Application of matched filtering to identify behavioral modulation of brain oscillations

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Abstract

Brain oscillations modulated by motor behaviors are coupled to steady-state and other potentially unrelated to movement oscillations, with energy in the same frequency bands as the signals of interest. We applied matched filtering, a quasi-optimum signal detection technique, to decouple and extract movement-related signals from local field potentials (LFPs) recorded in monkey motor cortical areas during the execution of a visually instructed reach-out task. Using a matched-filterbank, we examined coupling and interference of pre-movement and initial steady-state oscillations with movement-induced signals. Once these signal contributions were eliminated, we were able to identify significant correlations of the residual signals with behavioral parameters, which appeared attenuated by pre-movement signal interference in the raw LFPs. Specifically, the maximum and minimum amplitudes of filtered LFPs were directly modulated by peak movement velocity and micro-movements, respectively, identified in recorded hand velocity profiles. In addition, we identified phase correlations between signals during the delay (when the instructional cue was presented) and movement intervals, as well as modulation of LFP phase by movement direction. For pairs of orthogonal movement directions, corresponding LFP signals were consistently out of phase. Finally, β-band energy which is typically reduced during movement execution, possibly partly due to destructive interference between the modulated by behavior signal and unrelated oscillations, appeared to be recovered in the filtered signals.

Keywords

Motor system; Local field potentials; Brain oscillations; Matched filtering

1 Introduction

Extracellularly recorded local field potentials (LFP) in the brain represent aggregate neural activity from many neurons in the neighborhood of the recording site. LFPs recorded in motor cortical areas have been shown to be modulated by motor behavior parameters, such as speed and direction of movement (Baker et al. 2003; Rickert et al. 2005; Hatsopoulos et al. 2006; Richardson 2007), and specific temporal events related to the preparation and execution of motor tasks (O'Leary and Hatsopoulos 2006; Roux et al. 2006). During the execution of movement, an LFP signal recorded in motor cortical areas is composed of behavior-related components which may be coupled to background oscillations and other unrelated to the

behavior signal components. This coupling has been previously addressed using bandpass filtering, to extract the energy of the LFP signal in frequency bands in which the LFP is believed to be modulated predominantly by behavior (Hatsopoulos et al. 2006; O'Leary and Hatsopoulos 2006; Roux et al. 2006). However, in frequency ranges in which both the behavior and unrelated processes contribute to the LFP energy, it may not be possible to decouple distinct signal contributions.

Matched-filtering is a theoretically optimum detection technique for extracting a transmitted signal from an observed, corrupted by noise signal. If the noise spectrum is white, the matched filter is the time-reversed signal (Van Trees 2003). The filtering operation involves the convolution of the known (template) signal with the unknown signal in order to extract the template from it (Allen and Mills 2004). The technique is widely used in communications, radar, sonar and pattern recognition problems (Juday 2001; Spiesberger 2001). In theory, the difference between the known transmitted signal and the received signal is only the noise component. In practice, dispersion and propagation effects also distort the source signal, resulting in the loss of the matched-filter gain. In repeatedly recorded brain oscillations there are several sources of noise. The most prominent is the natural system variability. Signal contributions associated with task events prior to the behavior, background (steady-state) and stimulus-induced oscillations may also be treated as noise sources, which corrupt the behavior-induced signal. Alternatively, the motor behavior may be viewed as a perturbation to the steady-state brain oscillations, in which case the behavior-related signal becomes the noise. Irrespective of the assumption of what constitutes signal and what is noise, it is of interest to isolate the contribution of movement to the LFP signal during the execution of movement, in order to understand its modulation by behavioral parameters.

In this study we applied matched-filtering to movement-related LFPs recorded in monkey motor cortical areas, to assess their modulation during a visually-cued reach-out task. Initial steady-state (base-line) oscillations were recorded during a reference interval prior to cue onset. Although distinct background oscillations are present at different task-related intervals, we were interested in determining the contribution of initial steady-state signals, as well as respective contributions of other pre-movement intervals on movement-related signals. We, therefore, constructed a matched-filterbank to sequentially filter the movement signals, isolate these contributions and eliminate them. Residual signals, modulated primarily by movement and by other unobserved, potentially unrelated but coupled processes, were then used in further analysis. Our hypotheses were that a) behavioral correlates are more clearly identified in the filtered residual signals and b) background and pre-movement oscillations may destructively interfere with neural activity during behavior, resulting in the attenuation of specific frequency components of the recorded LFPs. Matched-filtering has also been applied to EEG signals, but for purposes unrelated to the extraction of behavioral correlates, e.g, to extract signal artifacts (Niedermeyr and Lopes da Silva 2004; Lopes da Silva et al. 1976; Stamoulis and Chang 2009). To the best of our knowledge, this technique has not been applied to LFP signals for biologically-relevant purposes. In addition, the use of baseline and pre-movement recordings as template signals and subsequent analysis of residual signals is entirely novel.

