Neural mechanisms of intermuscular coherence:

Implications for the rectification of surface electromyography

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Abstract

Oscillatory activity plays a crucial role in corticospinal control of muscle synergies and is widely investigated using corticospinal and intermuscular synchronization. However, the neurophysiological mechanisms that translate these rhythmic patterns into surface electromyography (EMG) are not well understood. This is underscored by the ongoing debate on the rectification of surface EMG prior to spectral analysis. Whereas empirical studies commonly rectify surface EMG, computational approaches have argued against it. In the present study we employ a computational model to investigate the role of the motor unit action potential (MAUP) on the translation of oscillatory activity. That is, diverse MUAP shapes may distort the transfer of common input into surface EMG. We test this in a computational model consisting of two motor unit pools receiving common input and compare it to empirical results of intermuscular coherence between bilateral leg muscles. The shape of the MUAP was parametrically varied and power and coherence spectra investigated with and without rectification. The model shows that the effect of EMG rectification depends on the uniformity of MUAP shapes. When output spikes of different motor units are convolved with identical MUAPs, oscillatory input is evident in both rectified and non-rectified EMG. In contrast, a heterogeneous MAUP distribution distorts common input and oscillatory components are only manifest as periodic amplitude modulations, i.e. in rectified EMG. The experimental data showed that intermuscular coherence was mainly discernable in rectified EMG, hence providing empirical support for a heterogeneous distribution of MUAPs. These findings implicate that the shape of MUAPs is an essential parameter to reconcile experimental and computational approaches.

Keywords: neural synchronization, corticospinal coherence, EMG rectification, alpha-motoneuron model, common drive, motor unit action potential
1. Introduction

Oscillatory activity plays an important role in the neurophysiological drive to the muscle (McAuley and Marsden 2000). In pathological conditions or effortful activity, this may be exaggerated and become evident as a tremor. Under many circumstances, however, oscillatory activity may not be directly noticeable, but can be discerned using spectral analysis of electromyography (EMG) and electroencephalography (EEG). In particular, many studies use corticospinal (EEG-EMG) and intermuscular (EMG-EMG) coherence to assess oscillatory input to the muscle (Grosse et al. 2002). Through these techniques a variety of oscillatory components have been identified, such as corticospinal synchronization at ~20 Hz during precision grip (Baker et al. 1997; Conway et al. 1995; Gross et al. 2000; Salenius et al. 1997) and intermuscular synchronization at ~10 Hz between homologous or synergetic muscles (Boonstra et al. 2007; Boonstra et al. 2008; Evans and Baker 2003; Poston et al. 2010; Sowman et al. 2006). Although many oscillatory components in the input to the muscle have been extensively validated, the physiological mechanisms that bring about these oscillations remain to be identified.

The ongoing debate on EMG rectification as a preprocessing step in assessing oscillatory activity underlines our incomplete understanding. A number of studies have addressed the rational of EMG rectification and the effects it has on power and coherence spectra (Farina et al. 2004; Myers et al. 2003; Yao et al. 2007; Yue et al. 1995). However, no general agreement has been reached and the debate on EMG rectification recently reemerged (Boonstra 2010; Halliday and Farmer 2010; Neto and Christou 2010; Reynolds and Lakie 2010; Stegeman et al. 2010). The discussion seems to divide experimental from computational approaches: Most empirical studies use and promote rectification of surface EMG (e.g. Boonstra et al. 2008; Mima and Hallett 1999; Yao et al. 2007), whereas simulation studies generally argue against rectification (e.g., Neto and Christou 2010; Stegeman et al. 2010). The disagreement suggests that either the experimental findings reflect other physiological processes than they intend to measure or that computational models have omitted crucial physiological properties.
The elucidation of this technical issue therefore contributes to our understanding of the mechanisms underlying oscillatory neuronal activity (cf. Boonstra 2010). A central question is how oscillatory activity is conveyed by the spike trains shaping the neuronal input to the motor unit (MU) pool and how these oscillatory components are transmitted by the MU pool and mapped into the surface EMG signal. The transfer function of the MU pool is largely linear and should hence transmit oscillatory input reliably (Negro and Farina 2011). Subsequently, the output spikes generate motor unit action potentials (MUAP) that are summed to generate surface EMG. Hence, while oscillatory components may be present in the output signals of the individual MUs, they may be distorted by convolution with the MUAP. A MUAP is determined by many factors resulting in a great diversity of shapes recorded by surface EMG (Baker and Lemon 1998; Farina et al. 2008; McGill et al. 2001; Stalberg et al. 1986). A heterogeneous population may average out oscillatory components in the aggregated surface EMG signal (Keenan et al. 2005), in particular if the polarity of MUAPs are equally distributed. We test the effect of a heterogeneous MUAP distribution in a basic model of two MU pools that incorporate key physiological properties. Both MU pools receive common input at a particular frequency and the effects on the rectified and non-rectified EMG are investigated by the coherence between simulated EMG signals. Simulated data are compared to empirical data acquired from healthy subjects during quiet standing to investigate whether using a heterogeneous MUAP shapes can reconcile experimental and computational approaches on the issue of EMG rectification. Such unification may help to improve the identification of oscillatory components in neuronal spike trains from surface recordings and better relate such measures to the underlying physiology.

2. Methods

A combined computational and empirical approach was carried out to investigate the mechanisms involved in the generation of common oscillatory input and its translation into surface EMG signals. The aim is to investigate the role of the heterogeneous distribution of MUAP shapes in general, not to model the MU pool of
a specific muscle. In this study we focus on intermuscular synchronization that has been observed in a number of studies (see Introduction). A computational model is presented consisting of two MU pools receiving inputs with various degrees of common input. The effect of heterogeneity of MUAP shapes on the effect of EMG rectification is tested for different input frequencies (2, 10, 25, and 40 Hz) and activation levels. Subsequently, the simulations for common input at 10 Hz are investigate in further detail and compared to experimental data obtained in healthy subject during quiet standing (Boonstra et al. 2008).

