

FIRING RATE INTERACTIONS AMONG HUMAN ORBICULARIS ORIS MOTOR UNITS

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(Received October 6, 1991)

Groups of human motor units from the same muscle exhibit joint fluctuations in firing rate during voluntary muscle contraction. In an effort to determine whether similar behavior would be observed in a muscle lacking muscle spindles, motor unit firing behavior was examined in the human orbicularis oris inferior (OOI) during mild voluntary effort. Motor unit activity was recorded with a quadrifilar needle inserted in the OOI. Firing occurrences were identified using a motor unit decomposition procedure. Cross-correlation of motor unit firing rates revealed a tendency for motor unit firing rates to covary, although the effect was somewhat more variable than that observed previously in other skeletal muscles. There was also a statistically significant tendency for pairs of motor units to fire at simultaneous or near-simultaneous (± 5 ms) intervals (synchronization). Firing rate variability in OOI motor units was not significantly different ($p > .05$) from that observed in the FDI. Thus, the present results suggest that the common drive of human motor unit activity may not depend on the presence of muscle spindles.

Keywords: Motor units, firing rate, facial muscles, synchronization, orbicularis oris, human.

The accurate identification of motor unit firing occurrences in human muscle has enabled us to attain considerable understanding regarding the manner in which the human motor system is controlled. Although the recruitment of new motor units into action is an important means by which some muscles can increase the force of a voluntary contraction (De Luca, LeFever, McCue and Xenakis, 1982), we now recognize that the ability to modulate motor unit firing rate is paramount for the precise regulation of muscular force.

During a constant-force isometric contraction, motor unit firing rates oscillate in-phase at a frequency of about 1–2 Hz. This joint fluctuation in firing rates, termed “common drive” (De Luca, 1985), seems to be a means by which activity among groups of motor units is tightly coupled. Common drive behavior has been observed in several different muscles including the first dorsal interosseous (FDI), tibialis anterior (TA), extensor pollicis longus (EPL), flexor pollicis longus (FPL), and the deltoid muscle (Creigh, 1984; De Luca, Kamen, Solar and Stashuk, 1987; De Luca

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We gratefully acknowledge the technical assistance of Ms. Nanette Paul and Mr. Andrew Roy in these experiments. This research was supported by funds provided by the Liberty Mutual Insurance Company and the Department of Veterans Affairs, Rehabilitation Research and Development Service (B594-RA).

and Mambrito, 1987). Since there have been few cases in which similar fluctuations in firing rates among groups of motor units have *not* been observed, this common drive phenomenon of motor unit firing rates seems to be a pervasive mechanism for the control of motor unit action.

The mechanisms underlying common drive behavior are ill understood. Numerous studies over the past decade have described a sensory partitioning in muscle, i.e., the notion that muscle spindle afferents are more tightly coupled to motor units innervated by the same primary nerve branch (Stuart, Hamm and Vanden Noven, 1988). So it is possible that muscle spindles might be an important contributor to the oscillation of firing rates among motor units in the same muscle compartment. It has also been suggested that bursts of activity from some central site might be contributing to this common drive phenomenon (Miles, 1987). Alternatively, some premotoneuronal site (located in either a spinal or a supraspinal region) might be delivering quantal pulses of excitation and/or inhibition to the active motoneuron pool.

A number of muscles innervated by the facial nerve seem to be devoid of muscle spindles. There is no evidence that muscle spindles exist in the *orbicularis oris*, although Kadanoff (1956) has suggested that there may be some stretch-like receptors in these muscles. We sought to determine whether the behavior in which motor unit firing rates co-fluctuate in a deterministic manner would be observed in a muscle devoid of intramuscular spindles—the *orbicularis oris*.

METHODS

Recordings were made from the *orbicularis oris inferior* (OOI) muscle in 4 young subjects (ages 20–29 yrs) with no known neurological disorders. Subjects were seated comfortably in a dental chair during the experiment. Informed consent was obtained from all subjects.

The subject was first instructed and trained to produce a moderate contraction of the OOI. A quadrifilar needle was then inserted into the OOI about 2 cm lateral to the midline, 5 mm below the vermilion border. The needle was then positioned into a suitable recording site while the subject maintained a mild contraction. In most cases, stable recordings were obtained when the subject attempted to produce an “ooh” sound. Recordings were stored on FM tape from sites in which two or more motor units could be successfully discriminated during a moderate contraction.

