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Changes in high-frequency neural inputs to muscles during movement cancellation

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Abstract

Objective. Cortical beta (13–30 Hz) and gamma (30–60 Hz) oscillations are prominent in the motor cortex and are known to be transmitted to the muscles despite their limited direct impact on force modulation. However, we currently lack fundamental knowledge about the saliency of these oscillations at spinal level. Here, we developed an experimental approach to examine the modulations in high-frequency inputs to motoneurons under different motor states while maintaining a stable force, thus constraining behaviour. *Approach.* Specifically, we acquired brain and muscle activity during a 'GO'/'NO-GO' task. In this experiment, the effector muscle for the task (tibialis anterior) was kept tonically active during the trials, while participants ($N = 12$) reacted to sequences of auditory stimuli by either keeping the contraction unaltered ('NO-GO' trials), or by quickly performing a ballistic contraction ('GO' trials). Motor unit (MU) firing activity was extracted from high-density surface and intramuscular electromyographic signals, and the changes in its spectral contents in the 'NO-GO' trials were analysed. *Main results.* We observed an increase in beta and low-gamma (30–45 Hz) activity after the 'NO-GO' cue in the MU population activity. These results were in line with the brain activity changes measured with electroencephalography. These increases in power occur without relevant alterations in force, as behaviour was restricted to a stable force contraction. *Significance.* We show that modulations in motor cortical beta and gamma rhythms are also present in muscles when subjects cancel a prepared ballistic action while holding a stable contraction in a 'GO'/'NO-GO' task. This occurs while force levels produced by the task effector muscle remain largely unaltered. Our results suggest that muscle recordings are informative also about motor states that are not force-control signals. This opens up new potential use cases of peripheral neural interfaces.

1. Introduction

Oscillatory synchronisation is a mechanism through which the activity of a population of neurons can be modulated. In the context of motor control and corticospinal interactions, this mechanism has been previously reported in different contexts involving muscle contraction, where significant levels of corticomuscular coherence have been reported in different frequency bands (Conway *et al* 1995, Schoffelen *et al* 2005, 2011, Baker 2007, Raethjen *et al* 2007). At present, it remains unclear how the corticomuscular transmission of high-frequency cortical oscillations (*i.e.* activity above 10 Hz, which has a negligible impact on force modulation) is involved in the neural control of movement (Baker 2007, Zicher *et al* 2023).

The most common way to study the corticospinal transmission of cortical rhythms in humans involves brain and muscle recordings during periods of sustained contractions to characterise

the corticomuscular coherence spectrum (Conway *et al* 1995, Kilner *et al* 2000, Baker 2007). This has provided consistent evidence of beta transmission between the brain and muscles. Interestingly, recent studies have shown that corticospinal beta transmission can be reliably characterised using motoneuron activity decomposed from muscle recordings (Ibáñez *et al* 2021). Extending the observations from sustained contractions, previous studies have also provided preliminary evidence about the transmission of neural oscillations in the gamma band (30–70 Hz) during states requiring participants to react in a pre-determined way (Schoffelen *et al* 2011).

However, while previous studies provide relevant information regarding the reliable transmission of certain neural oscillations between the brain and the muscles, we still have limited knowledge regarding the strength of the modulations of the signals transmitted along these connections, and we only have preliminary evidence about the possibility of using peripheral recordings of muscle signals to estimate cortical changes (Bräcklein *et al* 2022). To address this gap, here we characterised the changes of neural inputs in the 10–45 Hz band at the brain and muscle level, in a context of movement preparation and cancellation. Indeed, this framework is known to be associated with salient changes in cortical activity that relate to successful cancellation of impending actions (Alegre *et al* 2004, Wessel 2020). Specifically, we designed a 'GO'/'NO-GO' paradigm in which the effector muscle (the tibialis anterior (TA) muscle) was tonically active throughout the trials. Electroencephalographic (EEG) activity over the motor cortex and high-density electromyography (EMG) from the TA muscle were concurrently recorded. The latter was decomposed into the spiking activity of motoneurons innervating the studied muscle (Negro *et al* 2016). This information was used to analyse the spectral changes in the activity of pools of motoneurons and in the cortical activity during sustained contractions while participants were preparing a ballistic action and subsequently aborting it ('NO-GO' trials). We refer to this window after the 'NO-GO' cue as *cancellation* period.

2. Materials and methods

2.1. Experimental data acquisition

A total of 14 participants (all males, ages: 21–38 years) took part in this experiment and gave their written informed consent. Data from two participants were discarded from the analysis due to the presence of artifacts in the force signals. The study was conducted in accordance with the Declaration of Helsinki and was approved by the Imperial College Ethics committee (18IC4685).

An estimation of minimum sample size for this study could be estimated from results reported by Bräcklein *et al* (2022), which looked at conscious modulation of beta bursts from motor unit activity while force was held constant. They reported the partial η^2 to assess the effect size of the changes between beta burst modulations. The effect sizes for power, amplitude, duration and rate of bursting events at MU level ranged between 0.36 and 0.58. This would suggest an effect size parameter f larger than 0.7 (Cohen 1988).

A power analysis for repeated measures ANOVA with effect size $f = 0.5$, power of 0.9 and $\alpha = 0.05$ gives a total sample size of 11. An effect size of 0.7 would require a sample size of 6.

This power analysis was done using G*Power software (Faul *et al* 2007).