2.1 Computational approach

Overview

We study a model that includes the essential properties of a MU pool. The model consists of two MU pools of 100 $\alpha$-motoneurons each, which are modeled by leaky integrate-and-fire (IF) neurons (cf. Halliday 1998; Terry and Griffin 2010). Rate-modulated Poisson processes generate the inputs to the motoneurons. Although the spiking inputs to the muscle pools are independent, a common oscillatory modulation of this input is introduced, and parametrically increased from 0 to 100% of the background rate. The output spikes are convolved with a MU action potential (MUAP) waveform and summed to produce the EMG signal (see Fig. 1 for a schematic representation).

Motoneuron model

An IF neuron is a simple spiking model that is widely used and reproduces the basic neurocomputational features of neurons (Gerstner and Kistler 2002). It describes the membrane potential of a neuron in terms of the synaptic inputs and the injected currents it receives (Burkitt 2006; Izhikevich 2007). The membrane potential $V_i$ given by:

\[ V_i(t) = \int_{-\infty}^{t} I_i(t') dt' + V_i(-\infty) \]
\[
\tau \frac{dV_i}{dt} = -g_l(V_i - E_i) + \sum_{j=1}^{N} w_{ji} K_j,
\]

(1)

where \(i = 1, \ldots, M\), \(\tau\) is a time constant, \(g_l\) a leakage conductance, \(E_i\) the equilibrium potential, and \(w_{ji}\) the connection efficacy from input \(j\) to motoneuron \(i\) with \(j = 1, \ldots, N\). \(K_j\) is the excitatory post-synaptic potential of incoming spikes with exponential rise and fall (Gutig and Sompolinsky 2006) described by:

\[
K_j = V_0 \sum_{k=1}^{S} \exp \left( \frac{t_k - t}{\tau_{rise}} \right) - \exp \left( \frac{t_k - t}{\tau_{fall}} \right),
\]

(2)

where \(t_k\) denotes the spike times of the \(k\)th afferent and \(V_0\) a free parameter. Equation 2 determines the potential of incoming spikes based on the times of previous spikes \((k = 1, \ldots, S)\). An exact integration scheme was used to compute subthreshold membrane potentials (Morrison et al. 2007; Rubinov et al. 2011). Motoneuron \(i\) spikes if the threshold \(V_{\text{thresh}}\) is exceeded and its membrane potential then set to \(V_{\text{spike}}\) for duration of \(T_{\text{spike}}\), after which it is reset to the resting potential \(V_{\text{rest}}\) and held there for duration of \(T_{\text{refrac}}\). Each MU pool consisted of 100 motoneurons \((M=100)\), each receiving 60 inputs \((N=60)\) all with unit weighting \((w_{ji} = 1)\).

The parameters are set in general agreement with known physiology and the data presented by Gustafsson and Pinter (1984). In particular, the equilibrium potential \(E\) was set at -70 mV, the spike height \(V_{\text{spike}}\) at 40 mV and the reset potential \(V_{\text{rest}}\) at -80 mV. The membrane time constant \(\tau\) was set at 10 ms, the refractory period \(T_{\text{refrac}}\) at 25 ms and the spike duration \(T_{\text{spike}}\) at 1 ms. The parameters of the synaptic input filter were set following Rubinov and colleagues (2011): \(\tau_{\text{fall}} = 3\) ms, \(\tau_{\text{rise}} = 1\) ms, \(g = 0.1\) pS, \(V_0 = 20\) mV. The threshold \(V_{\text{thresh}}\) was set -52 mV and stochastically varied over time between -60 and -45 mV (corresponding to the 10-25 mV range used by Maltenfort and colleagues (1998)). Fluctuations in motoneuronal excitability and the mechanisms involved have been discussed in great detail (Rekling et al. 2000).

Importantly, in combination with the leaking conductance \((g = 0.1\) pS), a
stochastically fluctuating threshold assures that the coefficient of variation (CV) of the inter spike intervals (ISIs) is consistent with known physiology. The CV is an important determinant of the dynamic response of MUs to common input (Maltenfort et al. 1998; Nordstrom et al. 1992). To generate a heterogeneous population of cells, parameters for each motoneuron were independently drawn from a random Gaussian distribution centered at the prescribed parameter values.

Motoneuron input

Motoneurons receive 60 different inputs from a pool of 200 input traces such that each pair of motoneurons within the same MU pool received on average 30% of their input from shared inputs (Stegeman et al. 2010). There is no directly shared input to motoneurons in different pools. All inputs are modeled as rate-varying Poisson processes with a baseline firing rate plus rate modulations (cf. Zeitler et al. 2006). These oscillatory modulations may arise from fluctuations of the local field potential in motor cortex, although intermuscular synchronization at 10 Hz more likely arises from oscillations of subcortical origin (Boonstra et al. 2009). Poisson processes are the simplest of any point-wise statistical process and can be used to model neuronal discharge in which the intensity does not depend on history (Johnson 1996). The discharge likelihood can be constant, implying that events occur randomly at a fixed average rate (stationary), or it could vary with time (i.e. rate-modulated). In this study the Poisson processes that generate the input to the motoneurons are modulated by a common oscillation at different frequencies (2, 10, 25 and 40 Hz), with an intensity that varied from 0% rate-modulation (or stationary) to 100% rate modulation. In addition, the effect of the strength of motor drive is explored by varying the baseline firing rate (20, 40, and 60 imps/s). Figure 2 illustrates the input to the motoneurons and the effect of modulation by a common oscillation.

