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Cortical Activity Associated with Motor Unit Action Potentials: Motor Cortex Control of the Recruitment of Motor Units

By

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Abstract

This paper examines cortical involvement in the recruitment of motor units, rejecting a previous common drive theory, and supporting the theory that explains cortex as having a more specific role in the particular motor units that are recruited, showing a command rather than simply a drive. Results from this study demonstrate a relationship between cortical activity and individual motor unit firing in humans non-invasively by recording EEG and high-density surface EMG in parallel. EMG data, from 2 subjects, were decomposed into individual motor units and ERPs time-locked to the specific motor units were obtained. Inter-trial coherence was computed to further measure a direct relationship between cortical and motor unit activity. There was coherence at low frequency EEG oscillations around the time of the extracted motor unit spikes. Frequencies were also similar between subjects. Additionally, cross-validation analysis was done to demonstrate an ability to predict motor unit recruitment from EEG recordings. Results suggest cortical activity can be consistently associated with motor units and that there is a more precise relationship than just a readiness potential from movement onset. With this fine-grained control in the recruitment of specific motor units and the flexibility of recruitment, motor unit recruitment strategies are potentially trainable. This is important because of its potential for use in rehabilitation after injury or motor skill acquisition. This study sets forth foundational knowledge that allows for further research to better understand neuromuscular control.

Keywords: cortical activity, cortical control, motor cortex, motor unit action potential, motor unit, motor unit recruitment, EEG, high-density surface EMG

Cortical Activity Associated with Motor Unit Action Potentials: Motor Cortex Control of the Recruitment of Motor Units

The way in which humans control their neuromuscular system to perform complex motor tasks is an ongoing area of study. There is much yet to be discovered about muscle contraction, cortical control, and the specificity and flexibility in the recruitment of motor units. Motor units consist of a motor neuron’s cell body and dendrites, the axon’s branches, and the muscle fibers innervated by it (Del Vecchio et al., 2020). Generally, it is known that there is a consistent temporal relationship between cortical activity and movement onset through the use of electroencephalography (EEG) and electromyography (EMG) (Schurger et al., 2021). EEG measures electrical signals that vary in time and shows changes in electrical activity in the brain, while EMG measures electrical activity in a muscle in response to nerve signals. A temporal relationship refers to the event-related potential (ERP), a time-locked and phase-locked, responsive voltage, produced in the brain, to stimuli (in this case, motor events) (Luck, 2014; Sur & Shinha, 2009; Woodman, 2010). Time-locked means that cortical activity shows a pattern at the same time on each trial of the stimulus onset. Phase-locked means that cortical activity shows a pattern at the same angle on each trial of stimulus onset (exact timing of ongoing rhythmic activity). The timing of the frequency-bend specific activity is very similar on every trial. The known temporal relationship between cortical activity and movement onset is known as readiness potential, an ERP that shows a buildup of cortical activity leading up to voluntary muscle movement (Schurger et al., 2021). It is unclear, however, whether there is cortical activity associated with individual motor unit action potentials and the way in which the motor cortex is involved in the recruitment of motor units in muscle movement.

There are two competing theories regarding cortical involvement in the recruitment of motor units. One theory asserts that cortex sends a single homogenous drive to the motor neuron pool in the spinal cord and that the selection of specific motor units is determined entirely in the periphery. Because of the high correlation between the firing activities of motor units, as well as the short time delay in which units modulate their firing rates, it was surmised that motor unit activation was driven by the same source and any unshared inputs received by a single motor unit were classified as uncorrelated “noise” (separate from the common drive) (De Luca & Erim, 1994). Therefore, even though different motor units are recruited at varying times and in different ways, all individual motor units are affected, not by distinct command signals sent to these units, but by one common drive to which motor units respond differently. This is a way to avoid the central nervous system becoming overloaded by having to monitor and regulate motor units individually (De Luca & Erim, 1994). The concept of a common drive supplied to each pool of neurons by motor cortex provides that the cortex cannot control motor units separately and independently and the way in which cortex is involved is quite rigid (Kandel et al., 2013). Experiments in cats show that altering cortical activity does not change recruitment of motor units (Somjen et al., 1965). However, recent work in non-human primates demonstrates a shift in the perspective of cortical involvement in the recruitment of motor units (Marshall et al., 2021).

Competing with the homogenous drive theory, the other theory to explain cortical involvement in the recruitment of motor units maintains that cortex has a more specific role in the particular motor units that are recruited, which is to say it commands (directs and organizes) rather than simply drives. Support of this theory is shown first by being able to demonstrate a relationship between cortical activity and individual motor unit firing. Laine and colleagues (2012) have looked at the relationship between cortical activity and motor units in the human hypoglossal. Cortical entrainment (constant phase relationship between cortical signals to the same stimulus) is assessed by measuring phase-locking between single motor unit action potentials and EEG oscillations (neural brainwaves). They find that cortical entrainment of multiunit activity is detectable within the 15- to 40- Hz frequency range and cortical entrainment of single motor unit spike timing is reliable within the same frequency range. This means that cortical output to motor units can be measured directly and that this output contains frequency-specific influence on motor unit recruitment. In addition to being able to demonstrate this relationship, there is research that indicates that recruitment activity displays patterns that cannot be described by the common drive, demonstrating the flexibility of motor units. Intracortical recordings performed alongside intramuscular EMG in a rhesus macaque monkey show that motor unit recruitment is readily altered by cortical stimulations (Marshall et al., 2021). According to the common drive theory, stimulation of one electrode should activate, for example, motor unit one, as well as motor unit five. Furthermore, it should activate motor units with lower thresholds first. However, this is not the case in the rhesus macaque. Stimulation on one electrode activates motor unit one, but not motor unit five. Moreover, this stimulation activates motor units not according to threshold level. These findings demonstrate unexpected recruitment patterns, inconsistent with common drive recruitment. Additionally, neighboring motor units are differentially recruited by stimulation of adjacent electrodes. For example, stimulation of electrode one recruits motor unit eight, stimulation of electrode three recruits motor unit fifteen, and stimulation of electrode two recruits both. The results from the rhesus macaque study reject the theory that cortex merely sends a homogenous drive and the selection of specific motor units is determined entirely in the periphery. Rather the rhesus macaque study results support the theory that cortex not only drives, but also commands, and that motor unit recruitment is flexible. In other words, it is possible that individual motor units can be called independently from one another with separate command signals. However, it is unknown how much the ability for fine-grained control is typically used and whether cortical activity can be consistently associated with individual motor units.