A multichannel decomposition procedure was used to identify every firing occurrence of the motor units selected for study. Motor unit action potential trains (MUAPTs) were obtained by utilizing myoelectric (ME) signal acquisition and decomposition techniques. This procedure has been described in earlier papers (Mambrito and De Luca, 1983, 1984; Stashuk and De Luca, 1989). Briefly, a cannula in which four 50- μ wires were epoxied in a side port with 200 μ m between wires was used to record myoelectric (ME) activity during active muscle contraction using a bandpass of 1 kHz to 10 kHz. The resulting three channels of ME information obtained from this electrode were used to identify individual motor unit action potential (MUAP) firings from the composite myoelectric signal. An operator-interactive program was then used to decompose the signal into individual motor unit action potential trains. The algorithm also enabled us to identify simultaneous firings of two motor units.

Motor unit firing rates were estimated for the MUs successfully tracked throughout the contraction interval. The mean firing rate was estimated for each motor unit by taking the inverse of the mean interpulse interval during a stable five seconds of the contraction.

Motor unit firings comprise an impulse train composed of Dirac pulses. This impulse train was then passed through a low-pass filter to obtain a continuous-time signal. A filter consisting of a Hanning window with a typical length of 400 ms was used. The continuous signal was then dc-filtered and sampled at 100 Hz. Cross-correlation functions for pairs of sampled firing rate trains were then computed using each 5-s epoch in which there was activity in both motor units of the pair. Contractions in which two or more motor unit action potential trains (MUAPT) were present were recorded from four subjects. A total of 18 motor unit pairs were analyzed from these contractions.

The tendency for two motor units to fire in a time-locked fashion is termed synchronous firing behavior. Synchronization analysis was conducted using cross-interval histograms constructed using the first-order forward and backward firing interval between pairs of MUAPTs (Figure 1). The area in this cross-interval histogram within ± 1 interpulse interval (IPI) of the zero latency (simultaneous firing) bin was defined as the test region. Synchronous firing event occurrences were identified in the following manner: the number of event occurrences in each bin was counted and if a bin count exceeded that expected at the 95% confidence interval (C.I.), then the width of this peak was computed by determining the number of adjacent bins above the 90% C.I. If the resultant peak was only one bin wide, a synchronous event was declared only if the number of event occurrences in this one bin exceeded that expected at the 99% confidence interval (C.I.). Two adjacent peaks were declared a synchronous event if the number of counts in these bins exceeded the 97.5% C.I. If three or more adjacent bins exceeded the 90% C.I. and within this grouping, at least one 2-ms bin exceeded the 95% C.I., then a statistically significant synchronous event was identified. For each synchronous event, the peak location was identified as the bin at which the median number of firings occurred. These statistical tests were conducted based on a binomial distribution unique to each motor unit pair. In recognition of the large number of statistical tests conducted, these confidence intervals were chosen in an effort to minimize the type I statistical error rate, and minimize the number of false positive synchronous events.

RESULTS

Common Drive in the Orbicularis Oris Muscle

Cross-correlations among pairs of motor unit firing rates were somewhat more variable in the *orbicularis oris* than in other muscles we have studied. In some subjects the computed cross-correlation scores were moderately high (Figure 2). For example, four motor units were recorded simultaneously from subject LB and the resultant six motor unit firing rate cross-correlation values were among the highest we have recorded from any one subject in any muscle, ranging from 0.77 to 0.89 (Fig. 2A). In another subject, the pair of motor units recorded produced a low firing rate cross-correlation score at time lag 0 (Figure 2B). A histogram of all firing rate cross-correlation values obtained from 17 motor unit pairs in four subjects is presented in Figure 3.

Synchronous Firing Behavior

Cross-interval histogram plots were constructed to determine the extent to which motor units tended to fire either simultaneously or with a constant phase lag. Ten