Insert figure 2
Motor unit action potential

The spike trains of the integrate-and-fire motoneurons represents the neuronal output of the MU pool. The spike train of each motoneuron is convolved with a MUAP to yield a time series of electromuscular activity. The sum of these time series provides the EMG signal for that MU pool. Likewise, a single MUAP represent the summated activity of synchronously firing muscle fibers of a motor unit. The shape of a MUAP as measured by surface EMG is determined by numerous electrophysiological parameters, e.g. the location of the endplate and the muscle/tendon junctions in relation to the recording electrodes, the conduction velocity, semi-lengths and the angle of inclination of the fibers and the shape of the intracellular action potential (Bischoff et al. 1994; Keenan et al. 2006; McGill et al. 2001; Mesin et al. 2011; Stalberg et al. 1986). However, there is a lack of information regarding the range of motor unit properties in a muscle, with limited information on the distribution of these electrophysiological parameters across the entire population (Enoka and Fuglevand 2001). Moreover, these parameters differ considerably between different muscles.

In the present study, we therefore choose to parametrically vary the heterogeneity of the MUAP distribution to test its effect on the transmission of oscillatory common input. We implemented this by varying the polarity of the MUAP amplitude and the sign of the MUAP phases. We varied the uniformity of the polarity distribution from 100% (all positive, no negative polarity) to 50-50% (half of the MUs have a MUAP with positive polarity). Using bipolar surface recording, such a phase reversal of the MUAP can be observed when moving the electrodes over the endplate zone in the direction parallel to the muscle fiber (Kleine et al. 2007). Hence, different MUAP polarities may be observed in muscles where the endplates are distributed throughout the entire muscle, such as the gastrocnemius (Aquilonius et al. 1984). Note, however, that widely distributed endplates zones are not observed in all muscles.

Insert figure 3
As the MUAP morphology, we used the function proposed by Stegeman and colleagues (2010), in which half of the pulse shape is defined by:

\[ h(t) = 5 \sin \left( \frac{\pi}{d/2} \right) \exp \left( \frac{1}{\tau} \frac{t}{d/2} - 1 \right), \quad (3) \]

for \( 0 < t \leq d/2 \). For \( d/2 < t \leq a \) time and amplitude mirrored version of Eq. (3) is used. The duration of the MUAP \( d \) is set at 25 ms reflecting the wave shape of larger muscles and the damping \( \tau \) set at 0.18 ms (Fig. 3). The MUAP is scaled for each motoneuron individually to take into account variations in the number of muscle fibers innervated by different motor units and the position of the MU with respect to the EMG electrodes. To this end, the amplitude of the MUAP is randomly varied between 0 and 1. After the spike train of each motoneuron is convolved with the individually scaled MUAP, the electromuscular activity of all 100 MUs is summed to generate the surface EMG signal. Figure 4 illustrates the dynamics of the model by showing the input and output of a few motoneurons and the resulting EMG signal.

**Simulations**

In this study, we introduce a discretization of time in bins \( t \) of 0.5 ms, equivalent to a sample rate of 2 kHz used in the empirical study described below. The effect of four variables on intermuscular coherence is parametrically tested: percentage rate modulation (0-100%, in steps of 10%), percentage MUAPs with positive polarity (50-100%, in steps of 5%), frequency of common input (2, 10, 25, 40 Hz), and input rate (20, 40, 60 imps/s). For each parameter setting, 10 simulations of 45 s duration were generated, matching the number of experimental recordings.

*Insert figure 4*
2.2 Empirical approach

We briefly summarize the most important aspects of a study of EMG-EMG coherence in healthy human subjects, standing with eyes closed. The complete experimental protocol is provided in (Boonstra et al. 2008).

Participants

Ten healthy male students (age 19–23 yr) volunteered to participate in the experiment. All participants gave their informed consent after the experimental procedure and all accompanying instructions had been explained to them in detail. The experiment was carried out in full compliance with the Helsinki Declaration with prior approval by the ethics committee of the Faculty of Human Movement Sciences, VU University Amsterdam.

Procedure

The experiment included four blocks of quiet standing trials, each consisting of one eyes-open and one eyes-closed trial. Trial duration was 45 s. The first block was a baseline assessment in which participants were sober. In the subsequent blocks, low doses of alcohol were administered to investigate its effect on postural balance and intermuscular synchronization. For the present study, only the baseline recordings in the eyes-closed condition are studied.

Data acquisition

Participants were requested to stand barefoot on a force platform (9281B, Kistler, Reeuwijk, The Netherlands) to assess their center-of-pressure dynamics. Surface EMG was recorded bilaterally from three ankle plantar flexion or extensor muscles (i.e., lateral gastrocnemius [GL], medial gastrocnemius [GM], and soleus [SO]) and two ankle dorsiflexion or flexor muscles (i.e., tibialis anterior [TA] and extensor digitorum longus [ED]) in the lower legs. EMG data were amplified, on-line band-pass filtered (10–1,000 Hz), and stored on a disk with a sampling frequency of 2 kHz (Porti 5-16/ASD; TMS International, Enschede, The Netherlands).
2.3 Data analysis

Common oscillatory input to two MU pools was quantified by intermuscular coherence. EMG-EMG coherence was estimated using Welch’s periodogram method with a Hamming window of 2,048 samples length and 1,024 samples overlap (Welch 1967), resulting in a frequency resolution of 0.98 Hz. To investigate the effect of EMG rectification on the identification of common input, coherence was calculated both for non-rectified and rectified EMG (cf. Neto and Christou 2010). EMG signals were rectified using the Hilbert transfer\(^1\) (Boonstra et al. 2008; Myers et al. 2003). The Hilbert amplitude (or instantaneous amplitude) is defined as

\[
A(t) = \sqrt{x^2(t) + \hat{x}^2(t)} \text{ where } \hat{x}(t) \text{ is the Hilbert transform of } x(t).
\]

