EVOLUTION OF SURFACE ELECTROMYOGRAPHY: FROM MUSCLE ELECTROPHYSIOLOGY TOWARDS NEURAL RECORDING AND INTERFACING

Dario Farina[1] & Roger M. Enoka[2]

[1] Department of Bioengineering, Imperial College London, United Kingdom

[2] Department of Integrative Physiology, University of Colorado Boulder, CO, United States

Keywords: Electromyography, motor neuron, motor unit, decomposition

Correspondance:

Dario Farina

Department of Bioengineering

Imperial College London

London, United Kingdom

Email : d.farina@imperial.ac.uk

ABSTRACT

Surface electromyography (EMG) comprises a recording of electrical activity from the body surface generated by muscle fibres during muscle contractions. Its characteristics depend on the fibre membrane potentials and the neural activation signal sent from the motor neurons to the muscles. EMG has been classically used as the primary investigation tool in kinesiology studies in a variety of applications. More recently, surface EMG techniques have evolved from single-channel methods to high-density systems with hundreds of electrodes. High-density EMG recordings can be deconvolved to estimate the discharge times of spinal motor neurons innervating the recorded muscles, with algorithms that have been developed and validated in the last two decades. Within limits and with some variability across muscles, these techniques provide a non-invasive method to study relatively large populations of motor neurons in humans. Surface EMG is thus evolving from a peripheral measure of muscle electrical activity towards a neural recording and neural interfacing signal. These advances in technology have had a major impact on our fundamental understanding of the neural control of movement and have exposed new perspectives in neurotechnologies. Here we provide an overview and perspective of modern EMG technology, as derived from past achievements, and its impact in neurophysiology and neural engineering.

INTRODUCTION

Muscles are activated by sequences of action potentials discharged by motor neurons in the spinal cord. As Sherrington classically stated (Sherrington 1906), the motor neuron is the final common pathway of the neuromuscular system. It receives synaptic inputs from the entire nervous system and transmits its output to the muscle fibres, inducing their electrical activation and mechanical contraction. The neural signals sent from pools of motor neurons located in the ventral horn of the spinal cord to muscles are therefore the ultimate neural code for movement generation. Axonal action potentials reliably activate muscle fibres at the neuromuscular junction causing the depolarization of muscle fibres. The motor neuron and the fibres it innervates constitute the motor unit, which is the quantum of the motor system, as its smallest functional unit. The motor unit is a transducer of synaptic input (to the motor neuron) into forces (generated by the muscle fibres) (Heckman & Enoka, 2012) and therefore it is the frontier between the neural coding of motor tasks and movement mechanics.

The compound action potential of the fibres innervated by a motor neuron is the motor unit action potential. Each motor unit action potential produces an electric field in the surrounding space, as generated by the depolarised regions of the innervated muscle fibres (Plonsey 1977). This electric field can be detected with electrodes placed near the muscle fibres and, also, at the skin surface. With each action potential, the motor neuron in the spinal cord therefore generates a remote characteristic electric field on the skin surface. The body surface provides a screen of electrical activity timed with neural activations from the spinal cord.

The association between motor unit action potentials and the discharge of action potentials by motor neurons has been classically used to investigate motor unit

activity with selective intramuscular recordings. The concentric needle electrode, originally proposed by Adrian & Bronk (1929), marked the beginning of the era of in vivo motor unit investigations in humans. Intramuscular EMG recordings have provided a fundamental window for the study of motor units (for review, see Heckman & Enoka, 2012). However, although intramuscular EMG is a minimally invasive technique, the data yield is relatively low and in some countries the medical and technical constraints are prohibitive. As an alternative and, sometimes, complementary approach, the electric fields recorded with skin-mounted electrodes, which also provide direct information on motor unit activity, have allowed a simpler approach to motor unit investigations and a more widespread interest in the study of human movement at the motor unit level.

Here, we provide an overview of the advances in EMG technology that have led to currently established non-invasive methods for identifying the activity of individual motor units. These methods are progressively transforming surface EMG from a peripheral measure of muscle electrical activity into a neural recording system; a transition that is having an important influence on our understanding of the neural control of movement. In addition to providing a new methodology for physiological investigations, these advances in EMG technology have exposed new perspectives in neural interfacing and its attendant practical applications.

GLOBAL SURFACE EMG ANALYIS AND MOTOR UNITS

The function of spinal motor neurons over the last century has been studied in a series of studies that identified a few motor units in controlled laboratory conditions with invasive electrodes. The motor unit activity has been traditionally decoded with

time-consuming, computer-assisted manual decomposition methods (Merletti & Farina, 2009). Although the limited data yield from invasive EMG recordings has been partially resolved, much of our understanding of motor neuron function in humans is based on serial recordings of a small sample of motor units from each subject in standardized conditions. Although fundamental concepts on the neural control of muscles have been derived from this approach, it has been difficult to extrapolate these findings to the population level.

In contrast, surface EMG has been classically applied as a crude estimator of the global muscle activity, indirectly associated to the neural drive received by muscles. As recently as in the early 2000s, almost the entire surface EMG research was based on a few signal characteristics, such as amplitude or spectral moments, which provide indirect estimates of motor unit activity. At that time, the lack of validation of these techniques and fundamental flaws in their interpretation became evident, also because of a progressively increasing use of EMG computational models (Stegeman et al., 2000). In a review paper in 2004 (Farina et al., 2004), we wrote about "… the relations between global features of the surface EMG and the underlying physiological processes" and commented that "…. because direct measurements of motor unit activation are not available and many factors can influence the signal, these relations are frequently misinterpreted". Figure 1 shows an example of these difficulties. In this example, the amplitude of the surface EMG recorded from the vastus lateralis and medialis muscles is shown for four force levels (Figure 1A). The amplitude of the vastus medialis EMG is significantly greater than that of the vastus lateralis, which may be interpreted as a greater neural activation of the vastus medialis than lateralis. However, the differences in EMG amplitude can be almost entirely explained by differences in the amplitude of the individual motor unit action potentials between the

two muscles, as shown in Figure 1B, and not by differences in the level of neural activation. Indeed, the change in motor unit discharge rate with an increase in force was similar for the two muscles, indicating a similar amount of net excitatory input sent from the spinal cord to the two muscles. This example indicates the difficulty in separating the peripheral from the neural components in the interpretation of global EMG variables, such as amplitude.