In light of these relatively recent findings, the current study looks to further investigate whether cortical activity is associated with individual motor units and the way in which the motor cortex is involved in the recruitment of motor units in muscle movement. This study aims to examine this in humans using non-invasive methods. Through recording of EEG and high-density surface EMG in parallel, it will explore the relationship between cortical activity and motor unit action potentials. There is interest in seeing whether motor unit recruitment from EEG recordings can be predicted. Recordings from high-density surface EMG will be decomposed to identify individual motor unit action potentials during voluntary movement. Decomposition allows for action potentials to be compared, across subjects and over time, and knowing individual motor unit firing times provides a direct estimate of neural drive to the muscle (Del Vecchio et al., 2019; Del Vecchio et al., 2020).

While there are existing methods for decomposing surface EMG, motor unit recruitment using this method has not been directly related to human EEG (Hogrel, 2003, Kleine et al., 2000, Kleine et al., 2007). Laine and colleagues (2012) use EEG and EMG to look at the relationship between motor unit recruitment and cortical activity in humans but do so using intramuscular genioglossus EMG. Marshall and colleagues (2021) also use intracortical and intramuscular recordings. In contrast, the methodology in this study is noninvasive, which makes it more suitable for neuromuscular research, specifically motor unit action potential related studies. Although this method poses a potential issue with spatial resolution, recent work has shown methods of its improvement (Burle et al., 2015; Dupré La Tour et al., 2018; Michel & Brunet, 2019). New algorithms recover biological artifacts and topographic maps. Moreover, the current method can be used on humans with precise temporal resolution as opposed to other neuroimaging modalities. Additionally, extraction of motor unit action potentials from high-density surface EMG not only has been validated, but moreover maintains structural and functional information not provided by needle EMG (Hug et al., 2021).

It is hypothesized that in humans, there is a granular response-related or pattern of cortical activity associated with the firing of a motor unit, which is more specific than solely a big slow readiness potential. This would reject the common drive theory and further support that the motor cortex commands (directs and organizes) rather than simply drives. Moreover, it would provide a novel methodology for studying neuromuscular control in humans that can relate more directly than non-human primate literature. With this, motor unit action potential related studies can be replicated, and data can be more easily analyzed, which allows for new questions to be asked and further research to be done about neuromuscular control. Further answers to questions regarding how altering cortical activity can alter recruitment of motor units and motor unit flexibility can be sought. Additionally, if cortex has more fine-grained control in the recruitment of specific motor units, then motor unit recruitment strategies are potentially trainable. This is important because of its potential for use in rehabilitation after injury. Also, there is evidence that motor unit recruitment strategies change throughout skill acquisition (Bernardi et al., 1996). If this is the case, it is possible that manipulating cortical activity toward particular recruitment strategies can speed up motor skill acquisition, such as for training athletes.

Methods

Participants

Subjects are two adults. Subject 1 is female and Subject 2 is male. Although it is possible that neuromotor control varies between people, this does not pose an issue for this study.

Procedure

Data Collection

Subjects fill out a consent form following a short briefing of the procedure. An 8.5 mm HD-EMG Electrode Grid is prepared for application by ensuring that each electrode in the array contains conductive gel and the space in between the electrodes does not. The grid contains Ag/AgCl electrodes with high spatial resolution used to detect detailed muscle activity. It is placed on the muscle on the forearm associated with the movement of the subject’s ring finger. This is connected to the TMSi SAGA 32+/64+ Amplifier, a high-density electrophysiological amplifier used to acquire electrical signals. Next, after measuring the subject’s head size, an Infinity Gel Headcap that adheres to the international standard 10-20 EEG electrode positions and allows for passive acquisition of quality signals, low impedances, and for the least movement artifacts, is applied to the scalp and connected to the amplifier as well. Data are recorded on TMSi Polybench, a software application for quick recording application with graphical user interface for SAGA that includes configuration, data acquisition and data import/export (poly5). Impedance is checked before recording begins. Because the amplifier only records 64 electrodes and is intended to only use one of these applications at a time, 32 electrodes will be assigned to the grid and the other 32 assigned to the headcap. This allows for recording EMG and EEG data in parallel. This means that although there are up to 128 passive gel sensors, only 64 will be recorded. All channels are unipolar. Participants are then asked to perform a repeated motor task (different between subjects, but one task per subject). The subject is asked to avoid performing the task with movement in intervals too close together and is informed that there is no need for consistent intervals. Moreover, as with standard recording of EEG, the subject is also asked to avoid unnecessary movement unrelated to the desired motor task.

Subject 1

For the repeated motor task, Subject 1 was instructed to open and close her hand in a grasping motion for 10 minutes. Data were sampled at 4000 Hz and later filtered at 500 Hz and downsampled to 1000 Hz.

Subject 2

For the repeated motor task, Subject 2 was asked to spontaneously press the button on the amplifier with his ring finger for 20 minutes. This motor task differed from that of Subject 1 in order to target a specific muscle (ring finger) as opposed to several muscles (entire hand) used by Subject 1. Data were sampled at 500 Hz and later filtered at 250 Hz and upsampled to 1000 Hz.

Analysis

This study is intended to examine whether it is possible to relate cortical activity and motor unit action potentials through noninvasive EMG and EEG methods in humans. EMG analysis will involve extraction of motor unit action potentials. EEG analysis will involve searching for an ERP specifically time-locked not only to movement onset, but specifically to the motor unit. The extent of which phase-locking occurs will be analyzed with inter-trial coherence. If EMG is able to be decomposed into individual motor units and if an ERP time-locked to a specific motor unit can be obtained and also shown with inter-trial coherence from these recordings, this will indicate the ability to associate cortical activity with motor units.