2.1.1. Recordings

Experimental signals were non-invasively recorded from the brain using EEG and from the right TA muscle using high-density surface EMG while participants performed isometric ankle dorsiflexions (figure 1(A)). In two participants, multi-channel intramuscular EMG signals were also acquired.

EEG signals were recorded using 31 active gel-based electrodes positioned according to the International 10–20 system with FCz used as reference (actiCAP, Brain Products GmbH), amplified and sampled at 1 kHz (BrainVision actiCHamp Plus, Brain Products GmbH). The signals were resampled at 2048 Hz offline.

Surface EMG was recorded using 64 channel grids (13x5 arrangement with one missing electrode in a corner) with an interelectrode distance of 4 mm or 8 mm (OT Bioelettronica). The signals were amplified (150 V/V), sampled at 2048 Hz (Quattrocento, OT Bioelettronica) and bandpass filtered (20–500 Hz). Various grid configurations were used to maximise the number of units decomposed from the EMG signals. Since the analysis was done on the CST and not EMG, the grid arrangement does not bias the results, as it only provides a cleaned version of the neural drive to the muscles (Bräcklein *et al* 2021 estimated beta from periphery with an average of 11.9 ± 2.3 MNs). In three participants, one large grid with 8 mm interelectrode distance was placed on the muscle. In seven participants, four smaller (4 mm interelectrode distance) surface grids were used to cover the same surface of the TA muscle (Caillet *et al* 2023). In two other participants, two small surface grids and respectively three and four intramuscular electrode arrays were used. These intramuscular arrays had 40 electrodes, with 20 electrodes located on each side of a flat thin-film and separated by an interelectrode distance of 500 μm (Muceli *et al* 2022). In the experiments involving intramuscular recordings, all EMG signals were sampled at 10 240 Hz, and intramuscular signals were bandpass filtered between 100 and 4400 Hz.

During the experiment, participants sat in a comfortable chair with their knee flexed at 75°, their

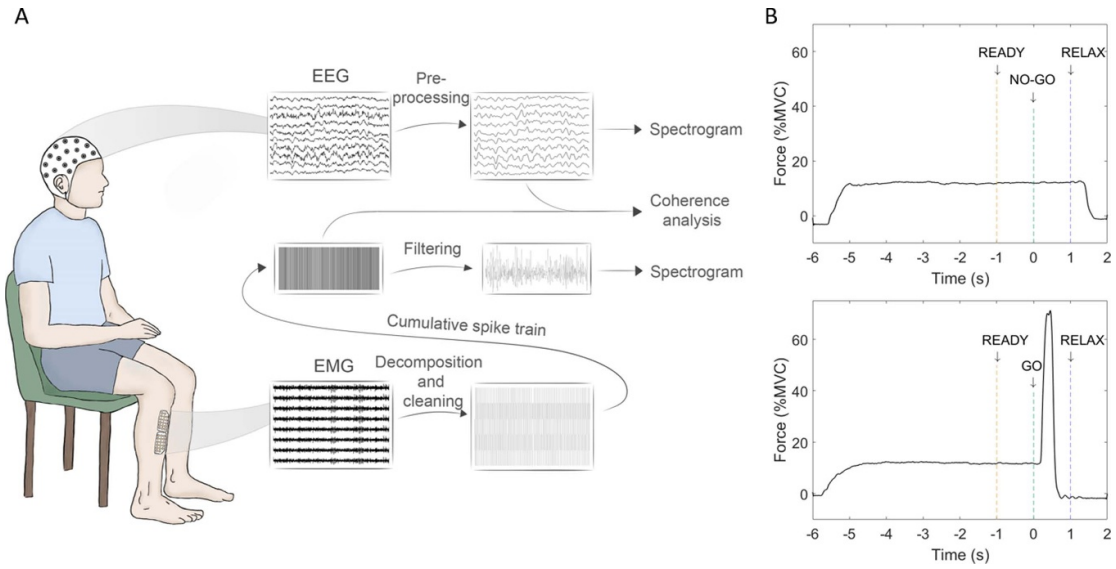

Figure 1. Schematic representation of the experimental protocol. (A), EEG, EMG and force (not shown) signals were concurrently recorded while participants were seated in a chair and were producing ankle dorsiflexions. EEG recordings were re-sampled and filtered offline (see methods). EMG signals were decomposed into MU trains of action potentials, which were then summed to get the cumulative spike train (CST). Spectral and coherence analyses were performed on EEG and CST. B, Example force traces from experimental tasks with 'NO-GO' (top figure) and 'GO' (bottom figure) trials. During each trial, the participants performed an isometric dorsiflexion at 10% maximum voluntary contraction (MVC) before reacting to an imperative stimulus. During 'GO' trials, participants performed a ballistic contraction, while during 'NO-GO' trials, they held the isometric contraction at 10% MVC until the last cue.

right leg securely fixed to an ankle dynamometer with Velcro straps, and their foot positioned onto a pedal at 30° in the plantarflexion direction, 0° being the foot perpendicular to the shank. A force transducer (TF-022, CCT Transducer s.a.s) fixed to the pedal recorded the force. During all tasks, participants received visual feedback with a target representing the level of force to reach and a trace representing the force they produced.

EEG, EMG and force signals were synchronised using a common digital trigger signal sent to the two systems.