2 Material and methods

2.1 Behavioral tasks and data acquisition

Data from two male rhesus monkeys (*Macaca mulatta*) were analyzed. Using a planar lever, the monkeys performed a visually-cued reaching task, divided into four behavioral intervals. The first interval was the center-hold period (1s duration in all trials and LFPs), when the monkey held a handle in the center of the workspace. It was followed by the instructed delay period, starting with the appearance of the visual cue, directing the animal to move the lever to one of eight directions (at 45° increments, starting at 22.5°), and ending with the

disappearance of the center target, i.e., the go signal. The third interval was the reaction time, a short period between the go signal and movement onset. The fourth interval was the movement time, during which the animal reached the desired target, held the lever at that target and then returned to the center-hold position. Monkey A repeated the task under three force field conditions, applied to its hand: null (control), in which both monkeys had been trained in the task, clockwise, and counterclockwise, both representing novel mechanical environments. Monkey B repeated the task with no applied forces. The task was repeated on average 60 times in each direction (20 times under each force condition), resulting in at least 480 trials for each recorded LFP (Richardson 2007). Given the inter-trial variability of the recordings, for each LFP, force condition and direction of movement, in time-domain operations, signals were averaged over all trials. In frequency-domain operations, individual trial spectra were computed and then averaged.

LFPs were recorded from primary motor cortex (M1) and dorsal premotor cortex (PMd), using tungsten micro-electrodes positioned with manual micro-drives. Up to eight micro-electrodes were used in each recording session and recording locations were changed in each session. Surgical and experimental procedures are described in detail elsewhere (Richardson 2007). All procedures were approved by the Committee on Animal Care at the Massachusetts Institute of Technology. We analyzed 33 LFPs recorded in the dorsal premotor cortex (PMd) and 48 LFPs recorded in area M1 of monkey A, and 54 LFPs in area M1 of monkey B, all sampled at 2,000 Hz and bandpass filtered in the range 1–1,000 Hz. Power-line noise was attenuated with a stopband filterbank, centered at the 60 Hz harmonics of the noise, in the range 60–480 Hz, with a 3 Hz bandwidth for center frequencies ≤150 and a 6 Hz bandwidth for center frequencies >150 Hz. Second order elliptical filters (30 dB attenuation in the stopband, 0.5 dB ripple in the passband) were used. Signals were filtered in both forward and reverse directions to eliminate potential phase distortions associated with the non-zero phase of the elliptical filter.

2.2 Matched filtering of LFP signals

The matched filter is a quasi-optimum linear filter $h(t)$ which maximizes the output signal-to-noise ratio *SNR*. It is not frequency band-specific but instead extracts a particular waveform from a contaminated by noise signal. The filter improves *SNR* by reducing the noise's spectral bandwidth to that of the template. At the same time, it reduces the in-band noise through the shape of the template's spectrum (Allen and Mills 2004). The *SNR* to be maximized is given by:

$$SNR(T) = \frac{\left| \int_0^T h(\tau) y(T - \tau) \, d\tau \right|^2}{\sigma^2 \int_0^T |h(\tau)|^2 d\tau}$$

(1)

where σ^2 is the variance of additive system noise. The observed signal, $y(t)$ is convolved with the time-reversed filter $h(-t)$ to obtain the matched-filtered signal $y_{MF}(t)$. This process corresponds to a normalized cross-correlation between the observed and template signals, though cross-correlation does not involve time reversal. The optimum filter that theoretically maximizes the *SNR* in Eq. (1) is the time-reversed signal $y(-t)$, under an assumption of white noise. In any realistic application, the selected match-filter is only quasi-optimum, given the non-white noise of physical and many mechanical systems as well as propagation and dispersion effects. The filtered signal y_{MF} is given by:

$$y_{MF}(T) = y(t) \star h(-t) = \int_{-\infty}^{\infty} y(t) h(t - T) \, dt$$

(2)

Recorded LFP signals during movement $y(t)$ were filtered with a matched-filterbank, shown schematically in Fig. 1.