Furthermore, it is challenging to demonstrate whether there is a clear relationship between a motor unit and an ERP. However, if a differentiating pattern can be extracted from part of the data and be applied to another part of the data (cross validation analysis) and if it predicts which ERP belongs to which motor unit, then this provides internal reliability and further indication that this activity in the cortex is selective for activity in the muscle, for particular motor units. If cortical activity can be consistently associated with motor units, it suggests that they can be called independently from one another with separate command signals, with cortex having fine-grained control of individual motor units.

In order to answer questions about the selectivity of motor unit recruitment in respect to cortical activity, there needs to be a way to isolate the cortical activity associated with particular motor units. Taking a neural decoding approach is a way to be able to do this. In this study, to reconstruct motor unit action potentials from the high-density surface EMG, convolutional dictionary learning is used, which involves decomposing the data into a set of convolutional kernels. This consists of identifying recurring temporal patterns from the data (which includes spike waveforms) and then recording when these patterns actually occur (spike times) (Dupré La Tour et al., 2018). Originally created for music recognition, convolutional dictionary learning is used as a way to learn and localize key patterns in signals or images. Multivariate convolutional sparse coding is an algorithm that has been applied to EEG and magnetoencephalography (MEG). Not only is it capable of learning temporal waveforms, but moreover, related spatial patterns, allowing their origin to be localized.

For EEG analysis, the EEG recording is compiled into epochs around the motor unit spike times and averaged over it to see an ERP locked to that particular motor unit. Furthermore, like Laine and colleagues (2012), inter-trial coherence for spike-locked epochs is computed to see if the spikes happen at a constant phase of ongoing cortical oscillations (Delorme & Makeig, 2004). This is a measure of phase-locking, measuring how consistent the oscillatory phase is across trials (how consistently they reach the same point in the cycle). It is calculated from a single trial EEG and reflects the temporal and spectral synchronization within EEG. For this study, it provides further a direct measure of cortical and motor unit synchrony and the power of the ERP. Additionally, cross validation analysis is performed by using different parts of the data to test and train a model on different iterations. By fitting a logistic regression classifier to four (out of five) parts of the ERP data, it is possible to predict which ERP belongs to which motor unit in the fifth part of the data. This is meant to test the classification model's ability to predict new data (prediction accuracy) and how it will generalize to an out-of-sample dataset as well (out-of-sample accuracy).

Python, Jupyter Notebook, MNE-Python and Scikit-learn packages, and the AlphaCSC package are the software that are used. MNE allows for computing intertrial coherence, Scikit-learn is used for cross-validation, AlphaCSC performs convolutional dictionary learning. The Poly5 file outputted by the TMSi Polybench is converted to a FIF file for ease and to gain more information about channel types.

Results

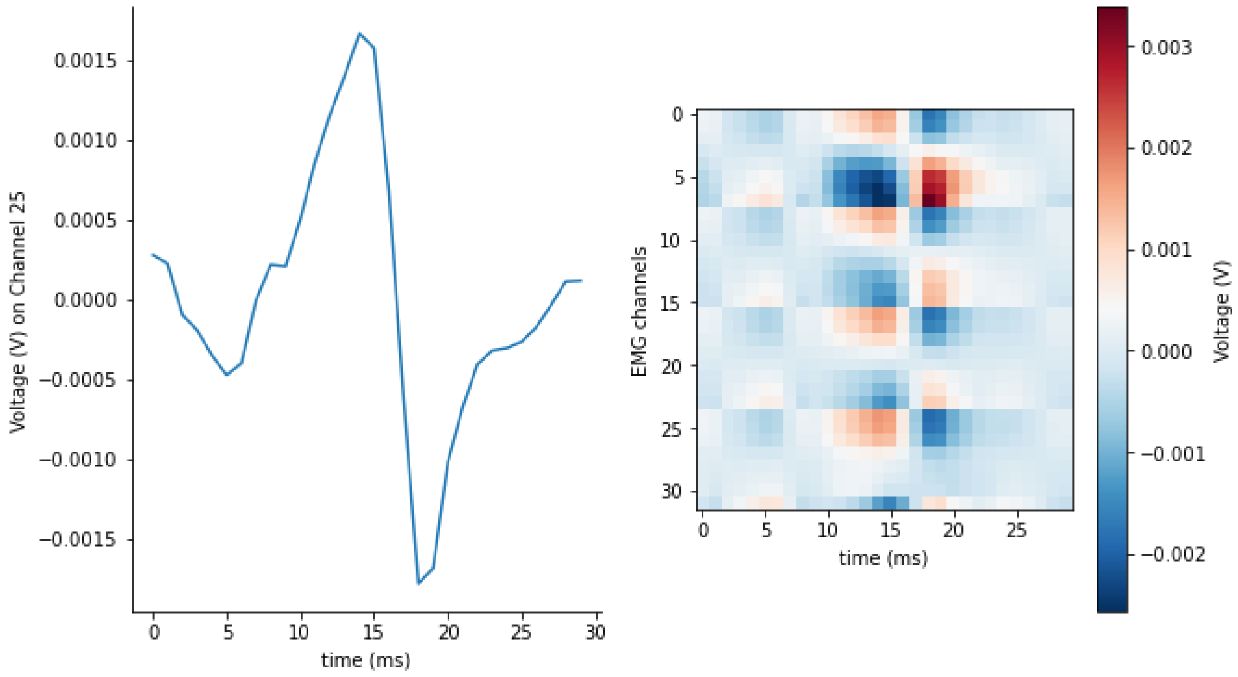
Subject results are reported individually.

Subject 1

Decomposition of the EMG data is shown in Figure 1. Only one clean motor unit was extracted. Using the AlphaCSC package and after specifying parameters, data was pulled out of the FIF file and the model was fitted to the data. This identifies patterns that are learned. All electrodes are referenced to the average of all EMG electrodes so anytime anything happens, polarity changes. Displayed in Figure 1 are a spike waveform (on the left) from a single channel from the EMG and a 2-D grid of the spike kernel (on the right). This demonstrates the ability to extract a motor unit action potential with convolutional dictionary learning and from this method of collecting EMG data. With this spike extracted, it can be related to the EEG data in order to evaluate whether the motor unit and EEG activity are coetaneous and an ERP is time-locked to the unit.