2.1.2. Task

The task was based on a movement preparation and cancellation framework that allowed us to explore changes in spinal motoneuron population activity during these brain states.

At the beginning of the experiment, participants were asked to produce an ankle dorsiflexion contraction with maximal force to estimate their maximum voluntary contraction (MVC) force level. This was repeated twice and the larger MVC value was used during the experiments. Then, the experiment was divided into three identical blocks with periods of rest in-between. Each block consisted of 35 trials, with one trial having a 50% chance of being a 'GO' or a 'NO-GO' trial. In both cases, throughout the trial, participants received four auditory cues of various lengths and frequencies. Note that participants were familiarised with the task before the recordings started and practiced responding to the cues until they were confident in their understanding of the task. For each trial, a first cue indicated to the participants that they had to produce a 10% MVC force. Then, after at least 4 s, a second cue (warning stimulus) was given, and this was followed by a third cue (imperative stimulus) 1 s later, which informed the participants about the trial type ('GO' or 'NO-GO'). A fourth cue, 1 s after the imperative stimulus, indicated the end of trial. At this point, participants had to relax and wait for the following trial (figure 1(B)). During 'GO' trials, participants produced a ballistic contraction above 10% MVC as soon as possible after the imperative stimulus. During 'NO-GO' trials, participants kept the level of force at 10% MVC until the end of the trial indicated by the fourth cue. The timing of the cues was fixed during all trials to ensure that the evolution of the neural states decoded from motoneurons were temporally aligned across trials, thus allowing the averaging of the results. Participants only received visual feedback on the force produced until the third cue. Additional visual feedback on reaction time was presented to the participants after the 'GO' cues to ensure fast and consistent reaction times through each block. Trials were separated by a period of rest of 7 s on average with a variation of ±20%. One block of 35 trials lasted about 8 min.

2.2. Data analysis

Spectral and coherence analyses were performed on signals recorded during 'NO-GO' trials, to be able to study the cancellation of a prepared movement. Force, EEG and EMG signals were cut relative to the

imperative cue before analysis. In addition, reaction time and coefficient of variation (CoV) of force were analysed from 'GO' trials to check that the tasks were done correctly.

2.2.1. Force analysis

The force data was low-pass filtered with a cut-off frequency of 15 Hz using MATLAB *lowpass* function (minimum-order filter with a stopband attenuation of 60 dB), baseline corrected, and normalised relative to the MVC. The reaction time was calculated during 'GO' trials as the duration of the interval between the imperative cue and the time point where the force signal exceeded 2 standard deviations of the steady mean force value preceding the 'GO' cue. The CoV of force was measured over a 3-s steady contraction interval preceding the imperative cue. Only trials in which the force remained between 7% and 13% MVC were kept for further analysis.

To check the performance of the participants, the percentage of valid trials was quantified. A 'GO' trial was considered valid if the onset of a ballistic movement was within ± 2 standard deviations of the participant's mean reaction time. 'NO-GO' trials were considered valid if the force did not exceed 15% MVC throughout the trial. Thus, we considered valid the trials in which subjects reacted correctly to the imperative cue. In addition, to discard from further analysis the trials in which participants did not perform the overall task optimally, specific criteria were defined. Overall, there were thresholds set for two main cases of errors in 'NO-GO' trial: one related to transient large changes in force (for example reacted to wrong cue), the other to overall variability in force. Overall, trials were discarded if during the steady contraction part, force went 2% MVC below or above the average calculated across all trials, or if the force standard deviation was above 0.5% MVC.

2.2.2. EMG decomposition

The EMG signals recorded from the different trials were concatenated and decomposed into constituent trains of action potentials using previously validated blind-source separation methods (Holobar *et al* 2014, Negro *et al* 2016). The signals recorded by each grid were decomposed separately, and the discharge series of motor units identified in more than one grid were removed. Duplicates were defined as units with more than 30% common discharge times. When two units were considered to relate to a same source, the unit with lowest CoV of interspike-interval was kept (Holobar *et al* 2010). The MU discharge times automatically detected by the algorithm were visually inspected and edited when necessary. Manual editing was done to units to improve their decoding accuracy to close to 30 dB. The manual editing consisted of the removal of artifacts falsely identified as discharge times and the addition of discharge times missed by the automatic steps, followed by automatic verification of the validity of the edits (Hug *et al* 2021).

2.2.3. Time-frequency analysis

Only the signals from the good'NO-GO' trials were included in the analysis (see the section 'Force analysis'). Furthermore, MU spike trains from trials in which the COV of discharge rate was above 30% were also excluded (Negro *et al* 2009).

EEG signals were first visually inspected, and trials in which movement artifacts were observed were excluded from the analysis (on average 10.58 ± 6.59), besides the ones that were not adequate according to the behavioural or MU discharge rate criteria (see above). The Laplacian derivation from channel 'Cz' was computed by subtracting the average electric potential recorded from the four closest equidistant channels, i.e., FC1, FC2, CP1, CP2 in our set-up. The surrogate 'Cz' channel was used to estimate the directional coherence (see the section 'Coherence analysis'). The resulting channel data was bandpass filtered before the analysis with a 3rd order Butterworth filter according to the bandwidth under investigation.