The use of the Hilbert transform renders the interpretation of rectified EMG straightforward as it equates to the instantaneous EMG amplitude. Hence, the question addressed in this study boils down to whether oscillatory activity is either present in the EMG signal or in the EMG amplitude. In the former, oscillatory input is directly transferred into the surface EMG signals, whereas in the later oscillations are reflected in amplitude modulations of high-frequency EMG signals, similar to the principle of the AM radio (Fig. 5; cf. Myers et al. 2003). The EMG amplitude is thought to reflect net MU activity – the recruitment and the discharge rates of the active MUs – and is regarded as an index of the level of activation provided by the spinal cord (Farina et al. 2004; Milner-Brown and Stein 1975). Likewise, it can be used an index of the net input to the MU pool (Boonstra et al. 2008; Schieber 1995). Note, however, that surface EMG underestimates the activation signal sent from the spinal cord to muscle as a result of the cancellation of positive and negative phases of MU action potentials (Keenan et al. 2005).

\[^{1}\text{We repeated all analyses using the absolute value to rectify surface EMG signals. The results were fully compatible with the present results using the Hilbert transform.}\]
The 95% confidence interval ($P < 0.05$) of the coherence spectra was determined by $1/(0.05)^{[(L-1)]}$, where $L$ is the number of disjoint segments used for the coherence analysis (Amjad et al. 1997). The confidence interval was then adjusted to account for the use of overlapping windows (Welch 1967). Computational and experimental data were analyzed identically.

3. Results

The effect of a heterogeneous MUAP distribution on the transmission of oscillatory input into surface EMG was examined in a computational model consisting of two MU pools. Intermuscular coherence was estimated from simulated EMG that is either rectified or not and compared to empirical data obtained during quiet standing. We will first summarize the findings of the computational model for the full parameter range. Subsequently, we will focus on the results using 10-Hz common input and compare it to experimental findings to test whether a heterogeneous MUAP distribution may reconcile both approaches.

3.1 Computational model

The effect of a heterogeneous MUAP distribution was tested for different input frequencies and input rates. The three different input rates (20, 40, 60 imps/s) result in a mean MU discharge rate of 7.3±1.7, 12.2±1.9, and 14.3±2.7 Hz, respectively (± reflects SD). The coefficient of variation (CV) of the inter-spike interval (ISI) for these input rates is 0.35±0.19, 0.17±0.03, and 0.14±0.04 without common input. These findings agree with experimental recordings showing a range of 10-30% and a decrease in CV at higher firing rate (Moritz et al. 2005; Nordstrom et al. 1992). The effect of common input on MU firing statistics is mainly apparent for common input at low frequencies (2 and 10 Hz) and high input rates (40 and 60 imps/s) revealing a decrease in mean discharge rate and an increase in the coefficient of variation. The latter is particularly evident for 2-Hz common input for which the coefficient of
variation increases to 0.7-0.8 with 100% common input: MUs are silent for most of the 500ms period length and then fire a few times in close temporal proximity.

A heterogeneous MUAP distribution was achieved by varying the polarity of the MUAP and the effect assessed using coherence analysis between the two MU pools. As an example, figure 6 shows the power and coherence spectra for three different parameter settings. With no common input, the power spectra of non-rectified EMG reveals the primary frequency content of the MUAP, whereas the peak at 8 Hz in the rectified EMG reflects the average firing rate of the motoneurons (Fig. 6A). The corresponding coherence spectra are not significant (Fig. 6B). With 30% common 10-Hz input and uniform polarity, both the power spectra (Fig. 6C) and coherence spectra (Fig. 6D) exhibit a peak at 10 Hz. However, when the polarity of MUAPs is evenly distributed (50% positive, 50% negative), only the power spectra of rectified EMG shows a peak at 10 Hz (Fig. 6E). The raw signal shows a much-reduced peak. Likewise, the coherence at 10 Hz is strongly reduced when using the raw (non-rectified) EMG signal (Fig. 6F). A 10 Hz peak in the coherence remains evident in the rectified EMG.

Figure 7 shows a systematic survey of the coherence at the frequency of common input for an input rate of 20 imps/s (corresponding to a mean firing rate of 7.3 Hz). Results are shown for both non-rectified (top) and rectified EMG (lower panels). The coherence at the frequency of the common input is displayed, which is generally the only peak observed in the coherence spectra. As expected, EMG-EMG coherence increases monotonically with periodicity (percentage common input) for both rectified and non-rectified EMG. However, there is large variability in the exact relationship across parameter settings. In particular, coherence estimated from non-rectified EMG is strongly affected by the heterogeneity of the MUAPs: for evenly distributed polarity of MUAPs (50-60%) coherence is strongly reduced for the non-rectified signal. In contrast, coherence estimated using rectified EMG is largely

Insert figure 6
constant over parameter settings. Coherence is somewhat reduced at higher
frequencies of common input. This effect is most pronounced for rectified EMG using
a uniform, or near uniform MUAP.

To highlight the effect of a heterogeneous MUAP distribution, we display the
difference in coherence between rectified and non-rectified EMG in figure 8. It is
evident that coherence is higher for non-rectified EMG with a uniform MUAP
distribution and higher for rectified EMG with a heterogeneous MUAP distribution
(50% of MUAPs with positive polarity and 50% with negative polarity). This pattern
is largely similar for different input rates (20, 40, and 60 imp/s) and different
frequencies of common input (2, 10, 25, and 40 Hz). These simulations show that
higher intermuscular coherence is generally obtained from non-rectified EMG if the
MUAPs are predominantly uniform. Coherence from rectified EMG is only higher
when surface EMG is generated from a heterogeneous MUAP distribution.