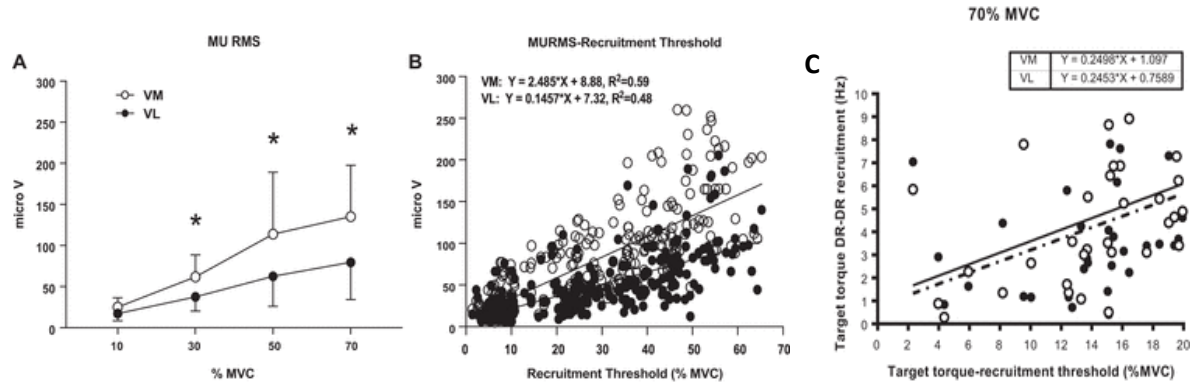


Figure 1. Characteristics of the global EMG and motor units during voluntary contractions with the knee extensors at increasing target forces. Surface EMG signals were recorded from the vastus medialis (VM) and lateralis (VL) during isometric contractions at forces ranging from 10% to 70% of the maximal voluntary contraction (MVC) force. The amplitude of the global EMG increased with target force for both muscles (A). However, the increase was greater for the VM compared with VL, so that at 70% MVC force the amplitude of the VM EMG was approximately double that for VL. From an analysis restricted to the global EMG only, this observation could be interpreted as a greater neural activation of VM with respect to VL. However, the amplitude of the single motor unit action potentials, which in this example were obtained by EMG decomposition, was also greater for the VM than VL (B), which likely indicates differences in the volume conductor filtering for the two muscles, rather than differences in neural drive. This is confirmed by the analysis of the relative changes of discharge rate of the motor units in the two muscles with respect to the changes in force, which were similar for the two muscles (C). Adapted with permission from (Martinez-Valdes et al., 2018).

Classic problems associated to the use of global surface EMG features as indirect measures of the neural drive to muscles include crosstalk (De Luca & Merletti, 1988; Solomonow et al., 1994; Farina et al., 2002), amplitude cancellation (Keenan et al., 2005), and the influence of the volume conductor on EMG amplitude and power spectrum (Farina et al., 2002b; 2002c). As shown in Figure 2, crosstalk is of particular concern. In this example, crosstalk between hand muscles resulted in high coherence values for two EMG signals, which may be incorrectly interpreted as indicating the level of common input to the sets of motor neurons innervating the two muscles.

The methodological limitations in global surface EMG analysis and interpretation can all be explained by the mixed influence of the neural activation and the waveforms of the action potentials. In brief, any mathematical descriptor of the EMG signal that does not separate the neural and muscle fibre contributions in the surface EMG cannot be used to infer neural control strategies. While early mathematical characterizations of surface EMG properties in the 70s clearly outlined the limitations of these approaches (e.g., Lindstrom & Magnusson, 1977), they constituted the only viable approach to the interpretation of surface EMG signals for quite some time.

Despite the development of many mathematical approaches to process the global surface EMG, the problems underlying its interpretation were not solved by an indirect analysis. Rather, it became evident that the core challenges with surface EMG interpretation were due to the global nature of the approaches (Farina et al., 2004; 2014), which contrasted with a direct access to the embedded neural information provided by invasive EMG methods.

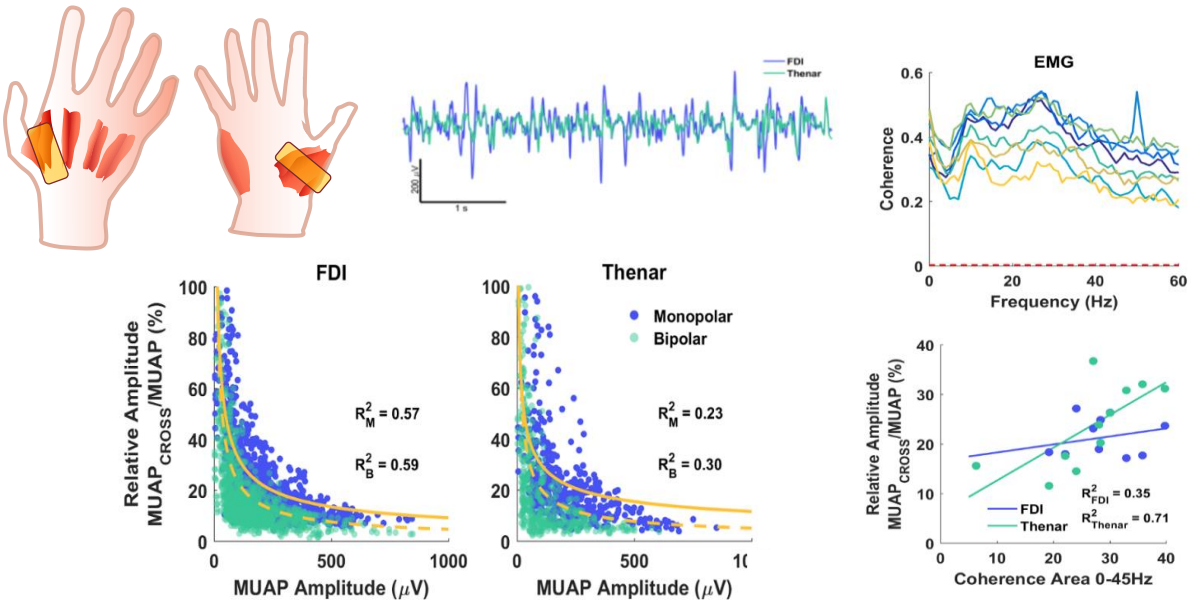


Figure 2. Crosstalk in surface EMG recordings. Surface EMG signals were recorded from the first dorsal interosseous (FDI) and the thenar muscles during concurrent activation of the two muscle groups. The EMG signals from the two muscle groups were relatively similar (top row, centre), leading to relatively high levels of coherence between them (top row, right) that might be interpreted as a high level of common input to the two sets of motor neurons. The signals were decomposed into single motor unit action potentials and used to estimate the amplitude of each action potential generated by one muscle but detected by the grid of electrodes over the second muscle (crosstalk motor unit action potentials, $MUAP_{CROSS}$). The $MUAP_{CROSS}$ values were compared in amplitude with the MUAPs directly generated by the second muscle (bottom row). The amplitude of the MUAPs due to crosstalk ($MUAP_{CROSS}$) could reach up to 100% of the amplitude of the MUAPs generated by the target muscle, indicating that a large proportion of the signals recorded from both muscles was influenced by crosstalk from the other muscle. A significant amount of the coherence value could be explained by the level of crosstalk (bottom row, right). Adapted with permission from (Del Vecchio et al., 2019).