For both signals (MU activity and EEG), the spectrograms were calculated with the segment length set to 0.25 s and a shift between adjacent segments of 10 samples. The results were averaged across trials before calculating the mean in each bandwidth (alpha: 8–12 Hz; beta: 13–30 Hz; gamma: 30–45 Hz). These values were then standardised in the window -3 s to 1 s relative to the 'NO-GO' cue. The average values for windows -2 s to -1 s, -1 s to 0 s and 0 s to 1 s were also calculated for each participant. To get the grand average results, first, for each participant separately, at each frequency sample, the average value was calculated in the window -3 s to -2 s. The value obtained was used as a reference of the level of activity at each frequency examined. At each following time point, changes relative to the reference were calculated and the values were standardised. The mean of these results was then calculated to get the grand average.

2.2.4. Coherence analysis

The transmission of high frequency oscillations between the brain and muscles was studied by calculating the directional coherence between the 'Cz' channel and the CST. The EEG signal was processed as for the time-frequency analysis, but a 1–45 Hz bandpass filter was used here. The same trials were removed from the EEG and CST and then the signals were detrended. The coherence was calculated over 1 s windows (-2 s to -1 s; -1 s to 0 s; 0 s to 1 s relative to the imperative 'NO-GO' cue) using the Neurospec 2.11 toolbox coded for Matlab (www.neurospec.org; Mathwoks Inc., USA). This toolbox

uses the multitaper method (3 tapers) for the spectral estimation and allows for the estimation of directional coherence. The toolbox also calculates the 95% confidence limit for the coherence estimate that was used here to evaluate significance.

2.2.5. Statistics

The statistical analysis was performed with SPSS (IBM). Three main windows were compared: −2 s to −1 s (referred to as *baseline*), −1 s to 0 s (*preparation*) and 0 s to 1 s (*cancellation*) relative to the imperative 'NO-GO' cue. To test for significant changes in power in these time windows, repeated measures ANOVA was performed for each recording type and frequency band, with time as the within-participant factor. The same test was used to check for changes in average discharge rate. The sphericity was checked with the Mauchly's test. Bonferroni correction was used to adjust for multiple comparisons. Results are reported as mean ± standard deviation, unless otherwise stated.

3. Results

3.1. Behavioural results

To confirm that participants were able to perform the task correctly, the percentage of valid trials was calculated (see Methods for criteria) (figure 2(A)). On average, 96.0% ± 1.5% and 95.1% ± 3.4% of 'GO' and 'NO-GO' trials were considered valid, meaning the participants reacted correctly to the imperative cue either reacting fast or keeping the force steady. After applying the task-specific criteria ensuring that stable contractions were held throughout the trials, 80.4% ± 11.4% of all 'NO-GO' trials were kept. Participants had average reaction times of 275.7% ± 43.1 ms in the 'GO' trials. The CoV of force was 2.42% ± 0.5% during the 3 s steady period before the imperative cues.

3.2. Decomposition results

On average, 28 (range 12–45) MUs per participant were identified from EMG signals. Out of these, an average of 26 (range 10–40) MUs fired steadily (without being de-recruited and recruited) during the contraction and were considered for further analysis. The average discharge rate of these MUs was 10.8 ± 1.1 spikes/s and the CoV of the interspike intervals was 14.5% ± 1.6%.

3.3. Changes in brain and muscle activity

We studied changes in power in alpha, beta and gamma bands in the MU firing activity, and in the EEG during the 'NO-GO' trials. The grand average from all participants showed changes in all bandwidths, while force stayed largely stable (figure 2(B)). A small drop in power was observed in the *preparation* period (−1 s–0 s), followed by a large broad-band increase post 'NO-GO' cue. To explore which changes were statistically significant, repeated measures ANOVA were performed on this data.

Overall, at the MU level, we found an effect of time on the power in the alpha ($F = 4.027$; $p = 0.032$; $\eta^2 = 0.268$), beta ($F = 35.711$; $p < 0.001$; $\eta^2 = 0.765$) and gamma bands ($F = 12.711$; $p = 0.001$; $\eta^2 = 0.536$). At the brain level, there was a significant effect of time on the power in the beta ($F = 19.844$; $p < 0.001$, $\eta^2 = 0.643$) and gamma bands ($F = 10.127$; $p < 0.001$; $\eta^2 = 0.479$), but not in the alpha band ($F = 1.473$; $p = 0.251$; $\eta^2 = 0.118$). There was no significant effect of time on the average discharge rate of the identified MUs ($F = 0.456$; $p = 0.563$; $\eta^2 = 0.040$).

In the *preparation* period we did not observe any significant changes relative to *baseline* in high frequency oscillatory activity in brain (beta: $p = 0.143$; gamma: $p = 0.344$) or muscle recordings (beta: $p = 0.093$; gamma: $p = 0.174$) (figures 3 and 4).

In the *cancellation* period, we observed a brief drop in the discharge rate in seven out of the twelve participants, but this did not significantly affect the average discharge rate in the studied windows. As mentioned before, we found an effect of time on the power in the alpha band (8–12 Hz) in the MU firing activity, which was not observed in the EEG activity. However, this change in the power within 8–12 Hz between *cancellation preparation* states was not significant in the pairwise comparison ($p = 0.052$).