We defined the recorded LFP signals during the center-hold, delay and reaction times as $h_c(t)$, $h_d(t)$ and $h_r(t)$ respectively, since they were used as filters in the proposed sequential matched-filtering. Noise terms u_1, u_2 and u_3 were assumed to be zero-mean, Gaussian additive system noise. We assumed that to a first approximation, there is a linear relationship between observed LFP signals at different task intervals. We first filtered the observed movement-related signal $y(t)$ using $h_c(t)$ as the baseline matched-filter. The resulting signal represented the best match between the baseline and the observed movement signal, i.e, the contribution of the background oscillatory activity. We then eliminated the matched from the original signal. The residual was then passed through $h_d(t)$ to eliminate the contribution from the delay signal, and subsequently through $h_r(t)$ to eliminate the contribution from the reaction time signal. Given the non-standard choice of filters in this process, we had to ensure that no resulting spurious phase shifts were introduced. Thus, throughout this analysis we compared the phase of the original and matched-filtered signals and corrected for phase changes accordingly. Movement-induced oscillations were assumed to be the dominant contributions to the resulting signal. Evidently the original signal also included noise associated with background activity during movement, as well as with other unrelated processes, which could not be independently observed and thus their waveforms were unknown. Contributions from these processes could not be attenuated through matched-filtering.

3 Analysis

We examined the effects of sequential matched filtering on the LFPs during movement preparation (delay interval) and execution (movement interval), in PMd and M1. For each movement direction, trial-averaged, individual movement-related LFPs were filtered in the order shown in Fig. 1. Original and once filtered signals (further averaged over all LFPs) are shown in Fig. 2, for PMd (top) and M1 (bottom), for the same direction of movement (22.5°), recorded under null force field conditions. The respective center-hold signals (the first filters) are superimposed on the left-side plots. Raw and once matched-filtered signals are superimposed on the right-side plots.

There are time-specific extrema in both raw and filtered signals and related amplitude gains. Specifically, there is an amplitude maximum 120–200 ms from movement onset, in both PMd and M1 raw signals, though barely distinguishable in the M1 signal given another local maximum at movement onset. These maxima are very clearly seen in the filtered signals and the amplitude gain at that point is >20 dB. In addition, there is a specific minimum 300–400 ms from movement onset, barely identifiable in the raw PMd signal but distinguishable in the M1 signal. In the corresponding filtered signals, these minima are very clearly seen with a gain of about 20 dB. Interestingly, these extrema appear to occur earlier in the PMd signal (50–100 ms earlier). To assess the correlation of these time-specific changes in LFP amplitude with behavioral changes, we examined movement velocity profiles, averaged over all successful trials for each direction of movement and null force field conditions, shown in Fig. 3. Indeed, the maximum speed of movement occurs at about 200 ms from movement onset and there is a local minimum at about 400 ms, associated with microvements, particularly clear in directions 22.5° and 337.5°. Thus, the amplitude distribution of the filtered LFP appears directly modulated by velocity of movement.

We also examined the effect of matched-filtering on LFP movement signals recorded when forces were applied to monkey A's hand. Two examples of LFP movement signals (averaged over both trials and LFPs for each movement direction), recorded in PMd and M1 respectively,

are shown in Fig. 4. Raw, once filtered and thrice filtered signals are superimposed, for a single direction of movement (292.5°).

Temporal changes that would reflect behavioral modulation are almost indistinguishable in the unfiltered signals, particularly those recorded in PMd. Also, the maximum amplitude at ~200 ms, is not clear in the raw signals but increasingly distinguishable in the once and thrice signals, the latter resulting from filtering the LFPs through the entire matched-filterbank in Fig. 1. The maximum filter gain is again of the order of 25 dB. Thus, the assumption of linear contributions of pre-movement, task-related intervals is appropriate, at least to a first approximation. It also appears that these contributions attenuate the modulation of the signal by the behavior. The modified amplitude distribution in the filtered signals is consistent with the *β*-band (12–27 Hz) spectral amplitude/power variation during movement, reported in (Richardson 2007).