CROSS-INTERVAL HISTOGRAM

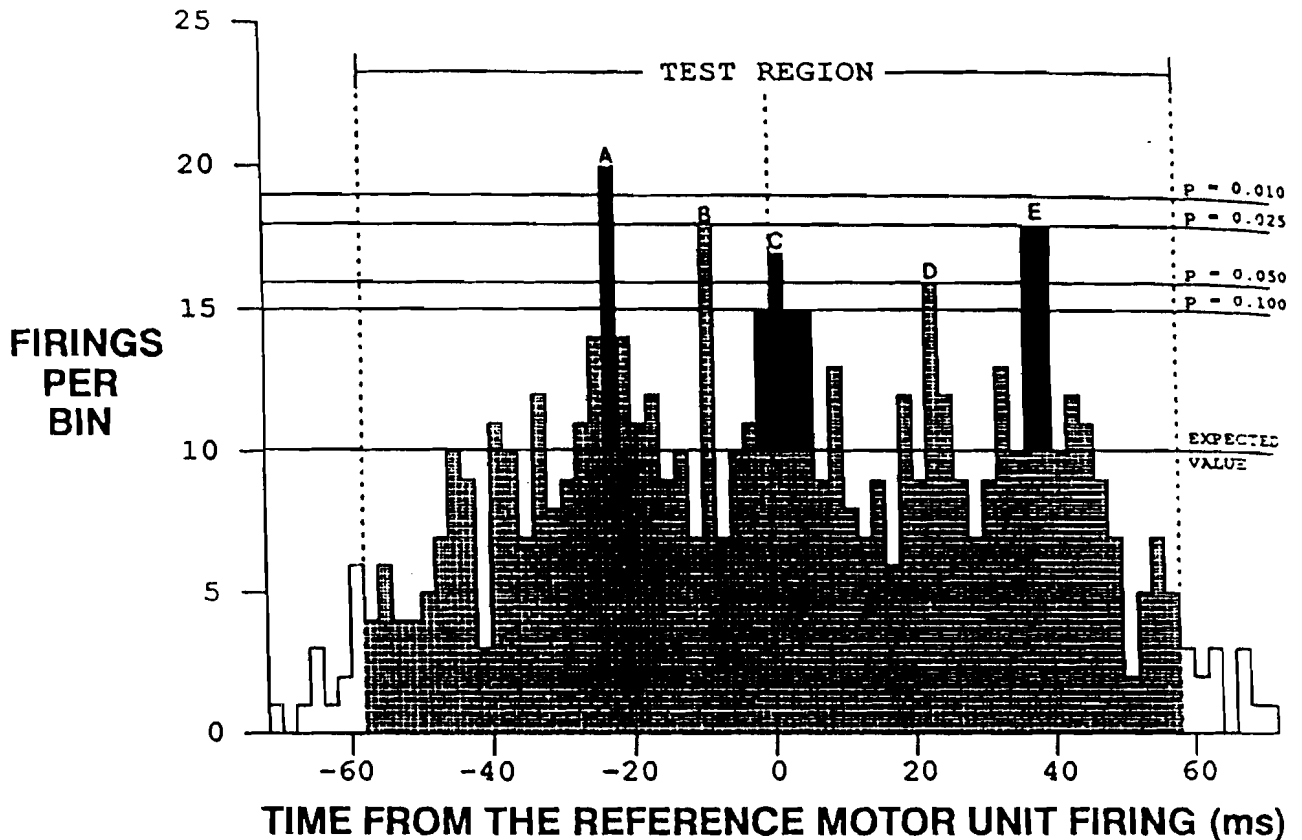


FIGURE 1 Example of a cross-interval histogram from one pair of motor units. The data in this example have been altered slightly to facilitate presentation of the criteria needed to declare a synchronous event. Starting at the beginning of the contraction, the interval between the firing of one motor unit and the closest firing of the alternate motor unit was measured. The corresponding bin in this histogram was then incremented. Event A shows an example of a single bin containing 20 counts in which the firing of one motor unit preceded the firing of the alternate unit by 24 ms. Events B and D demonstrate examples in which single bins fail to reach the 99% probability level required for a single bin event. In event C, four adjacent bins exceeded the 90% probability level, with one exceeding the 95% level needed to identify a significant synchronous event containing three or more bins. Finally, event E shows two adjacent bins in which the number of synchronous events equalled or exceeded the number expected at the 97.5% probability level. The test region corresponds to ± 1 interpulse interval (IPI).

of the 17 pairs examined showed a statistically significant tendency to fire either simultaneously or with a lag of ± 5 ms. Few synchronous events were found at delays longer than 5 ms (see Figure 4).