MULTI-CHANNEL EMG

Electrode arrays with multiple detection points provide multi-dimensional EMG signals. From these signals, it was possible to identify spatial distributions of motor unit activity that are repeated consistently over time (Masuda et al., 1985) (Figure 3A). These distributions are associated with single motor unit action potentials that can be

discriminated with simple algorithms (Masuda et al., 1985) (Figure 3A) and identified even in different contractions at multiple force levels (Merletti et al., 1999). Moreover, it was shown that healthy subjects can isolate the activity of individual motor units when provided with visual feedback from multi-channel surface EMG recordings (Farina et al., 2004b).

In addition to spatial sampling, the selectivity of surface EMG recordings can be increased with spatial filtering (Figure 3B). The simplest spatial filter for EMG recordings is the well-known bipolar derivation, which corresponds to the spatial discrete first-derivative operator. Higher-order derivative operators, such as the double differential filter, have also been classically applied, for example for estimating muscle fibre conduction velocity (Merletti et al., 1990; 1995). The extension of these filters to two spatial dimensions leads to the Laplacian filter and higher-order filters (Reucher et al., 1987a; 1987b), as well as customised spatial filters (Farina & Rainoldi, 1999). High-pass spatial filters are edge-detection filters in image processing and, when applied to surface EMG recordings, they sharpen motor unit action potential waveforms so that they are more easily identified in an interference signal (Farina et al., 2003). These filters also reduce the detection volume by attenuating the contribution of deep sources (Disselhorst-Klug et al., 1997); however, this does not necessarily imply a reduction of crosstalk by high-pass spatial filters (Dimitrova et al., 2002; Farina et al., 2002). A variety of spatial filters have been proposed for surface EMG detection (Figure 3B), which have improved the identification of motor unit action potentials, but usually not entire trains of action potentials (Disselhorst-Klug et al., 2000).

EMG signals recorded inside or in the vicinity of a muscle are convolutive mixtures of spike trains with the muscle fibre action potential waveforms (De Luca,

1979). The neural information embedded in these signals is the ensemble of the spike trains, whereas the waveforms of action potentials depend on the fibre membrane properties as well as on the anatomy and volume-conductor properties. Separating the neural information from the action potential waveforms makes it possible to eliminate the variability due to non-neural factors that influence the surface EMG. This separation also performs the transition of EMG from a muscle electrophysiological recording to a pure neural recording. Early approaches for full surface-EMG decomposition were based on a combination of spatial sampling and filtering, together with algorithms with a similar structure as those developed for intramuscular EMG decomposition (Figure 3C). These approaches can provide, in some instances, almost complete trains of action potentials, but fail when applied to high-interference EMG signals.

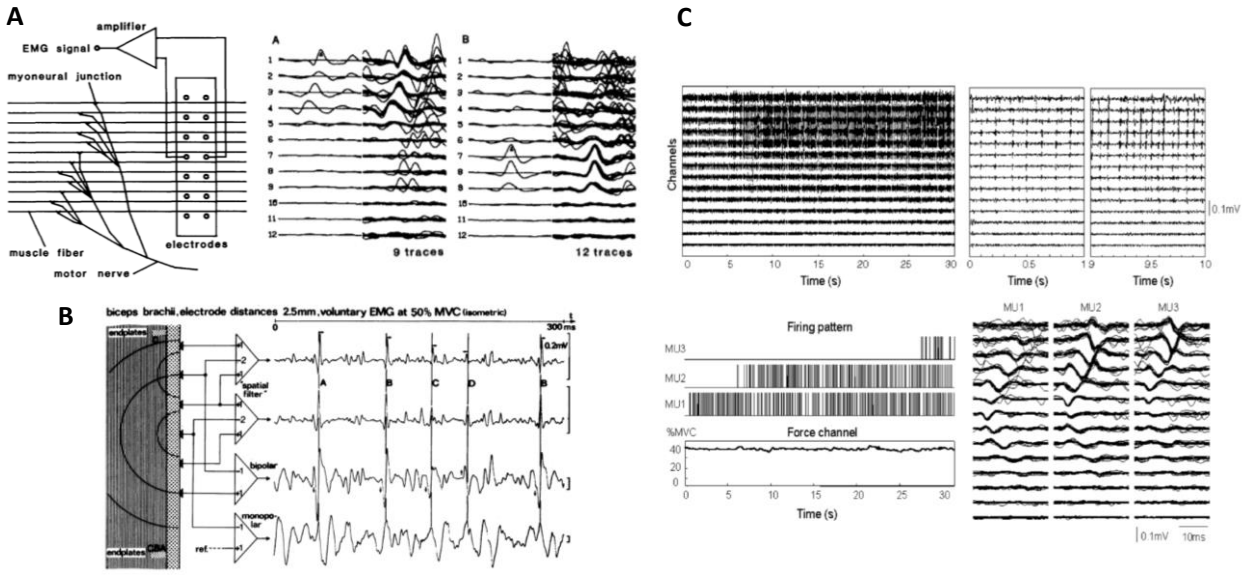


Figure 3. Early examples of the identification of motor unit action potentials from the surface EMG. One-dimensional arrays of electrodes allowed the identification of some repetitive action potentials of the same motor units over time and the estimation of the location of the neuromuscular junctions of the muscle units (A). Spatial filtering increases the selectivity of the recordings (B). The spikes associated with motor unit action potentials have a shorter duration when increasing the selectivity from a monopolar derivation to differential and Laplacian derivations (B). The concomitant use of spatial filtering and spatial sampling allows,

in some cases, the identification of almost complete trains of motor unit action potentials by decomposition algorithms (C). Reproduced and adapted from (A) Masuda et al., 1985, (B) Reucher et al., 1987a, (C) Gazzoni et al., 2004.

DECODING THE SURFACE EMG: FROM ELECTRIC FIELDS ON THE SKIN TO THE SPINAL CORD

Classic approaches to spatial sampling and filtering of the surface EMG were not explicitly derived from the EMG generation model, but instead were intended to increase the recording selectivity. However, the association between axonal action potentials in the efferent fibres of peripheral nerves and motor unit action potentials in EMG recordings can be described by a simple generation model that was defined mathematically in the 70s (De Luca, 1979). This well-known model, which is represented in Figure 4, can be expanded to multi-channel recordings, in which case it is expressed by the following equation (Farina & Holobar, 2016):

$$x_i(k) = \sum_{j=1}^{m} \sum_{l=0}^{L-1} h_{ij}(l) \sum_{r} \delta(k - \varphi_{jr} - l) + n_i(k), \qquad \text{with } i = 1, \dots, c; \quad k = 0, \dots, D_R \quad (1)$$

where i is the channel index, c the total number of channels, $x_i(k)$ is the EMG signal recorded by channel *i*, k is the discrete time variable, D_R is the duration of the recording (in samples), *m* the number of active motor units contributing to the EMG recording, $h_{ij}(l)$ the action potential of the j-th motor unit as recorded by the *i*-th channel, $\sum_r \delta(k - \varphi_{jr})$ the spike train of the j-th motor unit with spikes at times φ_{jr} (with $\delta(k)$ the Dirac delta impulse function), $n_i(k)$ the additive noise at channel *i*, and L the duration of the action potentials. The neural drive to the muscle *ND* is embedded in the EMG recordings:

$$ND(k) = \sum_{j=1}^{m} \sum_{r} \delta(k - \varphi_{jr}) \quad (2)$$

and is the ensemble of the series of discharge times of all active motor units.

