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Common Drive in Motor Units of a Synergistic Muscle Pair

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De Luca, Carlo J. and Zeynep Erim. Common drive in motor units of a synergistic muscle pair. *J Neurophysiol* 87: 2200–2204, 2002; 10.1152/jn.00793.2001. The interaction among the motor units of the extensor carpi radialis longus (ECRL) and the extensor carpi ulnaris (ECU) muscles in man was studied during wrist extensions in which the two muscles acted as synergists. Intramuscular recordings were obtained using special quadrifilar needle electrodes. Isometric wrist extensions at 20–30% of the maximal effort were studied. The electromyographic (EMG) signals were decomposed into the individual motor-unit action potential trains comprising the signal. The interaction among motor units were characterized by the estimated time-varying mean firing rate and the cross-correlation between the time-varying mean firing rates of pairs of motor units. Pairs of motor units within each muscle as well as pairs of motor units across the muscles were considered. In-phase common fluctuations, termed common drive, were observed in the mean firing rates of motor units within each muscle, consistent with earlier work on other muscles. Common fluctuations were also observed between the firing rates of ECU and ECRL motor units albeit with a variable phase shift. The existence of common drive across synergistic muscles was interpreted as implying that the CNS considers the muscles as a functional unit when they act as synergists.

INTRODUCTION

The observation that the firing rates of motor units fluctuate in unison with essentially no time delay between them has led to the concept of *common drive* (De Luca and Erim 1994; De Luca et al. 1982). This finding suggests that the CNS has evolved a relatively simple strategy for controlling motor units. Rather than controlling the activity of each motor separately, the CNS appears to control the excitation to the motoneuron pool. The common drive received by all the motor units in the pool is translated into individual firing patterns for each motoneuron by the input/output characteristics of the motoneuron (Erim et al. 1996). Fluctuations in the common drive are reflected in concurrent fluctuations in the firing rates of motor units of the same pool. This common behavior was studied by cross-correlating the time-dependent firing rate signals of pairs of concurrently active motor units. Common drive has been found in all muscles tested by our group, ranging from small distal muscles such as the first dorsal interosseous to large proximal muscles such as the deltoid (De Luca and Mambrito 1987; De Luca et al. 1982, 1996; Erim et al. 1996, 1999; Kamen and De Luca 1992). The existence of common drive has been verified by independent investigators (Guiheneuc 1992; Iyer et al. 1994; Miles 1987; Semmler et al. 1997;

Stashuk and de Bruin 1988). While the effects of handedness (Adam et al. 1998; Kamen et al. 1992; Semmler and Nordstrom 1995), different proprioceptive conditions (Garland and Miles 1997), exercise (Semmler and Nordstrom 1997), task and disease (Patten et al. 2000), and aging (Erim et al. 1999) on common drive have been studied, the commonality of fluctuations in the mean firing rates of motor units belonging to different muscles has received little attention. A previous study by our group showed common firing rate fluctuations among motor units belonging to different muscles when they were controlled as one functional unit during antagonist muscle co-activation (De Luca and Mambrito 1987). More specifically, an interaction was observed among the firing rates of motor units belonging to the extensor pollicis longus and flexor pollicis longus muscles while they were cocontracting to stiffen the interphalengeal joint of the thumb (De Luca and Mambrito 1987). The goal of the present work was to study common drive among motor units belonging to two muscles that are synergistically rather than antagonistically related in accomplishing a motor task.

METHODS

Data collection

Isometric constant-force extensions of the wrist were used to study the interactions of the muscles when they were functioning synergistically. The subjects were seated with the arm extended and pronated, the elbow at 20° of flexion, and the shoulder flexed at 25° and abducted at 15°. To ensure isometric contractions, the forearm was immobilized by a lightly padded plastic cast. Another plastic cast was placed around the hand to keep the fingers in a flexed position to reduce the contribution of the extensor digitorum communis to wrist extension. The hand cast was attached to a plate coupled to two force transducers measuring forces in wrist extension/flexion (y axis) and abduction adduction (x axis) directions. The transducers had a range of ± 200 N and a stiffness of 3.0×10^6 N/m. Maximal voluntary contraction (MVC) for wrist extension was determined, and specially designed quadrifilar needle electrodes (De Luca and Adam 1999) were inserted into each of the extensor carpi radialus longus (ECRL) and extensor carpi ulnaris (ECU) muscles. Intramuscular EMG signals from the two muscles and the wrist extension torque were recorded while the subjects traced specified trajectories with the aid of visual feedback. The trajectories had 15-s plateaus at 20–30% of the subject's MVC and the up and down ramps had slopes of $\pm 10\%$ MVC/s. Forces in both wrist flexion and abduction directions were recorded to ensure pure wrist extension, which is the direction for which the ECRL and ECU act as synergists.

