARREN, J. D., MILES, T. S. & TÜRKER, K. S. (1993). Properties of synaptic noise in tonically active human motoneurons. *Journal of Electromyography and Kinesiology* **2**, 189–202.
- WIEGNER, A. W. & WIERZBICKA, M. M. (1987). A method for assessing the significance of peaks in cross-correlation histograms. *Journal of Neuroscience Methods* **22**, 125–131.
- WILLIAMS, P. L. & WARWICK, R. (1980). *Gray's Anatomy*, 36th edn. Churchill Livingstone, Edinburgh.

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Author's email address

S. J. Garland: jgarland@julian.uwo.ca

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