3.2 Experimental findings

To evaluate the computational findings, the intermuscular coherence spectra obtained
from our model are compared to experimental data acquired from healthy subjects
during quiet standing. Bilateral EMG-EMG coherence was computed between five
homologous leg muscles (GL, GM, SO, TA and ED) with and without EMG
rectification. Of these five muscle combinations, only the three extensor muscles, i.e.
GL, GM and SO, exhibited significant intermuscular coherence (Fig. 9A-C). Bilateral
synchronization was observed in two distinct frequency bands: 0-5 and 10-15 Hz, but
in the context of the present study we focused on the higher 10-15 Hz frequency band.
Whereas synchronization at 10-15 Hz was significant when using rectified EMG,
intermuscular synchronization was reduced when estimated using non-rectified EMG
and was just below the 95% confidence interval. Coherence levels in both frequency bands estimated from non-rectified EMG were however slightly elevated compared to coherence at other frequencies, having a similar spectral distribution as coherence estimated from rectified EMG. The 50-Hz artifact from mains interference was strongly evident in all non-rectified EMG signals. To statistically test for similarity, the correlation coefficient between the coherence spectra of rectified and non-rectified EMG was determined for frequencies of 0-45 Hz (to exclude the 50-Hz artifact). The correlation coefficients computed for each subject individually were tested for significance using a one-sample t-test. For the three muscles showing significant intermuscular coherence, there was a significant correlation between the coherence spectra of rectified and non-rectified EMG (GL: $r = 0.53 \pm 0.07, T(9) = 7.6, P < 0.0005$; GM: $r = 0.24 \pm 0.08, T(9) = 2.9, P = 0.019$; SO: $r = 0.37 \pm 0.10, T(9) = 3.7, P = 0.005$; ± reflects SE). For muscles showing no significant coherence, the corresponding correlations were not significant ($P > 0.2$).

Insert figure 9

In the experimental data, intermuscular ~10-Hz coherence was thus revealed most clearly using rectified EMG. Although coherence was higher for rectified EMG in all three muscle combination, common 10-Hz input could also be observed in non-rectified EMG as evidenced by significant correlations between the coherence spectra. These findings indicate that common oscillatory input was mainly evident as ~10-Hz amplitude modulations of high-frequency EMG signals (see Fig. 5). In order to examine the frequency content of the EMG signal that carried these amplitude modulations, we performed further analyses comparing experimental and simulated results. EMG signals were hence high-pass filtered with a range of cut-off frequencies (10-990 Hz, in steps of 10 Hz) using a second-order Butterworth filter before EMG rectification and spectral analysis. The right-hand side panels of figure 9 show the coherence spectra after high-pass filtering at different frequencies. The coherence spectra remain largely equivalent after high-pass filtering the EMG signals up to 400-
600 Hz. In fact, intermuscular coherence increases after high-pass filtering compared to no filtering. For example, coherence at 11.7 Hz increased from 0.095 without filtering to 0.13 after high-pass filtering at 260 Hz for the SO muscles.

To facilitate comparison, parameter settings are selected that yield comparable coherence values and equivalent analyses are performed on simulated data using a heterogeneous MUAP distribution, low periodicity and common input at 10 Hz. Figure 10 shows the coherence spectra from simulations generated with an input rate of 20 imp/s, 15% periodicity and MUAP polarity distribution of 60-40%.

Intermuscular coherence at 10 Hz is significant for rectified EMG ($P<0.05$) but not for non-rectified EMG, although a smallish peak at 10 Hz is discernable. There is a significant correlation between the coherence spectra (0-45 Hz) estimated using non-rectified and rectified EMG ($r = 0.15 \pm 0.05$, $T(9) = 2.9$, $P = 0.008$). Coherence at 10 Hz increased after high-pass filtering with different cut-off frequency from 0.12 without filtering to 0.20 after high-pass filtering at 500 Hz (Fig. 10, right panel). Hence, for these parameter settings the simulated data are in close accordance with the empirical results. To investigate the general effect of high-pass filtering on coherence estimated from rectified EMG, we repeated the analysis for all parameter settings (i.e. input rate and frequency). These results reveal a consistent increase in coherence after high-pass filtering across parameter settings (data not shown).

Insert figure 10

4. Discussion

The aim of this study was to reconcile experimental and computational approaches on the issue of EMG rectification for the detection of common oscillatory muscle input. Whereas rectification is commonly used in experimental studies on corticospinal and intermuscular coherence, computational studies have argued against the use of rectification. Our hypothesis was that if MUAPs have heterogeneous shapes, oscillatory activity may cancel out in the aggregate EMG signal, in particular when the distribution has a near-zero mean. As a consequence, oscillatory input may then
only be discernable in the variance of the signal, i.e. in rectified EMG. We test this hypothesis with a basic computational model of two MU pools to simulate intermuscular coherence at different frequencies. Coherence spectra are estimated from both rectified and non-rectified EMG signal and judged against empirical findings. Although simulated oscillatory input can generally be identified irrespective of EMG rectification, the uniformity of the MUAP distribution strongly affects the identification of common input. With a uniform MUAP distribution coherence is higher for non-rectified EMG. In contrast, stronger coherence at the frequency of common inputs is only obtained for heterogeneous MUAP distributions in which the mean of the distribution tends to zero. Experimental data revealed that bilateral EMG coherence at ~10 Hz during quiet standing was clearly evident in rectified EMG, but diminished and non-significant in non-rectified EMG. Hence, a heterogeneous MUAP distribution may reconcile experimental and computational approaches. That is, although oscillatory components are present in the spike patterns of individual motoneurons, common oscillatory activity is canceled out in the aggregate EMG signal due to a heterogeneous MUAP distribution.