Data analysis

Intramuscular EMG signals were decomposed, i.e., separated into the individual action potentials of each motor unit, by using the precision decomposition technique (De Luca 1993; De Luca and Adam 1999; LeFever and De Luca 1982). For each reliably identified motor unit, the time-varying mean firing rate signal was estimated by passing the impulse train corresponding to the firing times through a Hanning window. The degree of correlation between the firing rate fluctuations of pairs of concurrently active motor units was examined by cross-correlating their mean firing rate signals. For each motor unit, the longest interval that did not include a sharp change (>8 pps) in the mean firing rate signal was determined. For each pair of motor units to be considered, the cross-correlation function was calculated over the intersection of the individual stable regions identified for each motor unit. The highest value of the cross-correlation function within ±100 ms of zero time lag was used to quantify the correlation among the signals, and the location of this peak indicated the lag/lead relationship between the signals. The cross-correlation functions were arranged so that for correlations within a muscle, a peak at a negative time lag represented fluctuations in later recruited motor units lagging similar fluctuations in earlier recruited motor units. Across muscles a peak at a negative time lag represented fluctuations in the ECRL lagging similar fluctuations in the ECU.

RESULTS

A total of 12 records from seven contractions were successfully decomposed (records from only 1 muscle were obtained for 2 of the contractions). A total of 70 motor units were isolated from the 12 records. Figure 1 shows typical firing rates during a wrist extension at 25% MVC. The *top half* of the plot shows the firing rates of three motor units from the ECRL, and the *bottom half* shows the firing rates of four motor units from the ECU. The darker, solid lines are the wrist extension and wrist adduction forces. Wrist extension and wrist adduction are represented in the positive direction, while flexion and abduction are in the negative direction. The wrist extension force trace rises up to 25% MVC. The wrist adduction force is less

than 3%MVC at all times, demonstrating that the contraction was essentially purely a wrist flexion with the two muscles acting synergistically. Common fluctuations can be seen between motor units of each muscle and to a lesser extent across the muscles.

Figure 2 shows plots of cross-correlation functions for a typical contraction. The *top left panel* displays cross-correlation functions between motor units of the ECU muscle, *top right panel* displays cross-correlation functions between motor units of the ECRL muscle, and the *bottom panel* displays the cross-correlation functions between motor units belonging to the ECU and ECRL muscles. The higher levels of correlation in ECU motor units as compared with ECRL motor units, which in turn was higher than the correlation between across-muscle pairs, was typical of other contractions observed. These patterns were quantified by maximal values of the cross-correlation functions that occur within 100 ms of *time 0*. Figure 3 shows histograms of cross-correlation peaks of motor unit pairs within each muscle and pairs across the two muscles, pooled from all the contractions. The following observations, summarized in Table 1, were made.

Within the ECU

The mean and SD of the maximal correlation values were 0.64 and 0.11, respectively. The mean and SD of the location of the peak were -6.0 and 27 ms. The mean of the time lag was not statistically different from zero using a two-tailed *t*-test ($P > 0.05$).