Figure 1

Spike Waveform from Single Channel and Spike Kernel for Clean Motor Unit

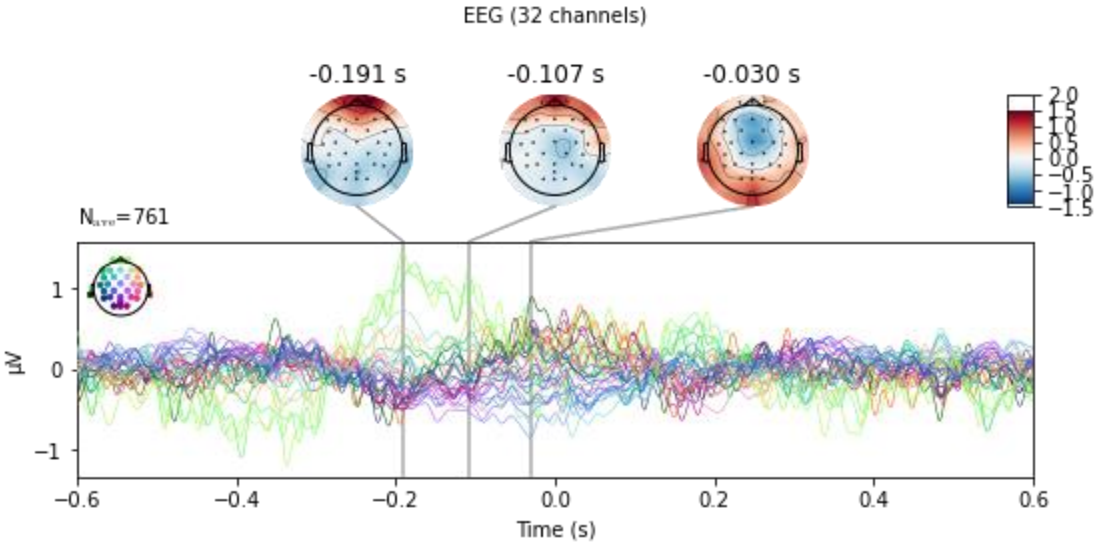


Note. On the left is an extracted spike waveform from just a single channel from the grid of the kernel on the right. The kernel shows the distribution of amplitude of the motor unit action potential waveform over the high-density surface EMG grid. The voltage (color) follows the pattern of a spike. The spike waveform happens in one place first and then moves across the array. The spike begins at 0.0 ms.

After loading the EEG data, bandpass filtering from 1 and 50 Hz, and thereafter resampling in the same frequency as above (to facilitate alignment with the EMG spike), 761 clean trials of EEG from 1,237 total spikes were obtained. Epochs (specific time windows extracted from the EEG) were made around the motor unit spike time and averaged. Averaging reduces the inclusion of voltage fluctuations not time-locked to the motor unit spike. It allows for the spike-related cortical activity to be evident. Figure 2 shows the resulting ERP. Results show the EEG ERP time-locked to the motor unit spike (the spike occurs at 0.0 seconds on the x-axis).

Figure 2

ERP Time-Locked to Motor Unit Spike



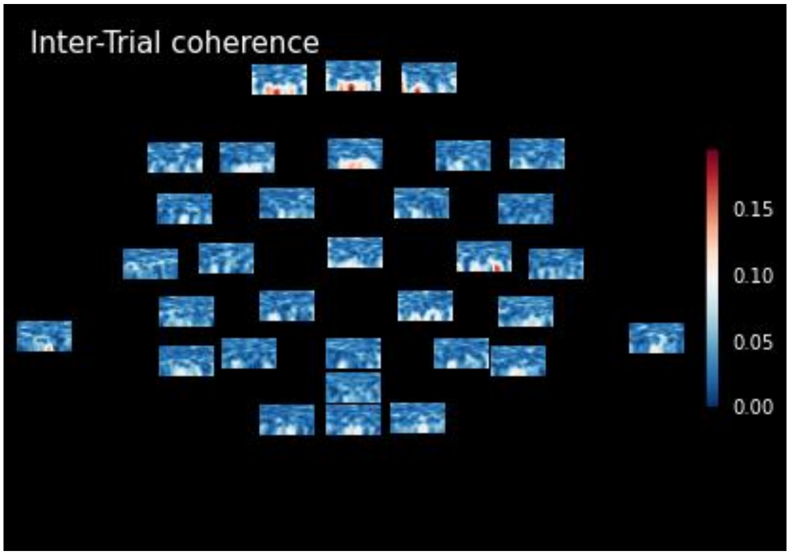
Note. Larger amplitudes show survival from the averaging operation, showing an ERP time-locked to the motor unit spike (the spike occurs at 0.0 s on the x-axis). It is within the range of being synchronous (no more than 0.15 ms off).

Figure 3 displays a topomap of inter-trial coherence. This coherence analysis (see Methods) shows a pattern of phase locking around the time of the spike from the motor unit at low frequencies. This can be seen by the red towards the center of the plots that contain red.

Figure 3 also shows inter-trial coherence in the frontal cortex, shown by the plots near the top of the topomap that contain red. Moreover, Subject 1 used her left hand, so it makes sense that there is inter-trial coherence in the right hemisphere as well.