We also found a difference in average beta levels in the MU firing activity, with the *cancellation* interval showing a significant increase in beta power relative to *baseline* ($p = 0.002$) and *preparation* ($p < 0.001$) (figure 3(B)). The timing of these rebounds was approximately aligned across participants (figure 3(A)). To explore whether these changes had a cortical origin, the same analysis was performed on the EEG recordings (figure 3(C)). EEG data showed similar patterns to what we saw in the MU firing activity, with an increase in beta levels after the 'NO-GO' cue. Beta power was significantly higher during *cancellation* (0 s to 1 s) than during *baseline* (−2 s to −1 s) ($p = 0.024$) and *preparation* (−1 s to 0 s) ($p < 0.001$) in all participants (figure 3(C)). The peak amplitude of the forward coherence (EEG-> MU) was also measured in the different windows considered. Seven out of twelve participants had significant coherence in beta during *baseline* (0.14 ± 0.12), four participants during *preparation* (0.15 ± 0.12) and eight participants in the *cancellation* window (0.17 ± 0.12). Five participants had non-significant coherence during preparation, that became significant post 'NO-GO'. Furthermore, Pearson correlation coefficient between average EEG

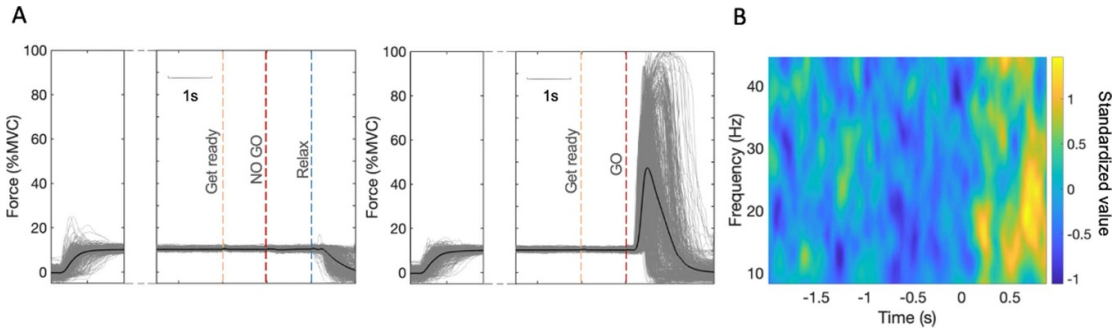

Figure 2. Average changes in MU activity observed while the force output was kept constant. (A), Force traces for correctly performed 'NO-GO' and 'GO' trials. Individual trials from all participants were plotted in grey and the average in black. The auditory cue timings are shown as vertical lines. (B), Standardised time-frequency changes during the 'NO-GO' trials averaged from all participants. Spectrogram shows average changes in bandwidth 8–45 Hz compared to the window −3 s to −2 s. Values were standardised per subject in the window shown here (−2 s–1 s) and then averaged.