The neural information is therefore contained in the recordings expressed by Eq. (1) but it is mixed by convolution with the waveforms of the motor unit action potentials $h_{ij}(l)$. Only recently has it been recognised (Holobar & Zazula, 2007; Holobar et al. 2009; Farina & Holobar, 2016; Negro et al. 2016; Holobar & Farina 2021) that this mixture problem can, in principle, be solved by inverting a mixing matrix and applying it to the multi-channel recording. This is essentially equivalent to estimating the inverse of the multi-channel motor unit action potentials across all channels and time samples and applying it to the signal to extract the target series of motor unit discharge times. We will not go into the mathematical details of this operation as recent reviews are available on the subject (e.g., Holobar & Farina, 2021), but note that the decomposition solution corresponds to filtering the surface EMG in the spatial and temporal domains concurrently (as opposed to a pure spatial filtering that was used in early approaches to enhance selectivity).

The decomposition problem is well-posed if the impulse responses $h_{ij}(l)$ [Eq. 1] are unique for each source; that is, the action potentials for each pair of motor units are different from each other in at least one EMG recording channel (Farina et al., 2008); this condition is intuitive as it is obviously not possible to discriminate the activity of motor units with identical action potentials. It is evident that this condition is likely to be valid for recordings with large numbers of channels, whereas fewer channels may easily lead to an ill-posed separation problem (Farina et al., 2008). This consideration led to the extensive use of high-density EMG systems for recording, as the systems most suited for processing by EMG decomposition algorithms. The solution of the

inverse problem of extracting the neural drive *ND* [Eq. (2)] from high-density EMG data [Eq. (1)] (Holobar & Zazula, 2007; Holobar et al. 2009; Farina & Holobar, 2016; Negro et al. 2016; Holobar & Farina 2021) has provided a new approach, complementary to the classic intramuscular EMG decomposition, for the study of motor unit activity.

High-density surface EMG provides several other advantages over classic individual bipolar recordings in addition to recording signals suited for decomposition. For example, the use of high-density EMG has shown that EMG amplitude varies substantially over the surface of individual muscles, both for anatomical reasons (e.g., De Luca, 1997) and because of spatial variations in muscle fibre activation (e.g., Madeleine et al., 2006). Therefore, the estimated intensity of muscle activity can be substantially improved when using multi-channel systems with respect to conventional single-channel recordings (Staudenmann et al., 2010). In general, global analyses applied to multi-channel recordings provide more reliable information than those obtained with fewer channels. Here, we will not focus on these applications but exclusively on the use of multi-channel EMG for decomposition into motor unit activity.

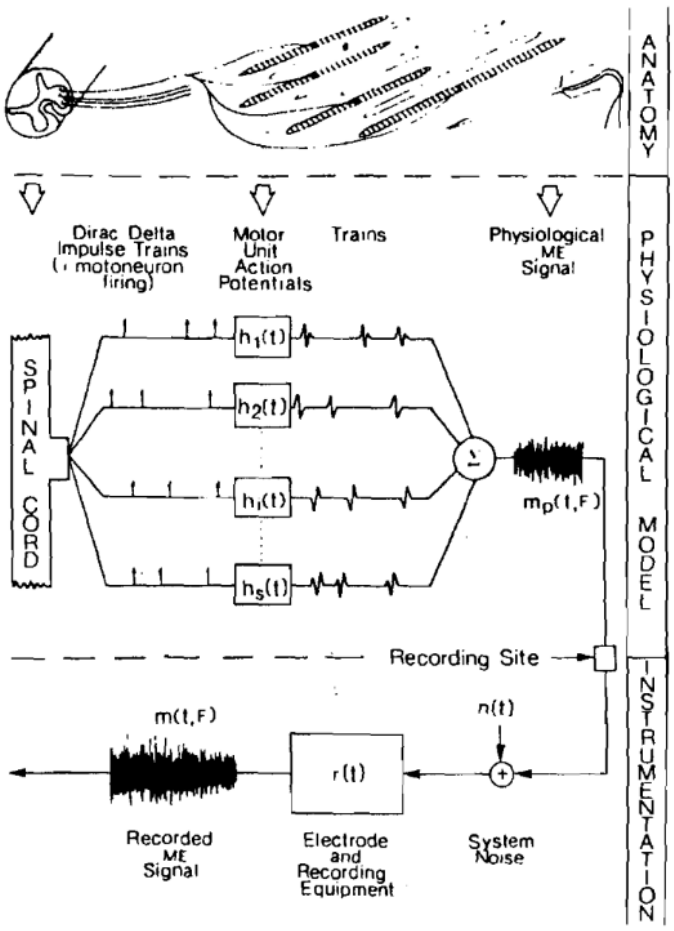


Figure 4. Classic model of surface EMG generation. The discharge times of motor neurons are mathematically represented as Dirac Delta functions (Eqs. 1 and 2 in the text). These are applied to filters representing the waveforms of action potentials of the innervated muscle units so that series of motor unit action potentials are obtained. These series are summed together to obtain the surface EMG, which is further influenced by the system noise (electronics and electrode-skin noise) and the frequency response of the specific EMG amplifier. This model underlies several contemporary decomposition methods. Although the model was proposed in the 70s, the realization that it could be inverted to estimate the discharge times of the motor neurons was only recognized in the last 15 years. Reproduced with permission from De Luca, 1979.

MOTOR UNIT INVESTIGATIONS

The availability of surface EMG decomposition algorithms has allowed a greater number of laboratories to perform motor control studies at the motor unit level. At the same time, several algorithms for surface EMG decomposition have been proposed. Although this greater effort has expanded our understanding of the neural control of movement, the ease with which surface EMG can be recorded and decomposed has also led to questionable uses of the approach. The issue of validation of surface EMG decomposition methods has therefore become central and is still debated (Farina et

al., 2014; Enoka, 2019). Moreover, contrary to intramuscular EMG decomposition, the accuracy and validity of surface EMG decomposition currently varies with muscle and volume conductor anatomy, which poses a severe limitation in the generalization of the approach. For example, the number of motor units that can be accurately detected by surface EMG decomposition decreases substantially with an increase in subcutaneous tissue thickness (Oliveira et al., 2022) and is on average lower in women than men (Del Vecchio et al., 2020b). In addition, while reaching high accuracy and reliability (Hug et al., 2021), the decomposition of surface EMG generally still shows lower accuracy than intramuscular decomposition when a similar amount of manual editing is applied to recordings obtained with the two techniques. Moreover, intramuscular EMG can be used to extract information that is currently not available from surface EMG, such as muscle unit territories and specific characteristics of the motor unit action potentials (e.g., polyphasic properties of the waveforms). Nonetheless, some other peripheral properties, such as muscle fibre conduction velocity, can be obtained more easily from surface than intramuscular EMG recordings.