Figure 3

Topomap for Inter-Trial Coherence

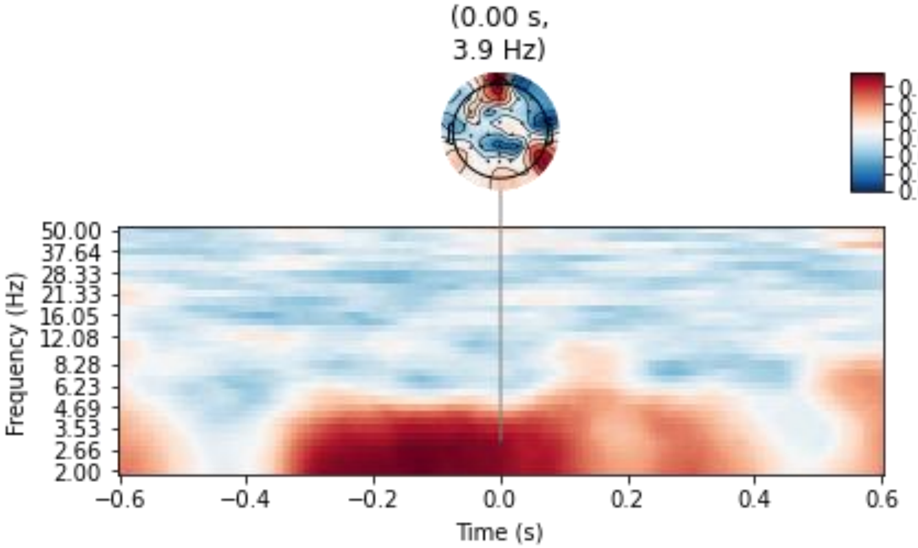


Note. The phase becomes predictable leading up to the motor unit firing, shown by the red towards the center of each plot that contains red. Each of the plots represents an electrode and the plots are arranged according to their location on the head. The x-axis of each is time (s), the y-axis is frequency (Hz), and the color is the inter-trial coherence for a given time-frequency.

Figure 4 represents the same information from Figure 3, but represented differently for clarity. The spikes from this motor unit appear to be occurring at a specific phase of low-frequency oscillations in the frontal cortex. Figure 4 displays the average of the individual EMG electrodes' coherence plots and a topomap for (0.0 s, 3.9 Hz). It shows coherence or phase clustering (shown by the color leading up to time of the motor unit spike).

Figure 4

Average Coherence Plot



Note. This shows that leading up to the time of the motor unit spike and at the time (0.0 s), there is coherence at low frequency oscillations.

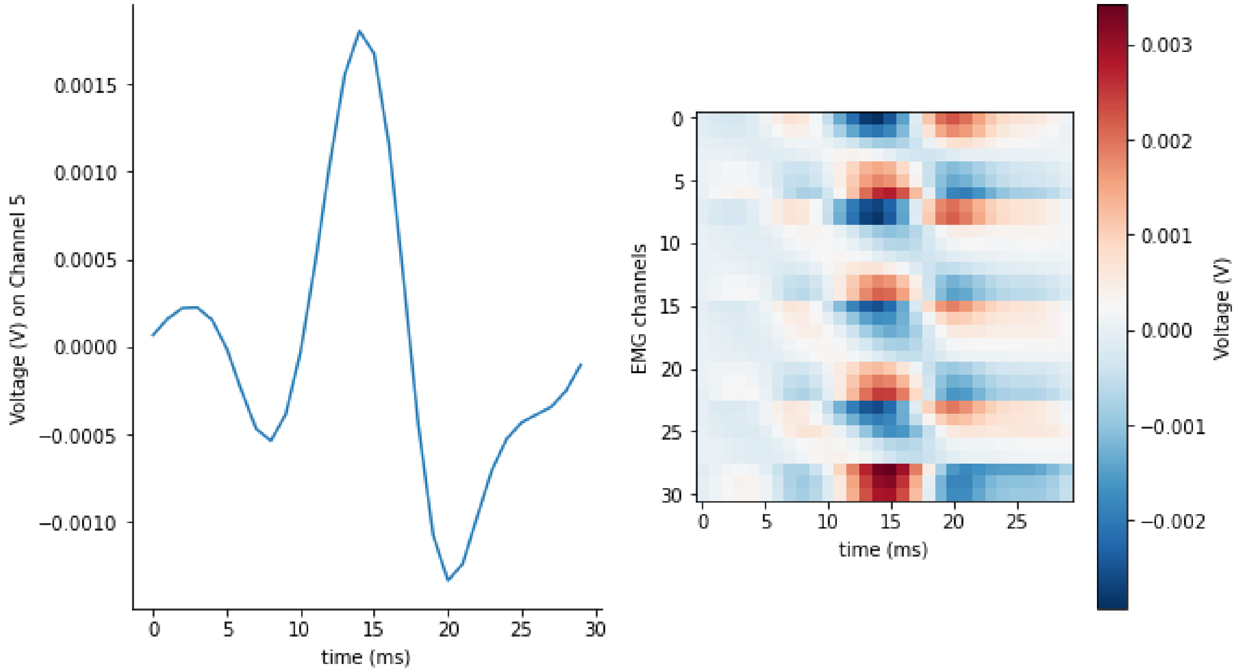
Inter-trial coherence analysis from Subject 1 provides further a direct measure of cortical and motor unit synchrony and the power of the ERP. Cross-validated analysis could not be performed for Subject 1 due to only being able to extract one clean motor unit.

Subject 2

Two clean motor units were extracted. Decomposition of the EMG data is shown in Figures 5 and 7. Displayed in Figure 5 are a spike waveform (on the left) from a single channel from the EMG and a 2-D grid of the spike kernel (on the right) for Motor Unit 1 in Subject 2. This shows that it was possible to extract a motor unit action potential from the high-density surface EMG using convolutional dictionary learning. This will be used to relate to cortical activity.