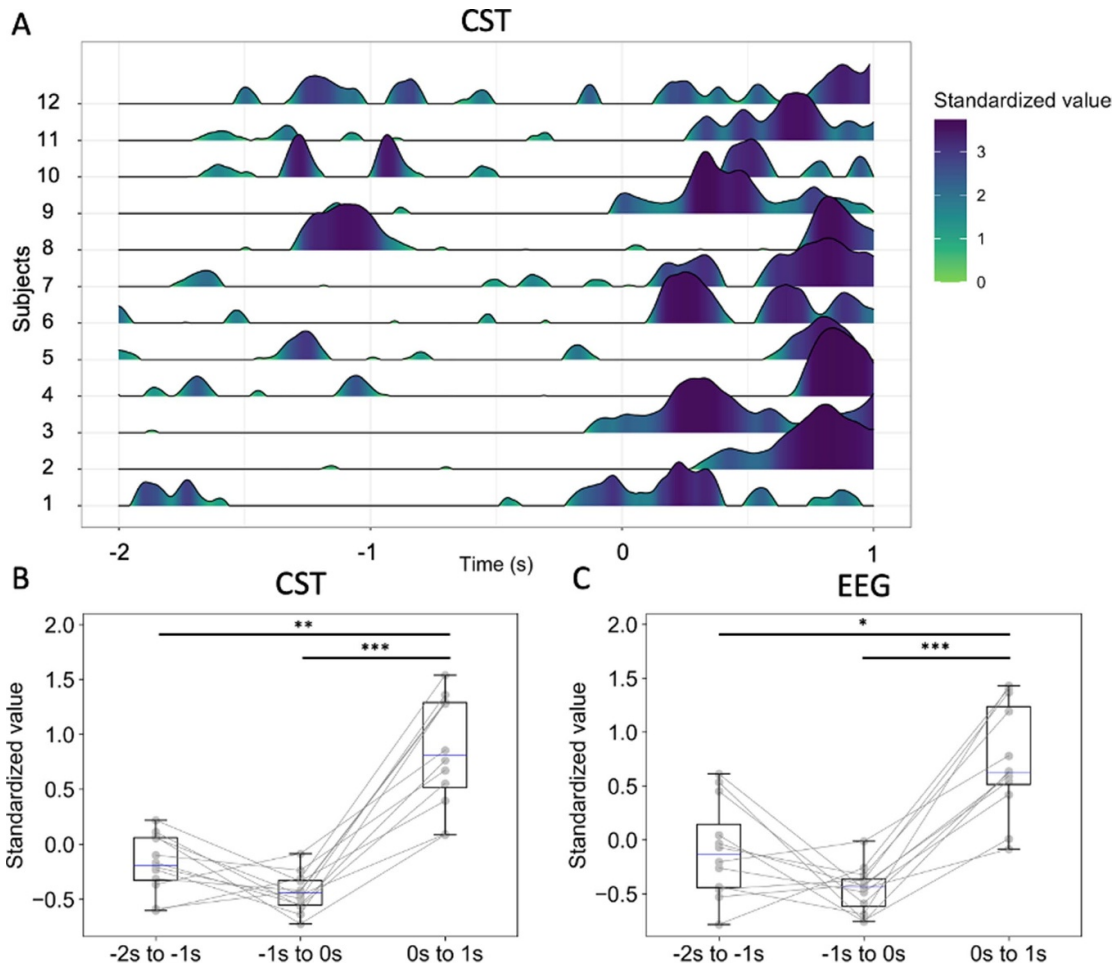

Figure 3. Changes in beta (13–30 Hz) levels at MU and brain levels. (A), Evolution of beta power in 'NO-GO' trials at muscle level. Each row represents data from one participant. Values were standardised in the window −2 s–1 s. Only positive values are plotted for clarity. (B), Changes in beta band MU activity in three windows relative to the 'NO-GO' cue shown as boxplot. Each point and line represent one participant. There is a significant increase in the last window compared to the first two, tested with repeated measures ANOVA. (C), Changes in beta observed in EEG recordings at subject level. Beta levels are significantly increased post 'NO-GO' cue, compared to the first two. $^{*}p < 0.5$; $^{**}p < 0.01$; $^{***}p < 0.001$.

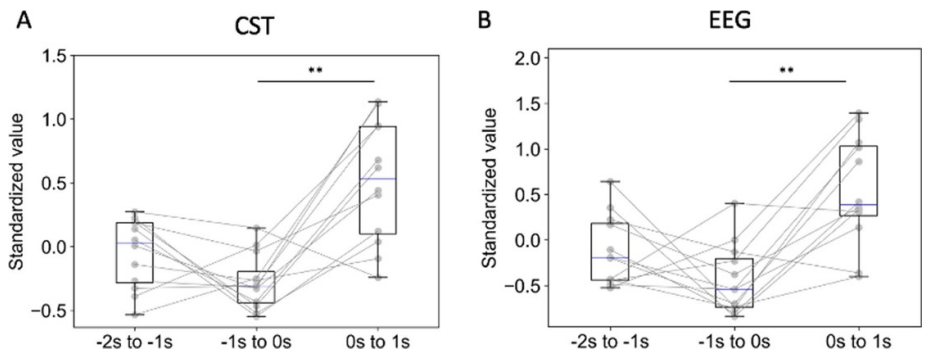

Figure 4. Changes in gamma (30–45 Hz) levels at MU and brain levels. (A), Average gamma level in MU activity in the three windows. Each point and line represent data from one participant. There is a significant increase in the preparation cancellation period compared to the previous window. (B), Gamma levels observed in EEG recordings. There is a significant increase in the last window. Repeated measures ANOVA was used for statistical tests. $^{**}p < 0.01$.

and CST beta changes post NO-GO in the subjects with significant coherence was 0.74 ($p = 0.03$).

Similar changes to the ones observed in the beta band were found in the low gamma band (30–45 Hz) activity (figure 4). There was a significant increase after the 'NO-GO' cue compared to *preparation* in MU activity ($p = 0.001$), with the change not being significant compared to *baseline* ($p = 0.058$) (figure 4(A)). In the EEG, the power in gamma was significantly increased in the last window compared to *preparation* ($p = 0.001$). As with the MU activity, there was a non-significant increase in gamma after the 'NO-GO' relative to *baseline* ($p = 0.100$) (figure 4(B)). Five out of twelve participants had significant forward coherence in the low gamma band during *baseline* (0.06 ± 0.03), six participants during *preparation* (0.05 ± 0.01) and six participants in the *cancellation* window (0.07 ± 0.01).

Overall, we found a significant increase in beta and low gamma at both muscle and brain level, while the change in the power in low frequencies (<12 Hz) was only present in the CST activity.

4. Discussion

We studied the activity of populations of MUs during states of movement preparation and cancellation. We showed prominent changes in high-frequency MU activity during the cancellation of a prepared ballistic movement. The observed changes were in part related to changes measured from the brain. Therefore, this study provides evidence for the possibility of extracting cortical information from the muscle signals when forces are unchanged. It also provides new information about the saliency of the modulations of high-frequency neural inputs that muscles receive.

Changes in cortical activity during movement preparation and cancellation have been studied in previous similar work (Schoffelen *et al* 2005, 2011, Wessel 2020). Here we focused on the transmission of this activity to muscles. We studied the MU population activity, which provides a robust characterisation of the spectral characteristics of the neural signals reaching the muscles (Muceli *et al* 2022). We observed a significant increase in beta power during the *cancellation* period (the window of time after a 'NO-GO' cue was given), which matched changes recorded at the brain level. Human studies looking at changes in the beta oscillatory activity using EEG recordings have previously reported increases in this frequency band after movement cancellation (Alegre *et al* 2004, Solis-Escalante *et al* 2012, Wessel 2020). In a stop-signal task, where participants had to rapidly cancel a movement they were previously prompted to do, beta bursting increased after successful cancellation (Wessel 2020). Also, in a similar 'GO'/'NO-GO' paradigm as the one used here, Alegre *et al* (2004) reported beta synchronisation in the fronto-central brain areas post 'NO-GO'. Our results are in line with these previous findings, even though there is one crucial difference between the tasks of most previous works and ours. In previous studies, participants were relaxed while preparing for movement, while here, participants were required to hold a stable contraction. Another study used a similar paradigm where local field potentials were recorded from monkeys while they were doing a lever depression task in a 'GO'/'NO-GO' paradigm (Zhang *et al* 2008). The monkeys had to initiate a lever depression and react to visual patterns by either releasing the lever ('GO') or maintaining the motor output. In line with our results, in the 'NO-GO' trials, the authors reported a marked beta rebound after a desynchronisation that appeared in all types of trials.