4.1 The efficacy of EMG rectification

Significant correlation between coherence spectra estimated with the EMG signal and EMG amplitude in both simulated and experimental data indicate that the effects of periodic input on surface EMG are wide-ranging and can be both identified in non-rectified and rectified EMG, although to various degrees (cf. Yao et al. 2007). In our model, the distribution of MUAP shapes plays a crucial role in determining whether full-wave rectification improves the identification of oscillatory activity from surface EMG. The current study shows that with a uniform MUAP, oscillatory input are generally augmented in non-rectified EMG, which explains the disparity between empirical and modeling studies on the use of EMG rectification. For instance, Stegeman and colleagues (2010) investigated the spectral transfer function of a MU pool as a function of the input frequency. They found a relative linear transfer function without EMG rectification, whereas rectification introduced a frequency
dependency (coherence was attenuated at higher input frequencies), and therefore concluded that rectification should be avoided. However, spike train output was convolved with an identical MUAP. Similar results are found in the present study revealing attenuated intermuscular coherence using rectified EMG for common input at higher frequencies (25 and 40 Hz) when using a uniform MUAP (Fig. 7). The attenuation of coherence at higher input frequencies is however much reduced when using a heterogeneous MUAP distribution. Experimental results on intermuscular coherence between bilateral lower leg muscles revealed higher coherence values for rectified EMG. In the simulations stronger coherence for rectified EMG is restricted to heterogeneous MUAP distributions. These findings implicate a heterogeneous MUAP distribution underlying the generation of the surface EMG in question. The wide use of rectification in experimental studies suggests that heterogeneous MUAP distributions may be the norm.

4.2 Motor unit action potentials

In the present study, the heterogeneity of the MUAP distribution was parametrically varied by changing the polarity of the MUAPs. In bipolar surface recording phase reversals of the MUAP can be observed when moving the electrodes over the endplate zone in the direction parallel to the muscle fiber (Farina et al. 2004; Kleine et al. 2007). Different MUAP polarities may be observed in muscles where the endplates are distributed throughout the entire muscle, such as the gastrocnemius and tibialis anterior muscles (Aquilonius et al. 1984). However, in other muscles the endplates form a fairly distinct and narrow band and phase reversals from fixed electrode locations are less likely to be observed. Variability in other electrophysiological parameters, such as differences in conduction velocity, have been shown to contribute to amplitude cancelation in surface EMG (Keenan et al. 2006). In this paper we show that this variability may also distort the transmission of oscillatory input into surface EMG. In particular, if the distribution of MUAPs tends toward a zero mean, oscillatory component become undetectable in non-rectified EMG and can only be observed as amplitude modulations of high-frequency content, i.e. in rectified EMG.
The MUAP is in itself a composite signal generated by summation of action potentials in single muscle fibers innervated by a single motoneuron (Dimitrov and Dimitrova 1998; McGill and Lateva 2001). Numerous factors affect the shape of a MUAP and recently new factors have identified that further complicate MUAP generation, such as innervation of multiple distinct endplate zones (Lateva et al. 2010) and the inclination of muscle fibers (Mesin et al. 2011). All these factors contribute to a heterogeneous MUAP distribution and hence distort the transmission of oscillatory components into the surface EMG signal. Likewise, electrode position affects coherence estimation showing attenuated coherence estimates when electrodes are placed over the endplate zone (Keenan et al. 2011). Whether the mean of the distribution indeed tends to zero for different types of muscles is currently hard to predict, as we only have limited information on the distribution of these electrophysiological parameters (Enoka and Fuglevand 2001). Full-wave rectified EMG provides the temporal pattern of grouped MU firing regardless of the MUAP shape (cf. Mima and Hallett 1999). Indeed, in our simulations oscillatory components can be robustly identified from rectified EMG robustly irrespective of the MUAP distribution, which may explain why rectification is generally used in empirical studies.

4.3 High-pass filtering

The present study confirms that, in general, oscillatory input to a MU pool causes oscillatory components in the EMG signal and rhythmic amplitude modulations of high-frequency EMG content (cf. Fig. 3). By high-pass filtering the EMG signals at different cut-off frequencies, we show that the amplitude modulations are present across a broad range of EMG frequencies. In fact, intermuscular coherence estimated from rectified EMG increases after high-pass filtering compared to no filtering across parameter settings. For example, simulations with a heterogeneous MUAP distribution, low periodicity and common input at 10 Hz show an increase in coherence from 0.12 without filtering to 0.20 after high-pass filtering at 500 Hz (Fig. 10, right panel). Likewise, empirical results show an increase in intermuscular
coherence from 0.095 without filtering to 0.13 after high-pass filtering at 260 Hz. These findings are inline with previous studies showing that high-pass filtering of the surface EMG signal improves the estimates of muscle force or torque (Potvin and Brown 2004; Staudenmann et al. 2007) and its correlation with the single motor unit signal (Riley et al. 2008). Whereas the current study uses rectified EMG to obtain a time-resolved estimate of the input to the MU pool, those studies used rectified EMG to estimate the output of the motoneurons. Together these results indicate that high-pass filtering before rectification improves both, in agreement with the almost linear transfer function of the MU pool (Negro and Farina 2011). It suggests that the bulk of the low-frequency content of the surface EMG signal may not provide a true representation of either the input or output of the MU pool, but may in fact arise from non-physiological processes (cf. De Luca et al. 2010). However, since the simulated data do not involve (non-physiological) noise and reveal the same effect, this explanation seems unlikely. Alternatively, high-pass filtering reduces the effect of amplitude cancellation, i.e. the underestimation of activation signal (Keenan et al. 2005). The present findings show that intermuscular coherence reflects concurrent oscillations in the activation level of different muscles, i.e. rhythmic rate-modulation of a very broad frequency carrier input to the muscle. High-pass filtering of surface EMG appears to improve the identification of oscillatory components in neurophysiological drive via intermuscular and corticospinal coherence.