Modulation of neural activity during the delay interval has been shown to be associated with motor planning (Roux et al. 2006). The true relationship between neural activity during the delay and movement intervals may be much more complex than the assumed linearity in this analysis. Nevertheless, by eliminating initial background activity from respective LFP signals we identified consistent phase correlations between them. Specifically, movement and delay signals were partially or entirely phase-correlated in 71% of LFPs under null force conditions, 60% under applied forces in monkey A, and in 67% of LFPs in monkey B. For both animals these relationships were identifiable for specific movement directions. Thus, for each of these directions of movement, we restricted averaging to trials and LFPs in which these phase relationships were barely identifiable in the raw signals. Figure 5 compares the original (top plots) and filtered (bottom plots) activity in the delay and movement intervals respectively, in M1 of monkey A, for a single movement direction, under no force (left plots) and clockwise force field conditions (right plots), respectively. Both movement and delay signals were filtered once to eliminate the center-hold baseline activity.

Throughout this analysis phase corrections have been made in every filtering operation, to ensure the elimination of spurious phase changes associated with the non-zero, non-linear phase of the baseline, delay and reaction time signals used to filter the movement signal. Thus, phase relationships identified when comparing the delay and movement signals are potentially biologically relevant. Specifically, we observed that matched-filtered movement and delay signals recorded under no force conditions, were in phase for approximately the entire duration of the time interval, particularly for movement directions in the upper half-plane of the working space (<180°). Corresponding signals under force conditions, appeared to be out of phase in the first 150–200 ms of the interval and in phase thereafter. These envelope phase changes were clearly distinguishable in the matched-filtered signals and to much lesser extent in the raw signals. Although the baseline activity during center-hold appears to primarily affect the amplitude levels of the delay and movement signals, secondary changes in the power distribution of the signal, as well as phase shifts can also be identified, suggesting the potential destructive interference of the background activity with the modulated by behavior movement signal. In a broad range of mechanical and physical systems, phase changes in their response are often associated with system perturbations. It is, therefore, possible that the observed differences in phase synchronization between movement and delay signals under null and clockwise force fields respectively, in the first 200 ms of the intervals, reflect the presence of the novel force field, a 'perturbation' to the learned task.

In addition to velocity of movement, several studies have shown that LFP signals are also modulated by movement direction. We thus examined the effect of matched-filtering in facilitating the identification of such modulation, by comparing filtered movement signals at different direction. In this part of the analysis, we only focused on signals recorded under no

applied forces. Figure 6 shows filtered pairs of movement-related signals for directions of movement orthogonal to each other.

LFP signals modulated by movements in mutually orthogonal directions appear to be out of phase. These phase relationships were not distinguishable in the raw signals. To extract the envelope phase of the LFP waveform during movement, low-pass filtering is typically used, which requires *a priori* selection of a frequency band of interest. Matched-filtering, and subsequent elimination of background activity and associated higher-frequency signal energy, also resulted in a lower-frequency signal from which it was easier to extract phase changes associated with behavioral modulation. This occurs at lower frequencies, in the *β*-and lower bands, and is reflected in the pairwise phase changes at orthogonal directions of movement. Previous studies predominantly report on the LFP amplitude modulation with movement direction (Richardson 2007; Roux et al. 2006). Here we report on the phase modulation of the signal. Note that the above results are for LFP signals decoupled from the background activity only. We also examined the matched-filtered delay signals for potential modulation by movement direction. Phase variability corresponding to orthogonal movement directions was not evident in these signals.

Although the *β*-band is the predominant frequency band of the precental cortex, energy in this band is significantly reduced during movement (Richardson 2007). This may reflect aspects of behavior, and similar results have been reported in regard to the attenuation of the *α*-band energy in the EEG, but it may also be in part associated with destructive interference of pre-movement signals with significant energy in the *β*-band. Thus, we finally examined the respective spectra of the center-hold signal as well as both raw and filtered signals during movement. Figure 7 shows an example of the three signals and respective spectra, averaged over trials and LFPs for one direction of movement, looking at the energy distribution predominantly at frequencies less than 40 Hz. The movement-related signal was matched-filtered only once.