Within the ECRL

The mean and SD of the maximal values were 0.54 and 0.13, respectively. The mean and SD of the location of the peak were -28 and 37 ms. The mean of the time lag was not statistically different from zero using a two-tailed *t*-test ($P > 0.05$).
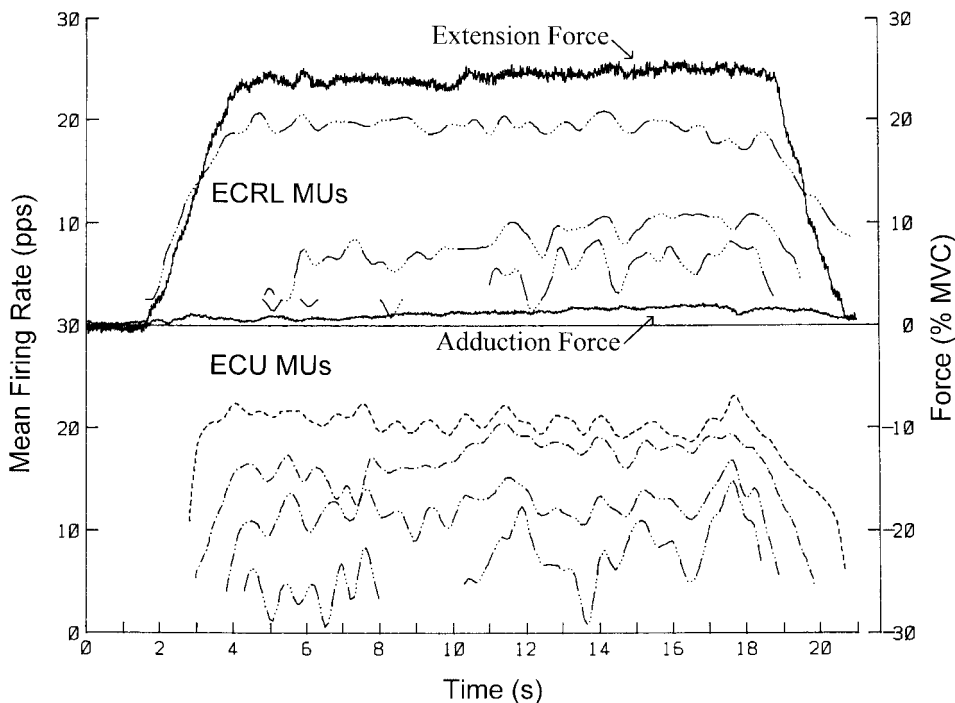

FIG. 1. Typical firing rates during wrist extension. *Top*: the firing rates of 3 motor units from the extensor carpi radialus longus (ECRL). *Bottom*: those from the extensor carpi ulnaris (ECU). The darker, solid lines are the wrist extension and abduction forces as marked. Forces are displayed as a percentage of the maximal voluntary contraction (MVC) value in their respective directions, and the force axis is displayed on the right hand side of the plot. Common fluctuations can be seen between motor units of each muscle and to a lesser extent across the muscles.
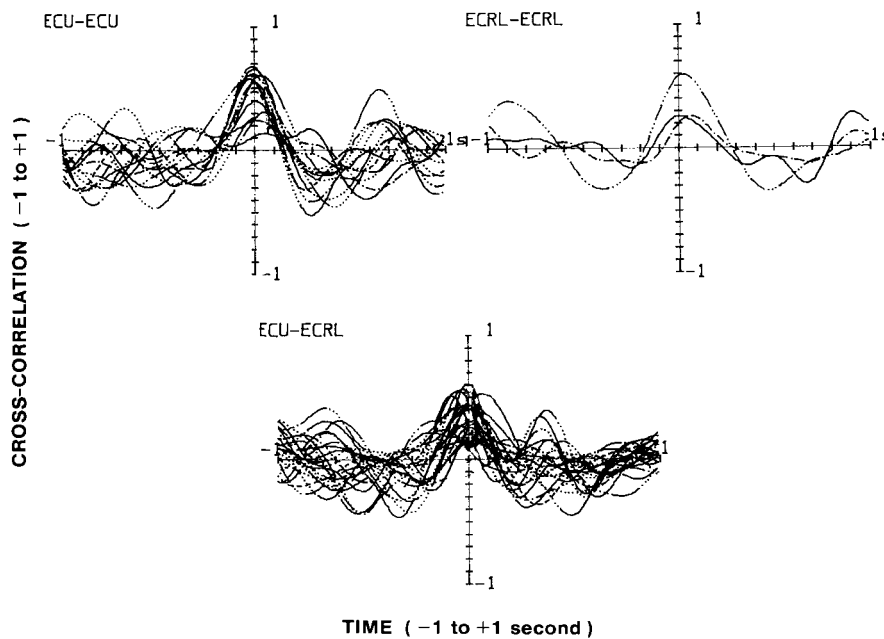
FIG. 2. Cross-correlation functions computed during a constant-force isometric contraction. Cross-correlation functions are computed between: motor units of the ECU muscle (*top left*); motor units of the ECRL muscle (*top right*); motor units of the ECU and ECRL muscles (*bottom*).

There was no statistically significant difference between the mean values of the correlations for the two muscles using a two-tailed two-sample *t*-test ($P > 0.05$), and the means were statistically different from zero ($P < 0.05$).