4.4 Neural oscillations
Oscillatory components in the input to the muscle were modeled as rate-modulated Poisson processes. That is, neural oscillations reflect an oscillatory hazard rate or spiking probability that does not necessarily depend on the precise timing of individual spikes or additional temporal correlations of inter-spike intervals (ISI) (cf. Kostal et al. 2007; Stein et al. 2005). This is not to say that spike trains do not contain a more complex temporal structure, but just that such correlations are not a prerequisite for neural oscillations. In fact, in perceptual systems the spike latency with respect to the phase of ongoing neural oscillations may provide a fast and
flexible temporal coding scheme (e.g., Fries et al. 2007). Similarly, neural oscillations
do not require for individual neurons to fire at the same frequency or the frequency of
the oscillations. Indeed, in case of 8- to 12-Hz amplitude modulation in EMG,
individual MU spike trains with firing frequencies up to 22 imps/s produce spectral
peaks at 8-12 Hz as a consequence of appropriately grouped discharges (Elble and
Randall 1976). However, the amount of synchronization may be affected by the
difference between the mean firing rate and the frequency of common input (Lowery
and Erim 2005). The independence of firing rate and modulation frequency is readily
established in Poisson processes by varying the baseline firing rate and rate
modulations independently. Hence, rate-modulated Poisson processes provide a very
simple and effective basis for modeling neural oscillations. The approach suggests a
connection with mean field models of cortical populations, whereby the oscillating
mean field is used to rate-modulate the Poisson process of Pyramidal output neurons
in motor cortex.

Oscillatory activity is thus reflected in oscillatory modulations of the firing
rate. As such, the input to the MU pool can be approximated by a DC shifted sine
wave plus white noise (e.g., Stegeman et al. 2010). Likewise, recent studies have
linked event-related EEG components to oscillatory activity by assuming asymmetric
or non-zero-centered neural oscillations (Mazaheri and Jensen 2008; Nikulin et al.
2007; van Dijk et al. 2010). These oscillatory components can be easily identified by
spectral analysis of spike trains (Jarvis and Mitra 2001). However, oscillatory activity
may not just be reflected in the firing rate, or first statistical moment, but may also
result in temporal modulation of the spiking variability, the variance or second
statistical moment. This study shows that the spatial configuration of the source has a
differential effect on the statistical properties of the recorded signal, that is, it mainly
affects the identification of oscillatory component in the non-rectified EMG. Hence,
oscillatory components in spike trains, in general, can be identified in the signal and
amplitude (or mean and variance) of neural signals. As a consequence, they should be
modeled by DC shifted sine wave plus time-varying noise.
4.5 Limitations and future work

Our objective was to model basic mechanisms underlying intermuscular coherence by including the essential properties of a MU pool and the current model lacks physiological detail of more realistic models (e.g., Farina and Merletti 2001; Williams and Baker 2009). This study may have thus omitted factors that could influence the identification of rhythmic components for surface EMG and should not be considered a complete account of intermuscular synchronization. In particular, further knowledge on the distribution of electrophysiological parameters across MUs will allow modeling the heterogeneity of MUAPs in more detail. Nonetheless we argue that it provides important insights into neuromuscular coupling.

A number of extensions to the model could be easily implemented. Firstly, neural mass or neural field models could replace the Poisson processes to explicitly model the direct corticospinal tract and extend the model to corticospinal (EEG-EMG) synchronization. Indeed, this is entirely consistent with prevailing models of population dynamics that assume synaptic inputs to differing neurons can be approximated by independent Poisson processes (Deco et al. 2008). Although the present study focuses on intermuscular coherence, we expect that the observed effect of the distribution of MUAP shapes will equally apply to corticospinal coherence. In addition, the source of the common input remained unspecified in the present study. Experimental studies indicate that common input at different frequencies may have a variety of origins (Boonstra et al. 2009; McAuley and Marsden 2000). In particular, Baker and colleagues recently identified how spinal interneurons play an important role in 10 Hz oscillatory input to the MU pool (Williams et al. 2010).

The computational model presented in this paper has generated a specific hypothesis that can be tested empirically. The heterogeneity of the MUAP distribution was recognized as a critical parameter that influences the efficacy of EMG rectification in the identification of oscillatory activity from surface EMG. As the heterogeneity is electrophysiological parameters varies across muscles, this hypothesis can be tested experimentally. For instance, the endplate zones are organized differently across muscles (Aquilonius et al. 1984; Saitou et al. 2000),
which will affect the polarity distribution of the MUAPs measured with a fixed electrode configuration.

4.6 Conclusion

The effects of periodic input on surface EMG are wide-ranging and can be both identified in the EMG signal and amplitude. The effect of EMG rectification is strongly dependent on the heterogeneity of the MUAP distribution. If the mean of the MUAP distribution tends to zero, oscillatory input to the muscle will be canceled out in the aggregate surface EMG signal. Under these circumstances, oscillatory components can still be identified as amplitude fluctuations of high-frequency EMG content reflected in rectified EMG. Higher coherence in rectified EMG compared to non-rectified EMG in experimental recordings indicates a heterogeneous MUAP distribution.

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Figure legends

**Figure 1.** Model schematic of two MU pools. A MU pool consists of 100 $\alpha$-motoneurons modeled as IF neurons. Each motoneuron receives 100 descending inputs modeled as Poisson processes, such that two motoneurons of the same MU pool receive on average 30% common input. The Poisson trains providing input to both MU pools are rate modulated by a common 10-Hz process. Note that there is no direct cross talk between the two MU pools: Only the rate modulation, when present, is common. That is, the rate modulation is in phase, but the individual spiking events are unique. The outputs of the motoneurons are convolved with a motor-unit action potential (MUAP) and summed to generate the EMG signal for that muscle.