Figure 5

Spike Waveform from Single Channel and Spike Kernel for Clean Motor Unit 1

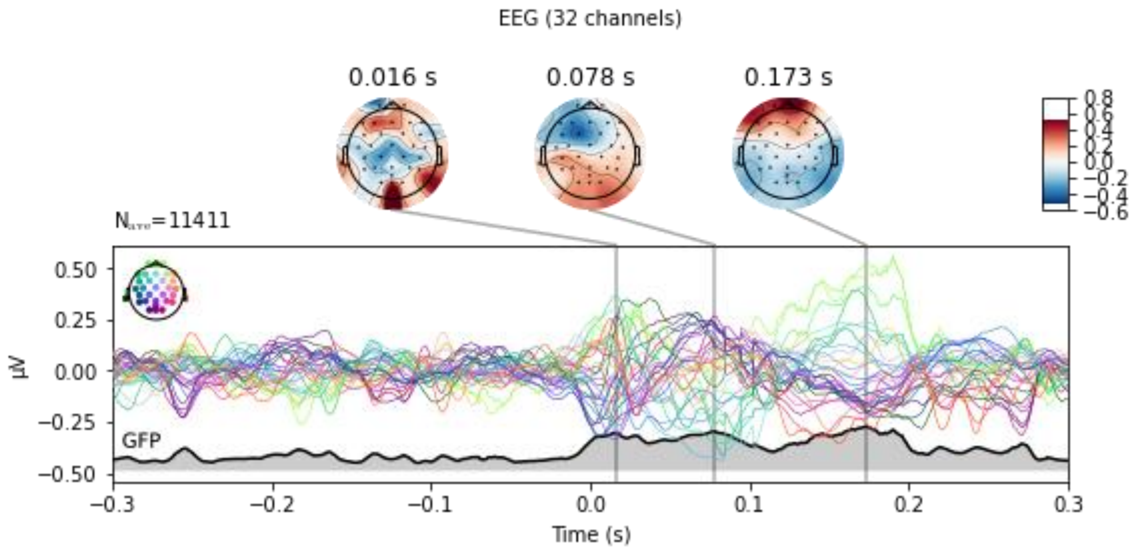


Note. On the left is an extracted spike waveform from just a single channel. The kernel shows the distribution of amplitude of the motor unit action potential waveform over the high-density surface EMG grid. The voltage (color) follows the pattern of a spike. The spike waveform happens in one place first and then moves across the array. The spike begins at 0.0 ms.

For Motor Unit 1 (Figure 5), 8,732 clean trials of EEG from 11,411 total spikes were obtained. Figure 6 shows the associated ERP. Results show the EEG ERP time-locked to the motor unit spike (the spike occurs at 0.0 seconds on the x-axis).

Figure 6

ERP Time-Locked to Motor Unit Spike 1

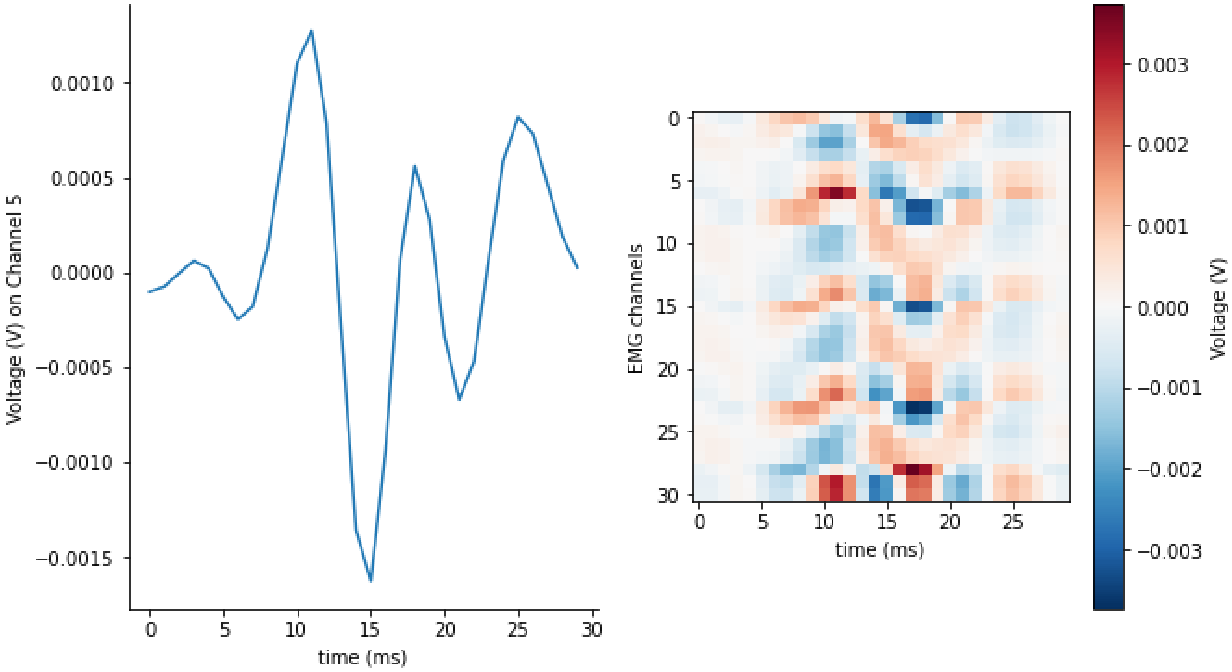


Note. Larger amplitudes show survival from the averaging operation, showing an ERP time-locked to the motor unit spike (the spike occurs at 0.0 s on the x-axis). It is within the range of being synchronous (no more than 15 ms off).

Subject 2 had two clean motor units that were able to be extracted. Figure 7 shows the decomposition of the second motor unit. Displayed in Figure 7 are a spike waveform (on the left) from a single channel from the EMG and a 2-D grid of the spike kernel (on the right) for Motor Unit 2 in Subject 2.