Overall, previous results clearly indicate that movement cancellation is characterised by a strong increase in beta power cortically, independent of the initial state (rest or stable contraction). Critically, here we show that this change in beta activity is also present at the spinal motoneuron level. The coherence in eight out of the twelve participants during the *cancellation* period is reflective of the cortical origin of the

beta activity in the muscle. Although we did not have significant brain–muscle coherence in the remaining four subjects, it is likely that corticomuscular transmission is still taking place. Even during long, stable contractions coherence varies greatly across subjects and is not always significant (Hashimoto *et al* 2010, Witham *et al* 2011). Furthermore, note that in biological signals, directional coherence will always yield smaller values than the overall coherence measure (Halliday 2015).

Similar changes to those found in the beta band, were observed in the low-gamma band (30–45 Hz) during the *cancellation* period. The level of the brain–muscle coherence was significant in half of the participants during this window. Previous work reported an increase in coherence over the gamma band during movement preparation (Schoffelen *et al* 2011), which was not observed here. However, one key difference between the paradigms used in studies that reported gamma activity in preparatory periods and our current work is the level of unpredictability of when the cue was presented (Schoffelen *et al* 2005, 2011). We used a fixed interval between the warning and imperative cues, while in previous studies, participants had to respond to cues with variable timings.

To explain how different types of inputs can explain the observed changes in MU, we ran a set of simulations testing simple conditions. By modelling the response of a pool of motoneurons ($N = 30$) to changes in the common inputs they receive, it is possible to study the motoneuron firing patterns. We can consider two scenarios relevant for the experimental results reported above: i) an instantaneous change in common input that transiently synchronizes units, or ii) an increase in higher-frequency oscillatory common inputs that do not impact the motoneuron discharge rate. The first case can be simulated as a short drop in the input to a pool of MUs, which then cases a brief drop in the discharge rates of the units (figure 5(A)). The second scenario can be represented by adding to the common drive a 300 ms oscillatory input, whose amplitude is not large enough to increase the mean discharge rate of units (figures 5(B)–(D)). As simulations show, both a drop in common input and an added high-frequency oscillatory input can affect the power of the CST at one or various frequencies simultaneously (figure 5). In the first scenario, the increase in power in the CST from the motoneurons is most evident at the frequency of the average discharge rates (11–12 Hz) (figure 5(A)). A transient change in common input at low frequencies may happen with movement cancellation (Rangel *et al* 2024) and the short drop in discharge rate we observed in some participants would point towards this possibility. However, we did not have a significant increase of power in the alpha band during the *cancellation* period. On the other hand, in the second simulation scenario, the effects of a short oscillatory input can be observed at the frequency of the input and at its harmonics (the power of which will depend on the strength of the inputs). For example, when the oscillatory input is at 10 Hz, an increase in power can be observed at 10 Hz, 20 Hz and 30 Hz, though the motoneurons did not receive common inputs at the higher frequencies (figure 5(B)). Similar changes are observed for higher frequency common inputs (figures 5(C) and (D)).

One concern that arises is that peaks at gamma frequencies in the spectrogram of CST could be partly produced as harmonics of other oscillatory synchronisations. Although it remains possible that strong beta synchronisation observed during the cancellation period could have affected the level of power in the gamma band, note that we also found significant forward coherence during this window in six out of twelve participants. This suggests that there was also a transmission of these descending oscillatory inputs to muscles at these frequencies, but the effects were not as strong as in the beta band. In addition, even though we identified on average 26 steadily firing MUs per participant, some of them had significantly fewer units. Thus, the estimation of power in higher frequencies, especially in the gamma band, could have been affected by their limited sampling by the CST of the identified motor units.

Overall, we observed significant changes in the firing activity of spinal motoneuron during movement cancellation. Moreover, the average discharge rate did not change during the three periods (*baseline, preparation, cancellation*), further supporting the idea that the significant changes in high-frequency modulation did not have a direct functional effect on force production and behaviour. This further raises the question of the role of these high-frequency rhythms. One hypothesis is that beta oscillatory activity has a role in transmitting state-related information by feedback to the brain (Baker 2007, Witham *et al* 2011), which is not in contradiction with our results, though such claim cannot be supported by our data.