Firing Rate and Firing Rate Variability in Orbicularis Oris Motor Units

Previous studies have suggested that motor unit firing rates in the *orbicularis oris* are more variable than in other skeletal muscles (Blair, 1988). We compared the mean interpulse intervals (IPIs) from 20 motor units in the OOI muscle with 29 motor units from the first dorsal interosseous (FDI) (Figure 5). Mean IPIs in the OOI during steady-state contraction (45.1 ms) were not appreciably different from those in the

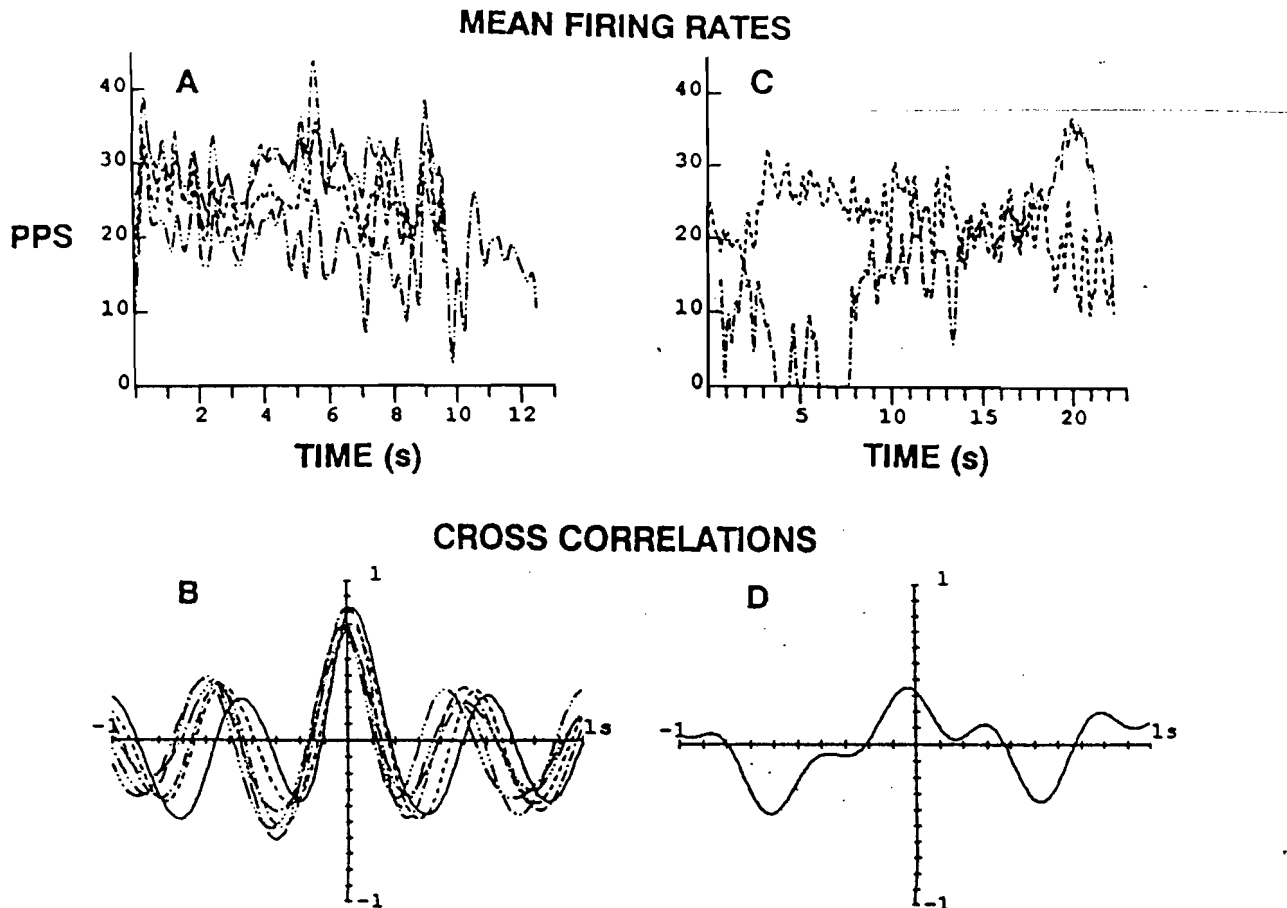


FIGURE 2 Firing rates and firing rate cross-correlations among orbicularis oris motor units in two subjects. A. Four motor units observed in one subject evidenced considerable in-phase fluctuation of motor unit firing rates. B. All firing rate cross-correlations in this sample exceeded 0.77 at time lag 0. C. In a second subject, one pair of motor units was observed whose firing rates were somewhat irregular and out of phase. D. In the interval during which both motor units were firing steadily a cross-correlation of 0.3 was obtained.

FDI (42.6 ms; $p > .05$). These values correspond to a firing rate of approximately 22 pulses/s. Moreover, the variability of firing as measured by the standard deviation (sd) of these interpulse intervals was also similar in the two muscles (11.8 in the FDI vs 14.2 in the OOI; $p > .05$).