Despite these limitations, surface EMG recordings enable the sampling of a greater number of motor units than is typically possible with intramuscular recordings. One key finding from these population-level measures of motor unit activity has been the fundamental role of common synaptic input to motor neurons for force produced by muscle (Negro et al., 2009; Farina et al., 2014b; 2015). This observation is the extension of the classic concepts of common drive (De Luca & Erim, 1994) and short-term synchronization (e.g., Semmler et al., 1997), which are both quantified for motor unit pairs, to the analysis of hidden dimensionality in the activity of populations of motor neurons (Negro et al., 2009).

It was recognised that the transmission of common input to a large number of motor neurons results in an approximately linear transformation into the motor neuron output (Negro et al., 2009). Despite the non-linearity of motor neurons in processing synaptic inputs, the central nervous system can linearise the transmission of neural information through motor neurons by projecting correlated input to sets of motor neurons. Because the muscle acts as a low-pass filter in transforming the neural drive into mechanical output, it is the low-frequency portion of the correlated input that determines the muscle force. Therefore, interestingly, the fluctuations in muscle force correspond to the low-frequency portion of the correlated input (common input) that the motor neurons receive (Farina et al., 2014b; Enoka & Farina, 2021). The distribution of common input to motor neurons linearises the association between input and output in motor neuron populations and is directly reflected in the generated force. Muscle force cannot be modulated without a certain proportion of common input. The presence of correlated input also explains both the observation of common drive and of short-term synchronization, as part of the same phenomenon but within different frequency bandwidths.

The association between the low-frequency component decoded from motor neuron output and muscle force is illustrated in Figure 5 (Thompson et al., 2018). The low-frequency component of the motor neuron cumulative spike trains, which is an estimate of the common input received by motor neurons, predicts the recorded force with high accuracy.

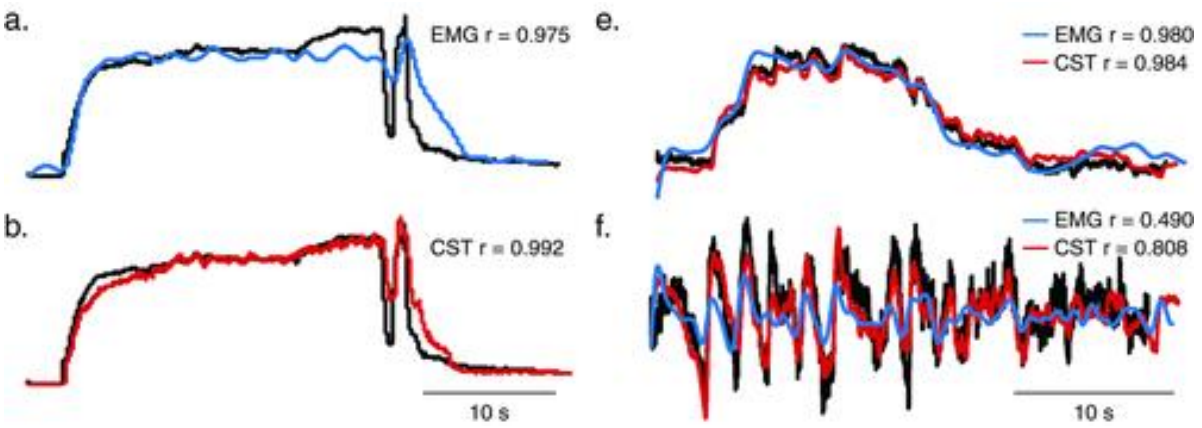


Figure 5. Relation between the effective neural drive to muscle and force. EMG and force were recorded from the left soleus muscle in a cat. The distal tendon of the isolated muscle was directly attached to a load cell to measure force. Muscle activation was induced, in this example, by the crossed-extension reflex. The force (black trace) exerted by the muscle is compared with both the rectified global EMG and the cumulative spike train (CST) of the motor units identified by surface EMG decomposition (a and b). When considering time intervals with large force variations (e) both the rectified EMG and the CST are correlated with force to a high degree. However, when analysing small force variations (f), the CST, as an estimate of the neural drive to the muscle, shows a greater correlation with force than rectified EMG. Reproduced with permission from Thompson et al., 2018.

Linearity in the transmission of common synaptic input also implies that groups of motor neurons may receive multiple synaptic inputs and that these can be identified from the motor neuron outputs by linear factorization methods. From the identification of a common input to groups of motor neurons, it was later possible to detect multiple synaptic inputs to multiple groups of motor neurons (Tanzerella et al., 2021). The identification of the structure of these inputs is possible with simple linear algorithms because of the linearization of the system by common input projections. It is therefore now possible to apply a variety of linear approaches to estimate the distribution of common inputs to motor neurons that innervate the same and other muscles, both synergists and antagonists (Tanzarella et al., 2021; Hug et al., 2021; 2022; Madarshahian & Latash, 2022; Del Vecchio et al., 2023). Interestingly, these findings

suggest that classic theories of muscle synergies, as derived from whole-muscle EMG recordings (Tresch et al., 1999), will need to be revised.

A population approach to the study of the input-output relation of motor neurons has also led to the observation that motor neurons receive synaptic inputs in a much greater frequency bandwidth than that associated with force production. Although the presence of beta oscillations (13-30 Hz) outside the force generation bandwidth (<10 Hz) was initially observed in the global surface EMG with coherence methods between cortical recordings and EMG (Conway et al., 1995), in more recent studies beta and higher oscillations have been directly detected from the discharge times of populations of motor units (for recent work, see Bräcklein et al., 2021; 2022). As with the low-frequency inputs to motor neurons, correlated higher-frequency inputs are linearly transmitted by motor neurons when they are distributed to many neurons. Indeed, beta and higher-frequency oscillations usually cannot be identified in the discharge series of a few motor neurons due to the non-linearity of the transmission or, equivalently, because they are sampled at a rate that is too slow (Negro et al., 2009). Rather, these frequencies can only be identified in a population analysis, so that the observable input bandwidth increases with the number of decoded motor units (Muceli et al., 2022).

The novel observations made possible by sampling more motor units with surface EMG than it was usually possible with conventional intramuscular EMG have also led to the development of intramuscular methods that can exceed the limited-sampling constraint. As early surface-EMG processing methods attempted to increase selectivity that matched invasive approaches, recently developed invasive technology has been able to increase the number of recording sites (spatial sampling) to match the capacity of high-density surface EMG (Farina et al., 2008b; Muceli et al., 2015; Muceli et al., 2022; Chung et al., 2023).