Finally, the transmission of cortical oscillations substantiated in this study supports the idea that muscle readings can provide information on brain activity. The oscillations identified from MUs could be used to estimate the corresponding supra-spinal oscillations. The motoneuron, as the final common pathway of the neuromuscular system, receives a variety of inputs from the full nervous system, which could allow researchers to partly infer the activity of

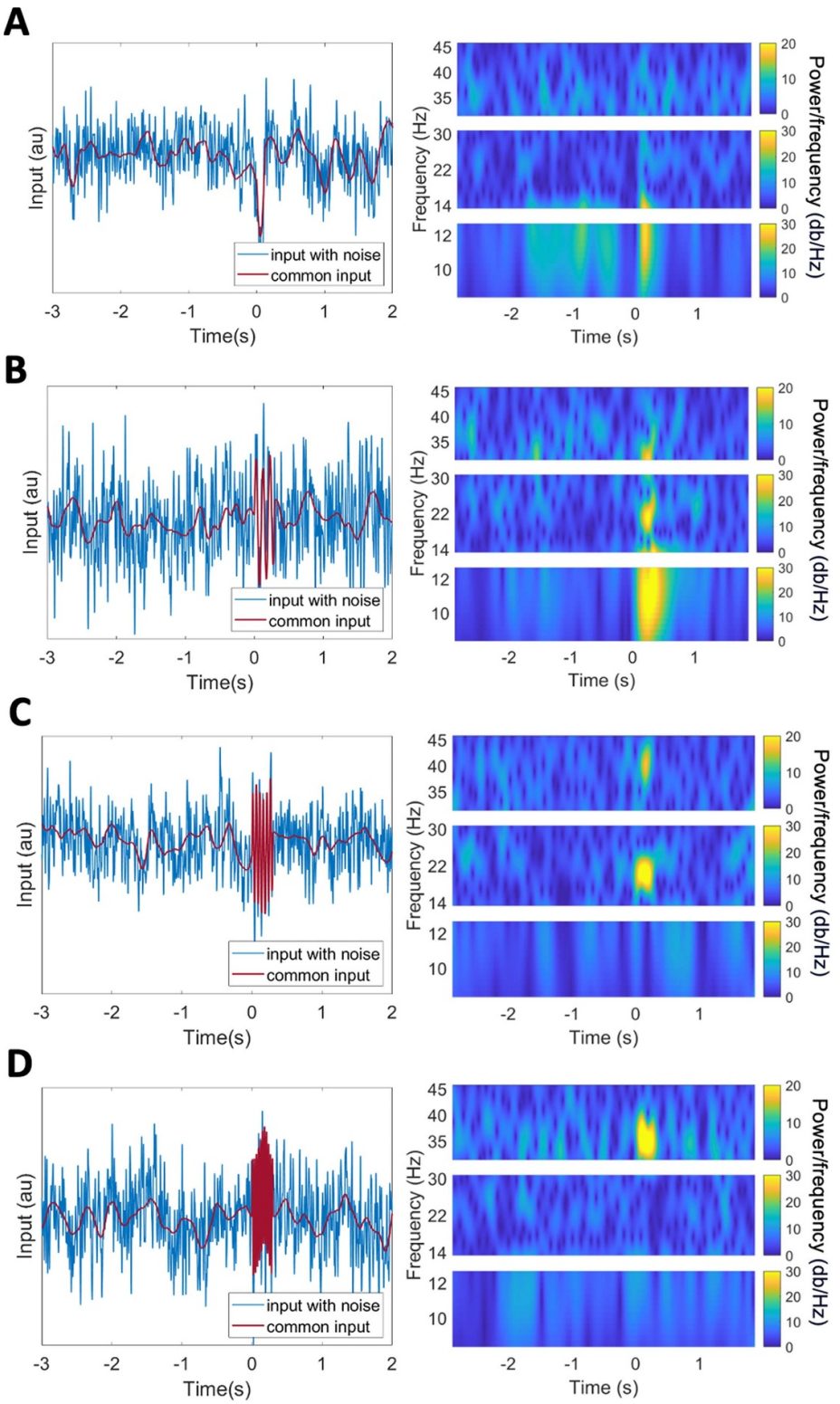

Figure 5. Spectrograms of the activity of a simulated pool of motoneurons receiving various common inputs. (A), Left panel shows common input to a motoneuron pool and example full input to one MN with independent noise added. A drop in the amplitude of common inputs at low frequencies (red trace; left panel) causes the synchronisation of the firing activity of motoneurons, and thus increases the power at frequencies that match their average discharge rate. The spectrogram of the cumulative spike train (CST) is shown separately on the right for alpha (8–12 Hz), beta (13–30 Hz) and gamma (30–45 Hz) bands. (B), Low frequency common input with an additional 300 ms oscillatory activity at 10 Hz caused an increase in power at 10, 20 and 30 Hz. (C), Low frequency common input with an additional beta oscillatory input at 20 Hz increased the power in CST at 20 Hz and 40 Hz but did not affect lower frequencies. (D), Low frequency common input with an additional low gamma input at 35 Hz temporarily increased the power at 35 Hz only.

other regions of the nervous system, including brain activity that does not directly drive muscle force.

5. Conclusions

This study provides novel information about the modulation of spinal motoneurons in stable contractions, during changing brain states. We show for the first time that an increase in beta oscillatory activity can be recorded from the motoneuron population during the cancellation of a prepared action.

Data availability statement

All data that support the findings of this study are included within the article (and any supplementary files).

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Author contributions

B Z: Conceptualisation, Methodology, Investigation, Analysis, Writing—original draft, review & editing; S A: Investigation, Writing—review & editing; J I: Conceptualisation, Methodology, Analysis, Writing—review & editing; D F: Conceptualisation, Resources, Writing—review & editing

Conflict of interest

The authors declare no competing interests.

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