DISCUSSION

We sought to determine whether the phenomenon of common drive, an in-phase fluctuation of motor unit firing rates, would be exhibited in a muscle lacking neuromuscular spindles, the *orbicularis oris*. Our results do indeed indicate that firing rates among motor units in most subjects are moderately well cross-correlated with little or no phase lag, suggesting that some common source is driving groups of motor units.

We have observed common drive in both young and old subjects (Kamen and De Luca, 1989), and in a variety of different muscles (Creigh, 1984; De Luca et al., 1987; De Luca and Mambrito, 1987). Indeed, it appears to be a quite robust phe-

MOTOR UNIT FIRING RATE CROSS CORRELATIONS

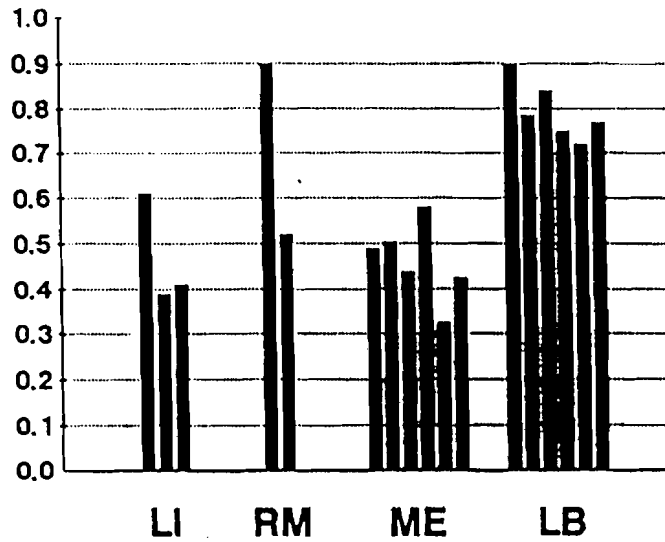


FIGURE 3 Peak motor unit firing rate cross-correlation values at time lag 0 (± 5 ms) are shown for all 17 motor unit pairs studied in four subjects

nomenon, at least during the types of isometric contractions we have utilized. There are several explanations for the joint fluctuations in motor unit firing rates.

The muscle spindle has been implicated as a candidate contributing to common drive behavior. The periodic firings of an individual motor unit may produce a transient unloading in neighboring muscle spindles. Inasmuch as any one spindle afferent synapses with almost every motoneuron in the pool (Mendell and Henneman, 1968, 1971), these oscillatory length changes may be responsible for the subtle fluctuations in motor unit firing rate.

Muscle spindles have never been observed in the *orbicularis oris* in human cadaveric preparations (C. Blair, personal communication). Neither have muscle spin-

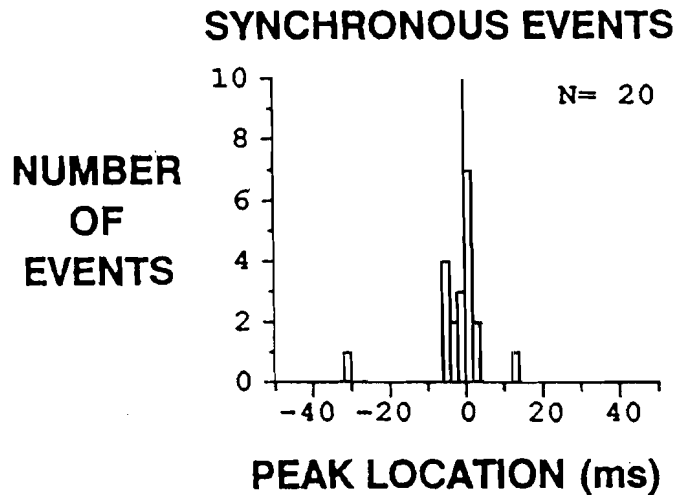


FIGURE 4 Synchronization of motor unit firings. Most synchronous events occurred around time zero, i.e., motor units exhibited a statistically significant tendency to fire at the same time or within an interval of less than 3-4 ms.