Across the ECU and ECRL

The mean and SD of the maximal values were 0.46 and 0.10, respectively. The mean and SD of the location of the peak were 33 and 74 ms (with the fluctuations in the ECRL leading those in the ECU). The mean of the time lag was statistically different from zero ($P < 0.05$).

The mean value of the cross-correlation across muscles was significantly less than the mean values for cross-correlations within muscles ($P < 0.05$) using a one-tailed two-sample *t*-test but was significantly greater than zero ($P > 0.05$).

DISCUSSION

The present work demonstrates that common drive exists between motor units belonging to two synergistic muscles. Albeit to a lesser degree than the *intra*muscular common drive exhibited within the ECU and ECRL muscles, the *inter*muscular motor unit pairs formed across the ECU and ECRL displayed significant common fluctuations in their firing rates

during wrist extension. This finding builds on our previous work, which showed that motor unit firing rates of antagonist muscles (flexor pollicis longus and extensor pollicis longus) were cross-correlated during voluntary coactivation to stiffen the interphalangeal joint (De Luca and Mambrito 1987). The suggestion that the motoneuron pools of an antagonist muscle pair may be controlled as if they were one pool when both are performing the same task is further corroborated by the present results. Here we show that the motor unit firing patterns of a *synergistic* muscle-pair also display a high level of commonality.

Our results demonstrate that the correlation among motor unit firing rates across muscles is lower than that within a muscle. A likely, albeit not exclusive, scenario is presented in Fig. 4. It is proposed that the common drive to each muscle can be broken down into a part that is received by both muscles (A) and a part that is unique to that muscle (B_1). [Each motor unit within either muscle also receives an input unique to that motor unit, denoted by $n_j(t)$.] Hence while the motoneurons within a given muscle share a larger portion of their net excitation (A + B_1 or A + B_2), motoneurons in different muscles nonetheless share a common drive (A). This common command signal A is analogous to the "coactivate" command proposed by De Luca and Mambrito (1987).

While it is speculative to attempt to distinguish the central and peripheral components of A, it is likely that there is a
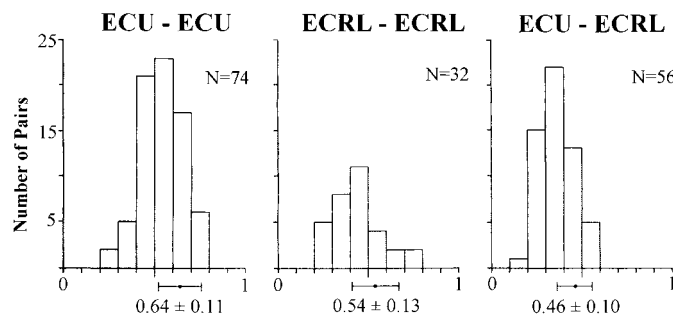

FIG. 3. Histograms of maximal correlations among motor unit pairs (within time lags of ±100 ms).

TABLE 1. *Common drive values among inter- and intramuscular motor-unit pairs*

Pairs Location	No. of Pairs	Common Drive	≠0?	Lag, ms	≠0?
ECU motor units pairs	74	0.64 ± 0.11	Yes	-6.0 ± 27	No
ECRL motor unit pairs	32	0.54 ± 0.13	Yes	-28 ± 37	No
ECU-ECRL motor unit pairs	56	0.46 ± 0.10	Yes	33 ± 74	Yes

Values are means ± SD. ECU and ECRL, extensor carpi ulnaris and radialus longus.
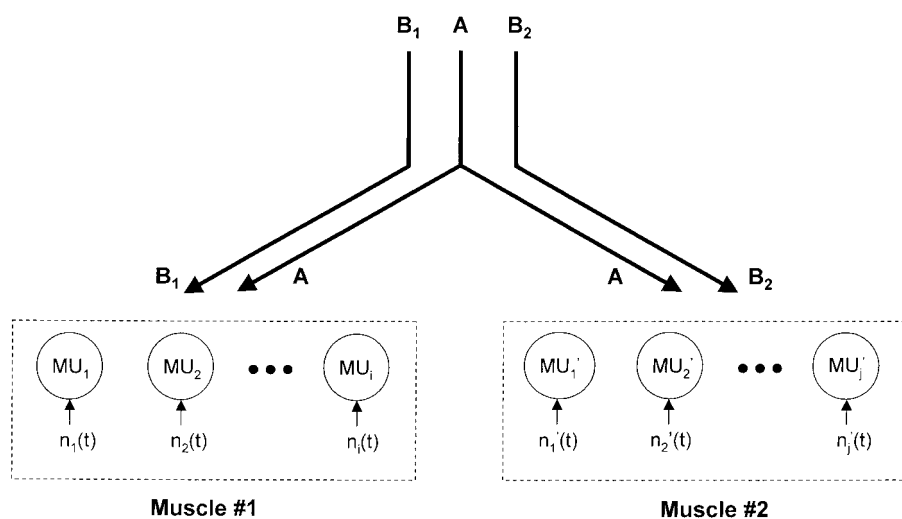
FIG. 4. A schematized diagram showing that some of the common drive (A) received by the motoneurons of the two muscles is shared, while there are portions of common drive (B_1, B_2) to the two motoneuron pools that are unique to the given muscle. In addition, each motoneuron receives an input unique to it (n).