In the original movement signal, spectral power below ~25 Hz significantly decreased about 200 ms after movement onset, in agreement with previous studies (Richardson 2007). In contrast, part of the signal energy was restored in the matched-filtered signal and *β*-band power was present beyond the initial 200 ms, for the entire duration of the interval. In addition, given the enhanced amplitude of the filtered signal, power below ~25 Hz in the first 200 ms also increased. Spectral power in the center-hold interval was on average ~10 dB lower. Contamination of the movement signal by pre-movement baseline activity, such as that during center-hold, and their destructive interference due to phase differences may in part cause the suppression of *β*-band energy after 200 ms from movement onset. This hypothesis is supported by the fact that spectral energy in this band was restored in matched-filtered signals from which background activity was eliminated.

4 Discussion

Movement-modulated LFP signals may be coupled not only to background, steady-state oscillations in the brain but also to activity related to the history of the behavioral task, i.e., to pre-movement events. To assess LFP modulation by behavioral parameters, it needs to be decoupled from unrelated processes. Band-pass filtering based on *a priori* knowledge of frequency bands predominantly associated with movement may not be appropriate, particularly if signal components from distinct sources may share significant energy in the same frequency bands. To attenuate unrelated to behavior contributions in the LFP movement signal, we applied matched-filtering, a technique predominantly used in sonar and communications for signal pattern recognition purposes. We assumed that, although the movement signal may be affected by unobserved, simultaneously modulated processes, potential contributions from

observed pre-movement events, i.e., the initial baseline activity, the delay and reaction time signals could be extracted through matched-filtering. For this purpose, we matched recorded pre-movement waveforms to the movement signal, estimated their contribution and eliminated them. Our goal was to determine a) whether filtered signals correlated more strongly with behavioral parameters than raw signals, and b) to assess the potential interference between these different signals. Evidently, there are steady-state oscillations during movement and contributions from other processes which may be coupled to the behavior-induced signal and which cannot be decoupled from it without knowledge of their independent waveforms. However, our study only addressed the effects of measured processes on the movement signal.

Irrespective of motor cortical region, the mechanical environment in which the task was executed, or direction of movement, matched-filtering showed that background oscillatory activity, during the center-hold interval affects predominantly the amplitude of the movement signal and to a lesser extent the actual waveform. Elimination of its and other pre-movement signal contributions resulted in residual waveforms in which the LFP amplitude distribution was temporally modulated by behavior, particularly the time at which hand velocity reached its maximum, as well as later times of micro-movements. However, it also appears that pre-movement activity also destructively interferes with the movement signal in the 12–27 Hz β-band, resulting in attenuation of spectral power in this band. We showed that once the background activity was eliminated, the related spectral power increased, particularly during parts of the interval where β-band power was prominent in the center-hold interval which was used as the filter. Oscillatory activity during the delay period appears to have a different effect on the movement signal. The envelope of the latter appears to be in phase with the delay signal for LFPs recorded under null force field conditions. For LFPs recorded under clockwise force field conditions, the two signals appeared initially out of phase for the first 200 ms of the interval and in phase after that. This implies constructive interference of the two signals for the entire duration of the interval in the no force case, and 200 ms following the presentation of the visual cue, in the force field case. Movement intention and movement execution may be reflected in the phase agreement between the two LFP signals. In contrast, the initial phase difference between the two signals under force field conditions may reflect the occurrence of a 'perturbation' to the learned task associated with the novel mechanical environment. In the first 200 ms of movement, the animal reaches its maximum hand velocity, a measure of performance, which is influenced by the applied force. Although several studies have associated these two intervals, to our knowledge, the phase relationship between respective LFPs have not been studied, possibly due to the difficulty associated with analyzing raw LFPs for phase. We also examined modulation of matched-filtered movement signals by movement direction. We observed that these signals were out of phase for pairs of orthogonal movement directions, while this occurrence was not evident in the raw signals. All these results support our initial assumption that to a first approximation, pre-movement events, including initial steady-state oscillations contribute to the movement signal quasi-linearly, directly and progressively attenuating the modulated by behavior amplitude distribution of the signal and destructively interfering with its frequency content and waveform.