INTERFACING FOR NEUROTECHNOLOGIES

The association between neural drive and force has been exploited in man-machine interfacing systems. For example, motor neuron decoding has been used to predict joint moments of missing limbs in amputees (Farina et al., 2017). In this application, nerves originally innervating the missing limb are surgically transferred from the stump end to surviving muscles proximal to the amputation. Once the target muscles are reinnervated by the transferred nerves, they generate electrical activity associated with the neural activation of the new innervation. In this way, the muscle electrical activity can be detected and decoded into the contributions of individual motor units, and thereby establish a neural interface. Figure 6 schematically shows this application. Similar applications of surface EMG for interfacing have been described in spinal cord-injury patients (Ting et al., 2021), infants (Del Vecchio et al., 2020), and non-human primates (Del Vecchio et al., 2022). Moreover, other research and industry efforts are involved in the development of wearable EMG systems, for example wrist-mounted devices, for interacting with virtual reality or as an alternative means to control computers or smart phones for large consumer electronics applications (see, e.g., “Facebook Reality Labs” in References).

The future adoption of neural interfacing by surface EMG in medical and mass consumer systems will depend on the critical factors that still influence the application of surface EMG decomposition. As discussed above, the accuracy of surface EMG decomposition is still variable among individuals and muscles. In addition, it is limited to relatively constrained contractions, usually isometric tasks at constant or slow-varying forces. Moreover, interfacing technologies should require minimal calibration, which is a limiting factor in long-term uses when the EMG characteristics change substantially.

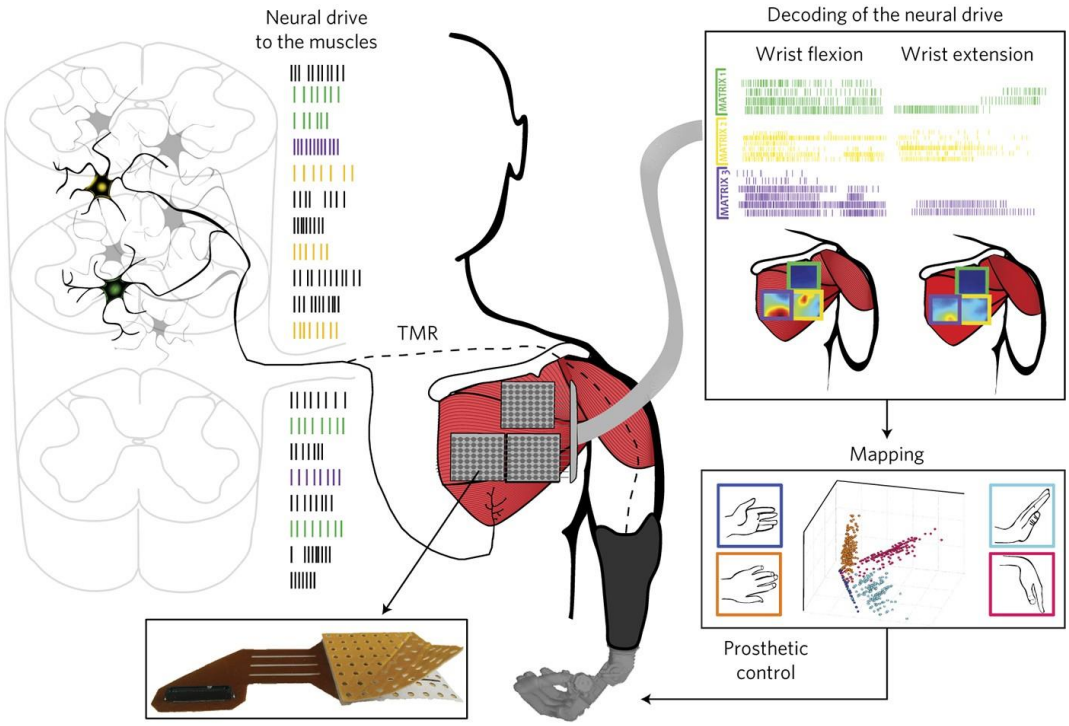


Figure 6. An example of neural interfacing for active prosthesis control based on high-density surface EMG decomposition. The nerves previously innervating muscles in the missing limb of an amputee are surgically transferred from the stump to proximal muscles. These proximal muscles are reinnervated by the transferred nerves so that their activity reflects the neural activation underlying the movement of the missing (phantom) limb (this surgery is called targeted-muscle reinnervation, TMR). In doing so, the reinnervated muscles are screens of the nerve activity that encodes the movement of the missing muscles. High-density surface EMG of the reinnervated muscles can be decomposed into the activity of motor units. These activities correspond to the activity of motor neurons in the spinal cord responsible for the activation of the lost muscles. Their decoding, therefore, allows the estimation of relevant commands for an artificial limb that reproduces the motor intention of the patient. Reproduced with permission from Farina et al., 2017.

CONCLUSION

The past 20 years have seen a profound increase in the information that can be extracted from surface EMG recordings. In contrast to global feature analysis and indirect associations to the neural drive to muscles that had earlier dominated EMG

processing, the field has transitioned to a direct extraction of motor unit discharge times from non-invasive EMG recordings over the last two decades. From the initial studies with concentric needle electrodes for intramuscular EMG recordings in humans (Adrian & Bronk, 1929), the decomposition of non-invasive EMG recordings has allowed motor unit analyses by many more laboratories, in less constrained conditions, and with larger yields of motor unit recordings. The evolution of this technology has provided advances in theories of neural control of movement and has shown potential for the future translation into neural interfacing systems. Nonetheless, limitations in the application of these methods remain and currently constrain their broad application across conditions. Surpassing these limits is a critical challenge for the future impact of surface EMG technologies.

ACKNOWLEDGEMENTS

This review covers work partly sponsored by the European Research Council (ERC) under the Synergy Grant Natural BionicS (810346) and the EPSRC Transformative Healthcare for 2050 project NISNEM Technology (EP/T020970/1) (to DF), and the National Multiple Sclerosis Society (to RME). The authors acknowledge the helpful comments of anonymous reviewers.

REFERENCES

Adrian, E.D., Bronk, D,W., 1929, The discharge of impulses in motor nerve fibres: Part II. The frequency of discharge in reflex and voluntary contractions. J. Physiol.;67(2):i3-151.

Bräcklein, M., Ibáñez, J., Barsakcioglu, D.Y., Farina, D., 2021, Towards human motor augmentation by voluntary decoupling beta activity in the neural drive to muscle and force production. J. Neural Eng.1 8(1).

Bräcklein, M., Barsakcioglu, D.Y., Del Vecchio, A., Ibáñez, J., Farina, D., 2022, Reading and Modulating Cortical β Bursts from Motor Unit Spiking Activity. J Neurosci. ;42(17):3611-3621.

Chung, B., Muneeb, Z., Thomas, K., Michaels, J.A., Jacob, A., Pack, A., et al., 2023, Myomatrix arrays for high-definition muscle recording. bioRxiv 2023.02.21.529200

Conway, B.A., Halliday, D.M., Farmer, S.F., Shahani, U., Maas, P., Weir, A.I., Rosenberg, J.R., 1995, Synchronization between motor cortex and spinal motoneuronal pool during the performance of a maintained motor task in man. J Physiol., 489 (Pt 3)(Pt 3):917-24.