Figure 7

Spike Waveform from Single Channel and Spike Kernel for Clean Motor Unit 2

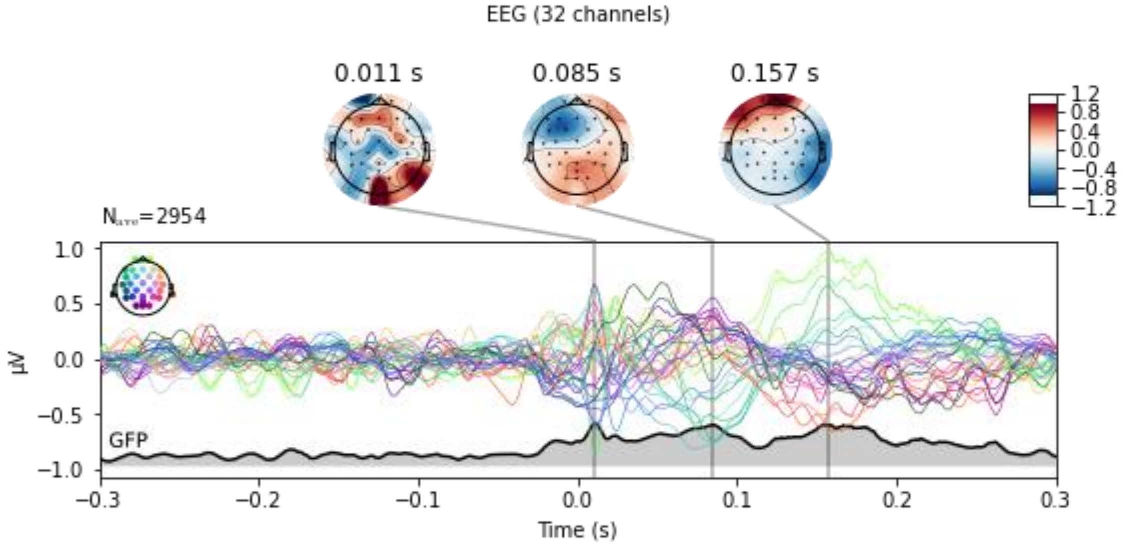


Note. On the left is an extracted spike waveform from just a single channel. The kernel shows the distribution of amplitude of the motor unit action potential waveform over the high-density surface EMG grid. The voltage (color) follows the pattern of a spike. The spike waveform happens in one place first and then moves across the array. The spike begins at 0.0 ms.

For Motor Unit 2 (Figure 7), 2,294 clean trials of EEG from 2,954 total spikes were obtained. Figure 8 shows the ERP. Results show the EEG ERP time-locked to the motor unit spike (the spike occurs at 0.0 seconds on the x-axis).

Figure 8

ERP Time-Locked to Motor Unit Spike 2



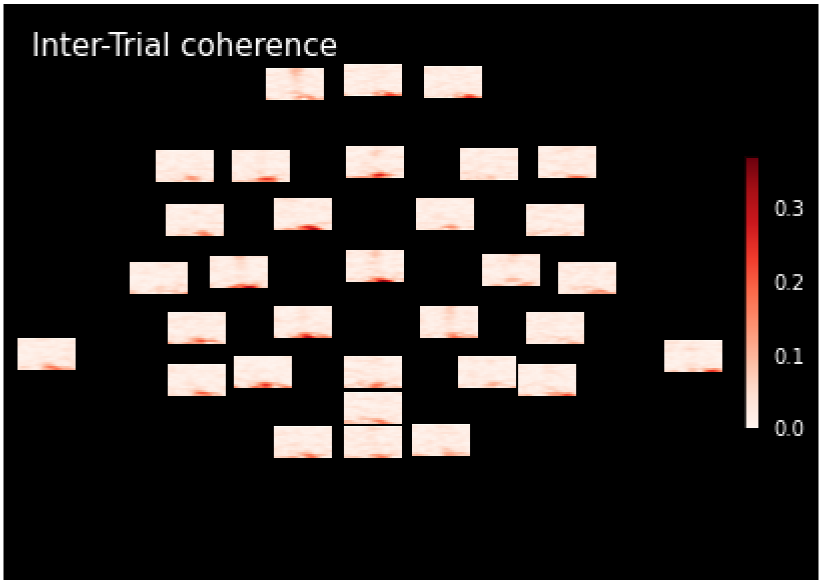
Note. Larger amplitudes show survival from the averaging operation, showing an ERP time-locked to the motor unit spike (the spike occurs at 0.0 s on the x-axis). It is within the range of being synchronous (no more than 15 ms off).

A difference between Subject 1 and Subject 2 is that Subject 2’s brain activity lags behind the motor unit action potential, whereas Subject 1's brain activity leads it.

Coherence analysis for Subject 2, like Subject 1, shows a pattern of phase locking around the time of the spike from the motor unit at low frequencies. Motor Unit 2 was used for analysis because it is the cleanest. Figure 9 shows inter-trial coherence in the frontal cortex. Moreover, Subject 2 used their right hand, so there is inter-trial coherence in the left hemisphere as well.

Figure 9

Topomap for Inter-Trial Coherence for Cleanest Motor Unit (Motor Unit 2)

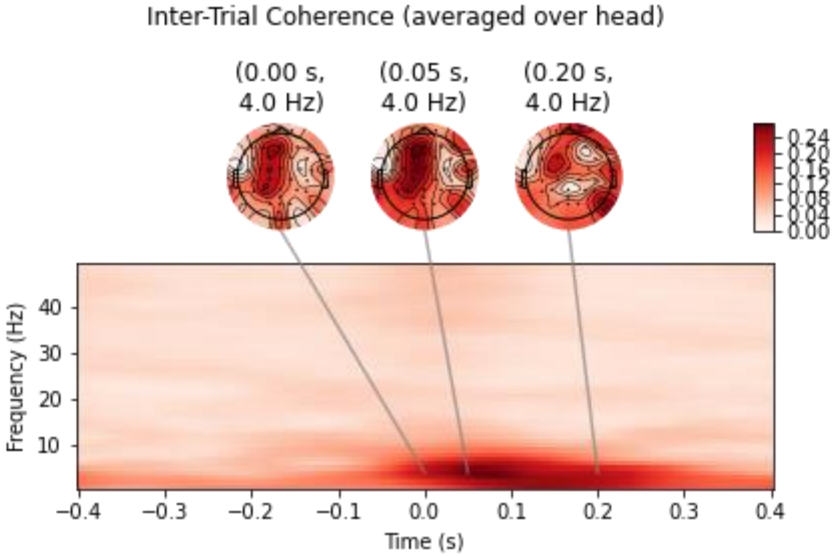


Note. Spikes from this motor unit are occuring at a specific phase of low-frequency oscillations with cortical activity lagging behind the motor unit firing, shown by the red towards the center of each plot that contains red. Each of the plots represents an electrode and the plots are arranged according to their location on the head. The x-axis of each is time (s), the y -axis is frequency (Hz), and the color is the inter-trial coherence for a given time-frequency.

Figure 10 represents the same information as Figure 9, but it is represented differently for clarity. It displays the average of the individual EMG electrodes' coherence plots and a topomap for (0.0 s, 4.0 Hz; 0.05 s, 4.0 Hz; 0.20 s, 4.0 Hz).