Matched-filtering cannot decouple signal components for which we have no waveform information. Thus, the residual movement signal will still be coupled to steady-state oscillations during movement as well to contributions from other unobserved processes. However, matched-filtering allows us to assess the presence and eliminate the contribution of observed waveforms. The underlying assumption of our analysis has been that movement-evoked potentials have at least one independent component which is unrelated to pre-movement events and the history of the trial, and is directly related to behavior. The origin and modulation of motor-evoked signals remain subjects of debate in the EEG literature (Mitzdorf 1985; Babiloni et al. 1999; Niedermeyr and Lopes da Silva 2004). However, our analysis and application of matched-filtering suggests that the LFP signal during movement may not be

solely the result of a series of phase correlations and modulation of steady-state activity, particularly given the strong alignment between specific features of its waveform with behavioral parameters and events. In addition, phase correlation between the delay and movement signals may again reflect previously identified relationships between motor planning and execution of a planned movement, rather than progressive phase correlations during the trial, particularly since such phase relationships were not present between the movement and reaction time signals. Match-filtering is, therefore, an adequate LFP signal analysis technique, to eliminate pre-movement signal contributions which appear to attenuate and distort the modulation of the LFP movement signal by behavioral parameters.

Acknowledgments

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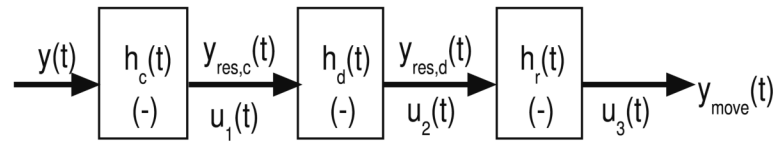
Fig. 1.