strong central component. The reports by Cheney and Fetz (1980), Belhaj-Saif et al. (1998), and McKiernan et al. (2000), stating that there exist corticomotoneuronal cells in the premotor cortex and rubromotoneuronal cells whose activity was correlated with motor unit action potentials in groups of simultaneously active muscles in the forearms of primates performing voluntary contractions, suggest a central source for the common drive observed between synergistic muscles. The anatomical intersection of the motoneuron pools of the ECU and ECRL muscles, which share the spinal nerve roots C_6–C_8 as the source of their innervation by the radial nerve, may also contribute to the commonality in the inputs to these muscles.

In addition to the central factors, peripheral inputs could conceivably contribute to A, the drive shared by both motoneuron pools. In fact, widespread distribution of Ia afferents to motoneurons within the muscle (Mendell and Henneman 1971) as well as in synergistic muscles (Baldissera et al. 1981; Munson 1990) might be a source of common excitation. Afferents from one muscle may supply Ia excitation to many motor nuclei, and it has been suggested that Ia pathways may be of special importance in movements that involve a cocontraction of muscle groups linked in Ia synergism (Baldissera et al. 1981). However, a report by Chalmers and Bawa (1997) describing a lack of a bidirectional reflex pathway between ECU and ECRL argues against the suggestion that Ia activity may be a source of common drive across muscles. These investigators reported that ECU motoneurons received no short-latency excitatory input from the ECR and that ECR motoneurons received some excitatory Ia input from ECU Ia afferents but with a latency that exceeded that observed in other muscles by several milliseconds. If Ia afferents were a major contributor to common drive across muscles, firing rates in the ECU would consistently lead firing rates in the ECRL. However, we found that ECRL motor units lead the ECU units. One viable explanation for the observed lead time would be that the electrode in the ECRL was located closer to the innervation zone than was the electrode in the ECU. If so, assuming an average muscle-fiber conduction velocity of 4 m/s, the 33 $\pm$ 74 ms delay we observed would correspond to a distance of 13.2 $\pm$ 29.6 cm. Such a distance spans most of the length of these muscles. The electrodes were placed in the middle of the belly of the muscles, hence this factor cannot account for the observed lead time. Thus our results in con-

junction with those of Chalmers and Bawa (1997) indicate that the Ia afferents are not likely contributors to the common drive across synergist muscles.

Shared recurrent inhibition could also be a contributing factor to common drive. Motoneurons innervating synergistic muscles are linked by strong mutual recurrent inhibition (Baldissera et al. 1981), which is more extensively distributed than the monosynaptic Ia excitation (Hultborn et al. 1971). Common recurrent inhibition could introduce commonality in firing rates by supplying the same negative excitation to motoneurons of both muscles. However, Katz et al. (1993) do not report any shared heteronymous Renshaw inhibition to the wrist extensors. Furthermore, it should be noted that previous work by our group showing common drive in the orbicularis oris muscle (Kamen and De Luca 1992), which lacks muscle spindles, and the first dorsal interosseous muscle (De Luca et al. 1982; Erim et al. 1999), which lacks Renshaw cells (Katz and Pierrot-Deseilligny 1999; Katz et al. 1993), indicates that neither spindle nor Renshaw activity are indispensable components of common drive, even within a muscle.

If neither the Renshaw recurrent inhibition and Ia afferent excitation is likely to mediate the common drive across synergist muscles, it remains that the most likely source is from higher levels. The finding of the present study indicates one more way in which the CNS displays efficiency in its operation. Muscles that contribute to the same task, whether they are acting as antagonists or synergists, are controlled as a functional unit and their respective motor units receive a common drive. This organization simplifies the management scheme of the CNS.

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