**Figure 2.** Example of 500 ms of input (at 40 imp/s) to a single motoneuron with different levels of 10-Hz modulation (A: 0%, B: 50%, C: 100%). The summed input from 100 input spike traces are depicted in gray, the low-passed filtered input is plotted in black to assist visual recognition of the 10-Hz modulation.

**Figure 3.** MUAP waveform (A) and the power spectral density of the MUAP (B).

**Figure 4.** Example of 500 ms of simulated data with a constant input rate of 20 imp/s (50% rate modulation). Spike train input to the MU pool in this example is modeled as a simple Poisson processes, showing the total input to five motoneurons on the left. The resulting membrane potential is shown in the second column and the output spike trains convolved with a weighted MUAP in the third column. The activity of 100 motoneurons is summed to produce the EMG signal generated by the MU pool as shown on the right.

**Figure 5.** Examples of signals with different types of 10-Hz modulations. Panel A displays a 10-Hz sinusoidal signal in grey with the rectified signal using Hilbert transform in black, reflecting the instantaneous amplitude. Note that the amplitude
envelope is constant, whereas rectification using the absolute value results in frequency doubling. Panel B displays the corresponding power spectral density on a logarithmic scale. Panel C displays an amplitude-modulated signal in which the amplitude of a 60-Hz carrier signal is modulated at 10 Hz, i.e. the principle used in AM radio. The 10-Hz modulation results in side bands in the power spectrum at 50 and 70 Hz, whereas the power spectrum of the signal amplitude reveals the 10-Hz modulation (D). Panel E displays amplitude-modulated white noise. Instead of a carrier signal, the amplitude of white noise is modulated at 10 Hz. The flat power spectral density shows no periodic components, which only become apparent after rectification (F).

Figure 6. Example of power spectral density (left column) and EMG-EMG coherence (right column) of simulation data. Top panels show the power (A) and coherence spectra (B) of data simulated with an input rate of 20 imp/s, no 10-Hz modulation and 100% positive polarity of the MAUPs. The second row shows the simulation results with 30% common 10-Hz modulation and 100% positive polarity of the MUAPs. The power spectrum of rectified EMG reveals a large peak at 10 Hz, whereas the peak is relatively small in non-rectified EMG (C). EMG-EMG coherence has a pronounced peak at 10 Hz both for both rectified and non-rectified EMG (D). Lower panels show data with a periodicity of 30% and positive polarity of 50%. Only the rectified EMG reveals a peak in the power spectrum at 10 Hz (E). 10-Hz coherence is strongly reduced in non-rectified EMG signal, but still evident in rectified EMG (F). The dotted lines in the coherence spectra depict the 95% confidence interval.

Figure 7. Effects of EMG rectification on quantification of common 10-Hz input. Simulated data were obtained for a range of parameter settings and EMG-EMG coherence was estimated using the rectified and non-rectified EMG. Each panel displays the coherence at the frequency of common input as a function of periodicity of the input on the y-axis (0%, no modulation; 100%, fully rate modulated) and polarity distribution on the x-axis (100%, all positive polarity; 50%, half positive...
polarity). Top row display results for non-rectified EMG and bottom row for rectified EMG. Columns display results for different input frequencies. All data is generated for the spike rate of the input of 20 imp/s.

**Figure 8.** The differences in coherence estimated from non-rectified and rectified EMG. Panels are similar to figure 7, but now only the differences are shown for all parameter settings. Columns show different input frequencies and rows different input rates (top: 20 imps/s, middle: 40 imps/s, bottom row: 60 imps/s). The figure reveals that for most settings coherence is higher when estimated from non-rectified EMG (corresponding to positive differences depicted in red). Only for a heterogeneous MUAP distribution (50-60 positive polarity) is coherence higher when estimated from rectified EMG (corresponding to negative differences or blue colors).

**Figure 9.** Intermuscular coherence from experimental data recorded during quiet standing with eyes closed. Left panels show coherence spectra estimated from the non-rectified EMG (black) and rectified EMG (gray) between left and right leg muscles (A: GL, B: GM, C: SO, D: TA, E: ED). The dotted line shows the 95% confidence interval. Intermuscular coherence estimated from rectified EMG revealed significant synchronization at 0-5 Hz and 10-15 Hz between bilateral calf muscles (GL, GM and SO). Right panels show coherence spectra estimated for rectified EMG after high-pass filtering at different cut-off frequencies (0-990 Hz, displayed on the y-axis). Qualitatively similar coherence spectra were found for a broad range of filtering settings with highest coherence values after high-pass filtering with a cut-off frequency between 100-300 Hz.

**Figure 10.** Intermuscular coherence from simulated EMG data obtained by integration of the computation model (input rate, 20 imp/s; periodicity, 10%; ratio of MUAP polarity, 60-40%). Left panels show coherence spectra estimated from the EMG signal (black) and EMG amplitude (gray) with the dotted depicting the 95% confidence interval. Right panels show coherence spectra estimated from the EMG
amplitude after high-pass filtering at different cut-off frequencies (0-990 Hz, displayed on the y-axis).
muscle 1

input

MU pool

convolve with MUAP

10-Hz modulation

EMG

∑

muscle 2

input

MU pool

convolve with MUAP

EMG

∑
input to MU

A

count

B

count

C

count

time [s]
Simulated MUAP

A

amplitude

\[ \text{time [ms]} \]

B

power

\[ \text{freq [Hz]} \]
A. Power spectra

B. Coherence spectra

C. Power spectra

D. Coherence spectra

E. Power spectra

F. Coherence spectra