Figure 10

Average Coherence Plot



Note. This shows that at the time (0.0 s) of the motor unit spike and following, there is coherence at low frequency oscillations.

Inter-trial coherence analysis from Subject 2 provides further a direct measure of cortical and motor unit synchrony and the power of the ERP. Because two motor units were able to be extracted from Subject 2, cross-validation analysis (see Methods) was performed. This is meant to test the classification model's ability to predict new data (prediction accuracy) and how it will generalize to an out-of-sample dataset as well (out-of-sample accuracy). The dataset was equally (same number of spikes) divided into five parts and for each combination of motor unit and part, the ERP was computed. All the channel times of each ERP were collapsed into a feature vector for classification and min-max scaling was used for all features to normalize, to avoid bias before model fitting. A logistic regression classifier was fitted to the ERP data from four (out of five) parts of the ERP data to predict which ERP belongs to which motor unit in the fifth part of the data. This was completed for all four times, each time holding out a different part for predicting, and prediction accuracies were recorded. Min-max scaling and fitting a logistic regression classifier five times was repeated 1,000 times in order to compute a p-value to determine whether the observed accuracy is significantly above chance. The p-value is the percentage of permutations for which the score obtained is greater than the score obtained using the original data. This permutation test is meant to randomly permute the ERP to motor unit pairings to know how well the classification model performs. Results showed an observed (averaged across parts) out-of-sample accuracy of 70%, exceeding the classification accuracy obtained on 95.8% of random permutations, resulting in a p-value of 0.042. At the nominal significance level of alpha = 0.05, that means the null hypothesis that motor unit recruitment cannot be decoded from EEG activity can be rejected. In other words, it is possible to relate cortical activity and motor unit action potentials, as well as show that motor unit recruitment from EEG recordings can be predicted.

Discussion

There are generally two competing theories regarding how the cortex relates to motor unit recruitment. Prior research explains cortical involvement as cortex sending a single homogenous drive to the associated motor neuron pool in the spinal cord and that situationally, the spinal cord will work out which motor units will fire (De Luca & Erim, 1994; Somjen et al., 1965). However, recent work suggests a new theory of cortical involvement, maintaining that cortex has a more precise role in the particular motor units that are recruited (Laine et al., 2012; Marshall et al., 2021). It has a greater capacity to influence recruitment, suggesting individual motor units can be called independently from one another with separate command signals. Therefore, cortex does more than just send a common drive.

In order to support this new theory, there first needs to be a way to demonstrate a relationship between cortical activity and individual motor unit firing and isolate it. This study hypothesized that in humans, a granular response-related or pattern of cortical activity associated with the firing of a motor unit is present. Not only were high-density surface EMG data from both Subjects 1 and 2 decomposed into individual motor units, but also, ERPs time-locked to a specific motor unit were obtained for both subjects and inter-trial coherence was computed to further measure a direct relationship between cortical and motor unit activity. There was coherence at low frequency EEG oscillations around the time of the motor unit spike. Furthermore, the frequencies were similar between Subject 1 (3.9 Hz) and Subject 2 (4.0 Hz). Moreover, for Subject 2, cross-validation analysis showed 70% out-of-sample accuracy, resulting in a p-value that allows for rejection of the null hypothesis that motor unit recruitment cannot be decoded from EEG. This association suggests that cortical activity can be consistently associated with motor units and that there is a more precise relationship than just a readiness potential from movement onset. It also demonstrates that motor unit recruitment from EEG recordings can be predicted. The results from this study reject the common drive theory and contribute to the theory that motor cortex has a more specific ability to direct and organize.

These results supply a novel noninvasive methodology for studying neuromuscular control in humans that can relate more directly than non-human primate literature. Motor unit action potential related studies can be replicated and data can be more easily analyzed, allowing for new questions to be asked and further research to be done about neuromuscular control. Knowing this association between cortical activity and motor unit action potentials and the potential control that motor cortex has on motor unit recruitment is a step towards understanding how altering cortical activity can alter recruitment of motor units and motor unit flexibility and the potential trainability of motor unit recruitment strategies. This is key for rehabilitation after injury or motor skill acquisition. For example, presently, it is known that muscle strength increases after strength training. Neural changes at the motor unit level after training is unknown; however, being able to relate cortical activity with a single motor unit opens up the research. Rehabilitation intervention is only possible if the same motor unit can be identified before and after the intervention (Del Vecchio et al., 2020). Therefore, results from studies like the current study can provide insight into the degree of corticospinal plasticity. Further knowledge of this could allow for intervening in cortical activity because there is a way to know what to target. In the future, one can reinforce certain patterns of neural activity by giving people feedback about patterns of neural activity about which they otherwise would be unconscious and people could learn different strategies (Ely et al., 2022). There is potential to be able to manipulate cortical activity toward particular recruitment strategies. This leads to research regarding whether cortical activity that is motor specific to particular motor units is large enough to be able to be trained consciously.

Recommendations for future studies to investigate are as follows. First, it would be beneficial to obtain a larger motor unit yield, to be able to extract at least 10 motor units from one person’s recording for analysis. With at least 10, it would be possible to reconstruct the activity of the rest of the spinal neuron pool and be able to predict the selectivity of motor unit recruitment by cortex (Heidlauf & Röhrle, 2013). The present study is meant to be a springboard for this future research of improved methodology. However, a possible way in which to do this could be to record off a larger muscle. Second, future work can look into individual differences. It can examine the variability in muscles and anatomy across subjects to further investigate the reason for leading versus lagging of cortical activity to motor unit spikes. This can be accomplished by having more subjects. Third, further development of software and hardware can help in this line of research. For example, the TMSi Polybench software used in this study expects all electrodes to be placed in one area and not in two areas, especially on either side of the heart. Although re-referencing can be done later, it blurs to some extent the initial visual of the recordings. Moreover, results from this study showed activity in the frontal cortex; however, the current setup does not have good coverage of this region. Work with 64 electrodes should be done to further investigate this. Despite its limitations, overall, this study contributes to research in this area, supplying foundational knowledge that allows for further experimental testing and the development of additional software and hardware to better understand neuromuscular control as a whole.

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