De Luca, C.J., 1979, Physiology and mathematics of myoelectric signals. IEEE Trans. Biomed. Eng., 26(6):313-25.

De Luca, C.J., Merletti, R., 1988, Surface myoelectric signal cross talk among muscles of the leg. Electroencephalogr. Clin. Neurophysiol. 69:568–75.

De Luca, C.J., Erim, Z., 1994, Common drive of motor units in regulation of muscle force. Trends Neurosci.;17(7):299-305.

De Luca CJ., 1997, The use of surface electromyography in biomechanics. J. Appl. Biomech.; 13: 135-163.

Del Vecchio, A., Germer, C.M., Elias, L.A., Fu, Q., Fine, J., Santello, M., Farina, D., 2019, The human central nervous system transmits common synaptic inputs to distinct motor neuron pools during non-synergistic digit actions. J. Physiol., 597(24):5935-5948.

Del Vecchio, A., Sylos-Labini, F., Mondì, V., Paolillo, P., Ivanenko, Y., Lacquaniti, F., Farina, D., 2020, Spinal motoneurons of the human newborn are highly synchronized during leg movements. Sci. Adv., 6(47):eabc3916.

Del Vecchio A, Holobar A, Falla D, Felici F, Enoka RM, Farina D., 2020b, Tutorial: Analysis of motor unit discharge characteristics from high-density surface EMG signals. J Electromyogr Kinesiol. 53:102426.

Del Vecchio, A., Jones, R.H.A., Schofield, I.S., Kinfe, T.M., Ibáñez, J., Farina, D., Baker, S.N., 2022, Interfacing Motor Units in Non-Human Primates Identifies a Principal Neural Component for Force Control Constrained by the Size Principle. J. Neurosci., 42(39):7386–99.

Del Vecchio, A., Germer, C.M., Kinfe, T.M., Nuccio, S., Hug, F., Eskofier, B., Farina, D., Enoka, R.M., 2023, The forces generated by agonist muscles during isometric contractions arise from motor unit synergies. J Neurosci. (In Press)

Dimitrova, N.A., Dimitrov, G.V., Nikitin, O.A., 2002, Neither high-pass filtering nor mathematical differentiation of the EMG signals can considerably reduce cross-talk. J. Electromyogr. Kinesiol., 12(4):235-46.

Disselhorst-Klug, C., Silny, J., and Rau, G., 1997, Improvement of spatial resolution in surface EMG: a theoretical and experimental comparison of different spatial filters. IEEE Trans. Biomed. Eng., 44:567-574.

Disselhorst, C, Bahm, J., Ramaekers, V., Trachterna, A., Rau, G., 2000, Non-invasive approach of motor unit recording during muscle contractions in humans. Eur. J. Appl. Physiol., 83:144-150.

Enoka, R.M., 2019, Physiological validation of the decomposition of surface EMG signals. J Electromyogr Kinesiol., 46:70-83.

Enoka, R.M., Farina D., 2021, Force Steadiness: From Motor Units to Voluntary Actions. Physiology (Bethesda)., 36(2):114-130.

Farina, D., Rainoldi, A., 1999, Compensation of the effect of sub-cutaneous tissue layers on surface EMG: a simulation study. Med. Eng. Phys., 21:487-496

Farina, D., Merletti, R., Indino, B., Nazzaro, M., Pozzo, M., 2002, Sur face EMG crosstalk between knee extensor muscles: experimental and model results. Muscle Nerve 26:681–95.

Farina, D., Fosci, M., Merletti, R., 2002, Motor unit recruitment strategies investigated by surface EMG variables. An experimental and model based feasibility study. J. Appl. Physiol., 92:235-247.

Farina, D., Cescon, C., Merletti, R., 2002, Influence of anatomical, physical, and detection-system parameters on surface EMG. Biol. Cybern., 86(6):445-56.

Farina, D., Arendt-Nielsen, L., Merletti, R., Indino, B., Graven-Nielsen, T., 2003, Selectivity of spatial filters for surface EMG detection from the tibialis anterior muscle. IEEE Trans. Biomed. Eng., 50(3):354-64.

Farina, D., Merletti, R., Enoka, R.M., 2004, The extraction of neural strategies from the surface EMG. J. Appl. Physiol. (1985)., 96(4):1486-95.

Farina, D., Gazzoni, M., Camelia, F., 2004., Low-threshold motor unit membrane properties vary with contraction intensity during sustained activation with surface EMG visual feedback. J. Appl. Physiol. (1985)., 96(4):1505-15.

Farina, D., Negro, F., Gazzoni, M., Enoka, R.M., 2008, Detecting the unique representation of motor-unit action potentials in the surface electromyogram. J. Neurophysiol., 100(3):1223-33.

Farina, D., Yoshida, K., Stieglitz, T., Koch, K.P., 2008, Multichannel thin-film electrode for intramuscular electromyographic recordings. J. Appl. Physiol. (1985).;104(3):821-7.

Farina, D., Merletti, R., Enoka, R.M., 2014, The extraction of neural strategies from the surface EMG: an update. J. Appl. Physiol. (1985)., 117(11):1215-30.

Farina, D., Negro, F., Dideriksen, J.L., 2014, The effective neural drive to muscles is the common synaptic input to motor neurons. J Physiol., 592(16):3427-41.

Farina, D., Negro, F., 2015, Common synaptic input to motor neurons, motor unit synchronization, and force control. Exerc. Sport Sci. Rev., 43(1):23-33.

Farina, D., Holobar, A., 2016, Characterization of Human Motor Units From Surface EMG Decomposition. Proc. IEEE 104:353-373.

Farina, D., Vujaklija, I., Sartori, M. et al., 2017, Man/machine interface based on the discharge timings of spinal motor neurons after targeted muscle reinnervation. Nat. Biomed. Eng. 1, 0025.

Gazzoni, M., Farina, D., Merletti, R., 2004, A new method for the extraction and classification of single motor unit action potentials from surface EMG signals. J Neurosci. Methods.;136(2):165-77.

Heckman, C.J., Enoka, R.M., 2012, Motor Unit. Compr Physiol 2:2629-2682.

Holobar, A., Zazula, D., 2007, Multichannel blind source separation using convolution kernel compensation. IEEE Trans. Signal Process., 55:4487-4496.

Holobar, A., Farina, D., Gazzoni, M., Merletti, R., Zazula, D., 2009, Estimating motor unit discharge patterns from high-density surface electromyogram. Clin Neurophysiol.;120(3):551-62.

Holobar, A., Farina D., 2021, Noninvasive Neural Interfacing With Wearable Muscle Sensors: Combining Convolutive Blind Source Separation Methods and Deep Learning Techniques for Neural Decoding. IEEE Signal Processing Magazine 38, 103-118.