SIMILARITIES IN INTERPULSE INTERVALS

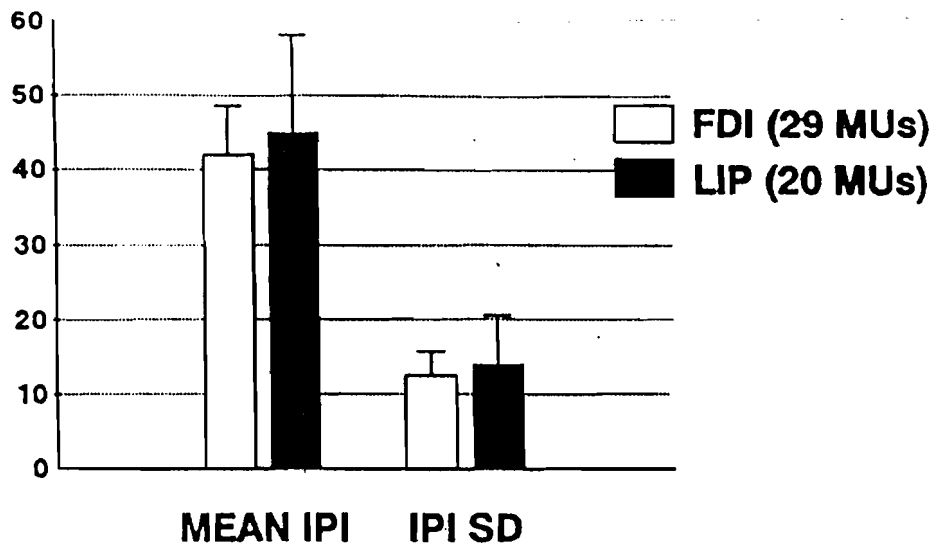


FIGURE 5 Firing rate variability in orbicularis oris and the first dorsal interosseous (FDI) muscles. Neither the mean interpulse intervals nor their standard deviations were significantly different in these two muscles.

dles or any large diameter afferents been observed in lower primate *orbicularis oris* (B. Munger, personal communication). There has been a report that other stretch-type receptors may exist in this muscle (Kadanoff, 1956), but the photographic evidence presented by Kadanoff is subject to alternative interpretations. Stretch reflexes can be evoked from the *orbicularis oris* using mechanical stimuli applied to the lower lip (McClellan, 1989) and individual motor unit activity has been shown to correlate with small mechanical displacements to the corner of the mouth (McClellan and Smith, 1982). Motor unit responses to these mechanical disturbances may be mediated by the rich supply of cutaneous receptors or other small-diameter afferents in *orbicularis oris*.

There are some reasons why other nonperipheral mechanisms may be viable in explaining the joint fluctuations in motor unit firing rates. For example, common drive may originate from a supraspinal source. Groups of corticomotoneuronal cells (CM) tend to exhibit synchronous firing behavior (Smith and Fetz, 1989), which might present a wave of excitation to the motoneuronal pool. Synchronous firing of CM cells with similar axonal conduction velocities might also explain the zero-latency motor unit synchronization we observed. Other investigators have also provided evidence that the firing of motor cortical cells is tightly coupled during free movement (Murphy, Kwan and Wong, 1985a, 1985b) as well as during isometric contraction (Allum, Hepp-Reymond and Gysin, 1982).

Common drive may originate from a spinal generator oscillator source. Wilson (1967) has discussed the idea that such a central oscillatory rhythm needn't be dependent upon proprioceptive feedback. Possible involvement of recurrent inhibition from the Renshaw cell circuit has also been implicated (De Luca, 1985; Loeb, Yee, Pratt, Chanaud and Richmond, 1987).

The presence of motor unit synchronization in most of the contractions suggests that muscle spindles are not necessary for synchronous firing behavior. Indeed synchronization has been observed under a variety of conditions, including slow walking

in quadrupeds (Loeb et al., 1987) and in respiratory muscles (Davies, Kirkwood and Sears, 1985). One possible mechanism for synchronization involves the recurrent collaterals among motoneurons. There is considerable anatomic (Cullheim, Kellerth and Conradi, 1977; Scheibel and Schiebel, 1966, 1969) and physiological evidence (Gogan, Geuritaud, Horchelle-Bossavit and Tyc-Dumont, 1977; Grinnell, 1966; Magherini, Precht and Schwindt, 1976; Nelson, 1966) to suggest that motoneuron axon collaterals terminate on other motoneurons as well as on inhibitory Renshaw cells (Baldissera, Hultborn and Illert, 1981). Two motoneurons sharing a common source of recurrent inhibition might exhibit a tendency towards zero-latency synchronization.

Muscle spindles may indeed contribute to synchronization and common drive behavior among motor units. However, the present data coupled with the observation that muscle spindles are lacking in the *orbicularis oris* support the notion that some central site might be capable of driving conjoint motor unit firing behavior.

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