Hug F, Avrillon S, Del Vecchio A, Casolo A, Ibanez J, Nuccio S, Rossato J, Holobar A, Farina D., 2021, Analysis of motor unit spike trains estimated from high-density surface electromyography is highly reliable across operators. J. Electromyogr. Kinesiol. 58:102548.

Hug, F., Avrillon, S., Sarcher, A., Del Vecchio, A., Farina, D., 2022, Correlation networks of spinal motor neurons that innervate lower limb muscles during a multi-joint isometric task. J Physiol. (In Press)

Hug, F., Avrillon, S., Ibáñez, J., Farina, D., 2023, Common synaptic input, synergies and size principle: Control of spinal motor neurons for movement generation. J Physiol., 601(1):11-20.

Keenan, K.G., Farina, D., Maluf, K.S., Merletti, R., Enoka, R.M., 2005, Influence of amplitude cancellation on the simulated surface electromyogram. J Appl Physiol (1985), 98(1):120-31.

Lindstrom, L., Magnusson, R., 1977, Interpretation of myoelectric power spectra: a model and its applications, Proc. IEEE, 65:653-662.

Madarshahian S, Latash ML., 2022, Reciprocal and coactivation commands at the level of individual motor units in an extrinsic finger flexor-extensor muscle pair. Exp Brain Res 240:321-340.

Madeleine P, Leclerc F, Arendt-Nielsen L, Ravier P, Farina D., 2006, Experimental muscle pain changes the spatial distribution of upper trapezius muscle activity during sustained contraction. Clin. Neurophysiol. 117(11):2436-45.

Martinez-Valdes, E., Negro, F., Falla, D., De Nunzio, A.M., Farina, D., 2018, Surface electromyographic amplitude does not identify differences in neural drive to synergistic muscles. J Appl Physiol (1985)., 124(4):1071-1079.

Masuda, T., Miyano, H., Sadoyama, T., 1985, A surface electrode array for detecting action potential trains of single motor units. Electroenc. Clin. Neurophysiol., 60:435-443.

Merletti, R., Knaflitz, M., De Luca, C.J., 1990, Myoelectric manifestations of muscle fatigue during voluntary and electrically elicited contractions. J. Appl. Physiol., 68:1657-1667.

Merletti, R., Lo Conte, L., 1995, Advances in processing of surface myoelectric signals: Part 1. Med. Biol. Eng. Comput., 33:373-384.

Merletti, R., Farina, D., Granata, A., 1999, Non-invasive assessment of motor unit properties with linear electrode arrays. Electroencephalogr. Clin. Neurophysiol., 50:293-300.

Merletti, R., Farina, D., 2009, Analysis of intramuscular electromyogram signals. Phil. Trans. R. Soc. A.367357–368.

Muceli, S., Poppendieck, W., Negro, F., Yoshida, K., Hoffmann, K.P., Butler, J.E., Gandevia, S.C., Farina, D., 2015, Accurate and representative decoding of the neural drive to muscles in humans with multi-channel intramuscular thin-film electrodes. J Physiol., 593(17):3789-804.

Muceli, S., Poppendieck, W., Holobar, A., Gandevia, S., Liebetanz, D., Farina, D., 2022, Blind identification of the spinal cord output in humans with high-density electrode arrays implanted in muscles. Sci Adv., 8(46):eabo5040.

2021, Inside Facebook Reality Labs: Wrist-based interaction for the next computing platform, Available at: https://tech.facebook.com/reality-labs/2021/03/inside-facebook-reality-labs-wrist-based-interaction-for-the-next-computing-platform/ , (Accessed 15 Mar 2023).

Negro, F., Holobar, A., Farina, D., 2009, Fluctuations in isometric muscle force can be described by one linear projection of low-frequency components of motor unit discharge rates. J Physiol., 587(Pt 24):5925-38.

Negro, F., Muceli, S., Castronovo, A.M., Holobar, A., Farina, D., 2016, Multi-channel intramuscular and surface EMG decomposition by convolutive blind source separation. J Neural Eng., 13(2):026027.

Oliveira DS, Casolo A, Balshaw TG, Maeo S, Lanza MB, Martin NRW, Maffulli N, Kinfe TM, Eskofier BM, Folland JP, Farina D, Del Vecchio A., 2022, Neural decoding from surface high-density EMG signals: influence of anatomy and synchronization on the number of identified motor units. J. Neural Eng. 2;19(4).

Plonsey, R., 1977, Action potential sources and their volume conductor fields. IEEE Trans. Biomed. Eng., 56:601-11.

Reucher, H., Rau, G., Silny, J., 1987, Spatial filtering of non-invasive multielectrode EMG: part I{Introduction to measuring technique and applications. IEEE Trans. Biomed. Eng., vol. 34, pp. 98-105.

Reucher, H., Rau, G., Silny, J., 1987, Spatial filtering of non-invasive multielectrode EMG: part II{Filter performance in theory and modelling. IEEE Trans. Biomed. Eng, 34:106-113.

Semmler, J.G., Nordstrom, M.A., Wallace, C.J., 1997, Relationship between motor unit short-term synchronization and common drive in human first dorsal interosseous muscle. Brain Res., 767(2):314-20.

Sherrington, C.S., 1906, The integrative action of the nervous system. New Haven, CT, Yale University Press.

Solomonow, M., Baratta, R., Bernardi, M., Zhou, B., Lu, Y., Zhu, M., Acierno, S., 1994, Surface and wire EMG crosstalk in neighbouring muscles. J Electromyogr Kinesiol 4:131–42

Staudenmann D, Roeleveld K, Stegeman DF, van Dieën JH., 2010, Methodological aspects of SEMG recordings for force estimation--a tutorial and review. J. Electromyogr. Kinesiol. 20(3):375-87.

Stegeman, D.F., Blok, J.H., Hermens, H.J., Roeleveld, K., 2000, Surface EMG models: properties and applications., Journ. Electromyogr. Kinesiol., 10:313-26.

Tanzarella, S., Muceli, S., Santello, M., Farina, D., 2021, Synergistic Organization of Neural Inputs from Spinal Motor Neurons to Extrinsic and Intrinsic Hand Muscles. J Neurosci., 41(32):6878-6891.

Thompson, C.K., Negro, F., Johnson, M.D., Holmes, M.R., McPherson, L.M., Powers, R.K., Farina, D., Heckman, C.J., 2018, Robust and accurate decoding of motoneuron behaviour and prediction of the resulting force output. J Physiol., 596(14):2643-2659.

Ting, J.E., Del Vecchio, A., Sarma, D., Verma, N., Colachis, S.C., Annetta, N.V., Collinger, J.L., Farina. D., Weber. D.J., 2021, Sensing and decoding the neural drive to paralyzed muscles during attempted movements of a person with tetraplegia using a sleeve array. J Neurophysiol., 126(6):2104-2118.

Tresch, M.C., Saltiel. P., Bizzi, E., 1999, The construction of movement by the spinal cord. Nat Neurosci., 2(2):162-7.