Diagram of the matched-filterbank. The output signal is a thrice filtered signal once the baseline, delay and reaction time contributions to the LFP signal have been suppressed. The *dash signs in parentheses* refer to the elimination of the matched from the original signal following convolution
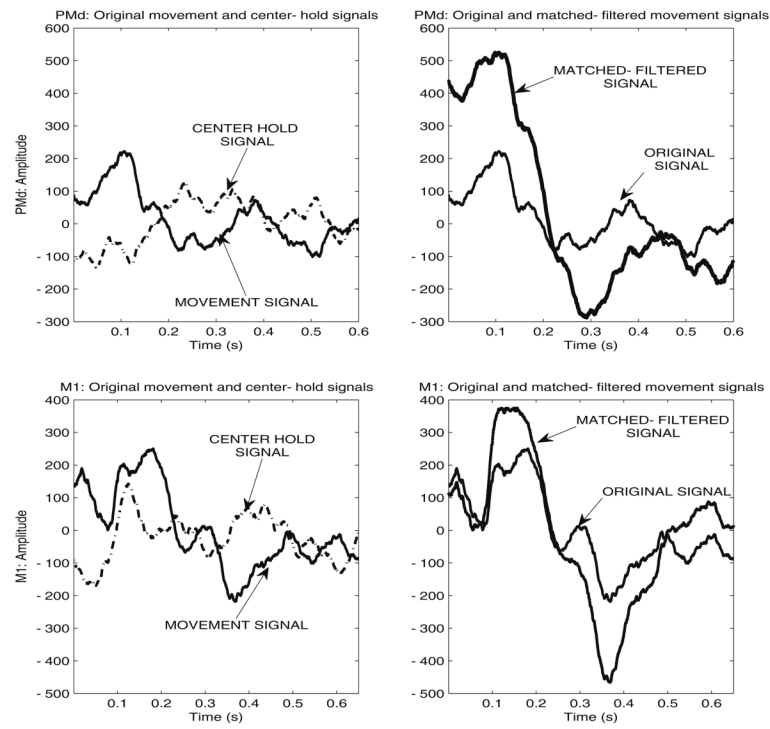
Fig. 2.
Background oscillatory activity (*dashed*)is superimposed to the PMd and M1 movement signals, respectively (*top* and *bottom*, *left plots*). Corresponding original and once-filtered signals are shown at *top* and *bottom*, *right-side plots*
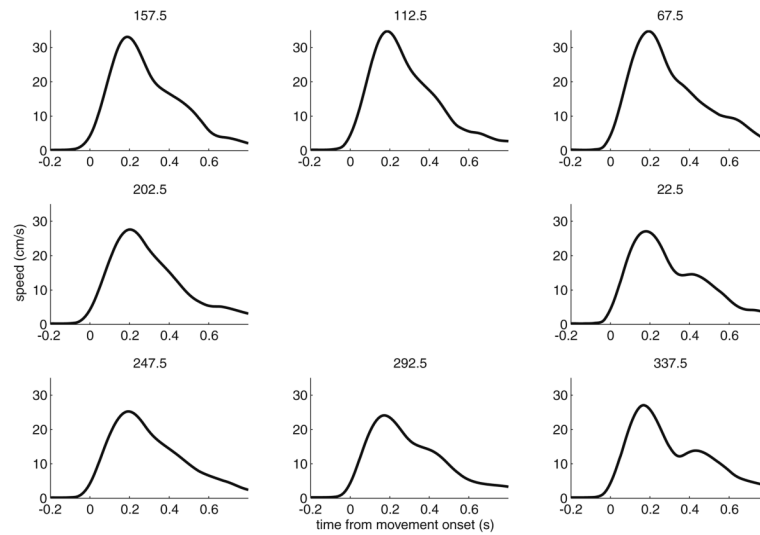
Fig. 3.
Averaged velocity of movement profiles of monkey B, under null force conditions, for each direction of movement
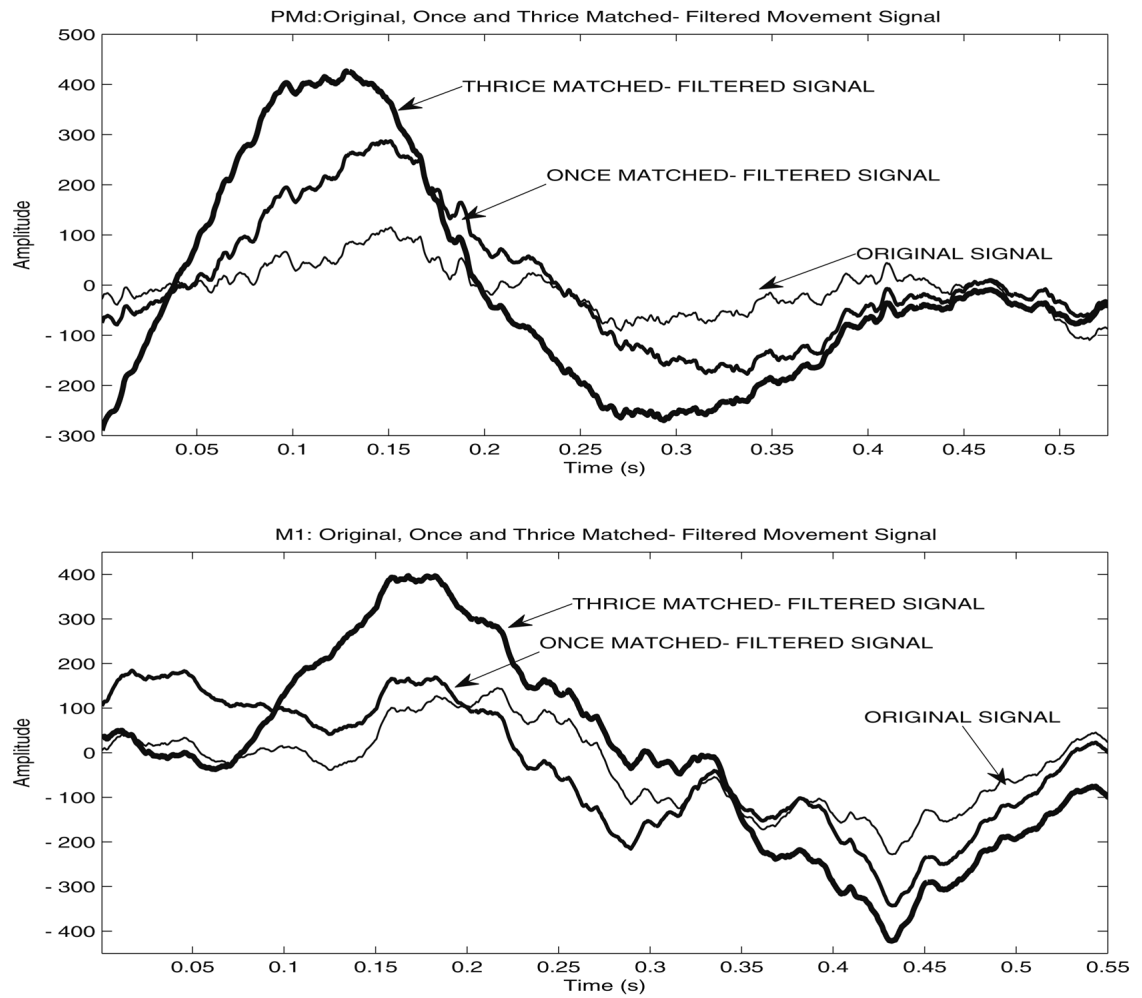
Fig. 4.
Original LFP signals and signals matched-filtered with baseline and all pre-movement waveforms, respectively, under clockwise forces
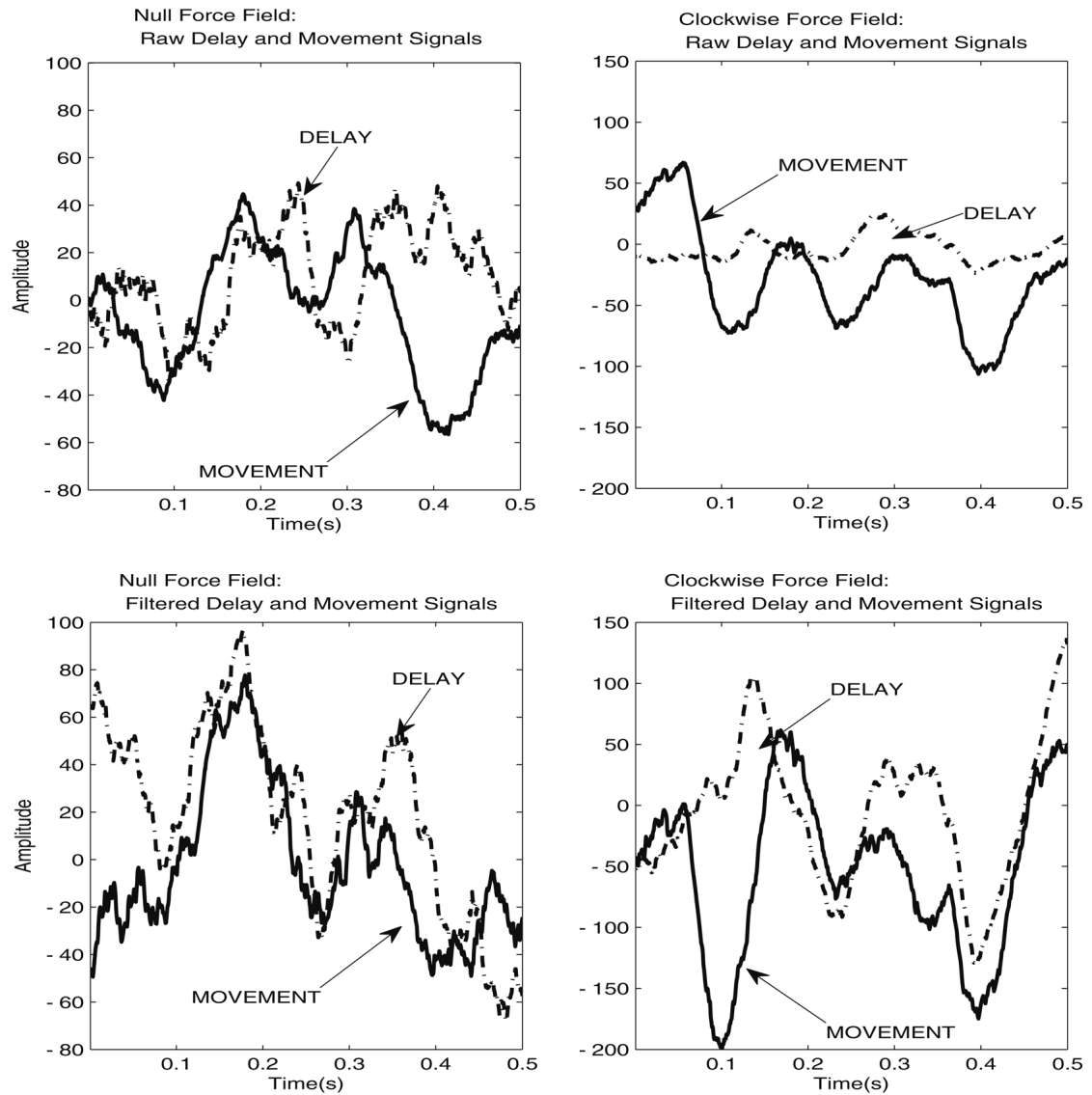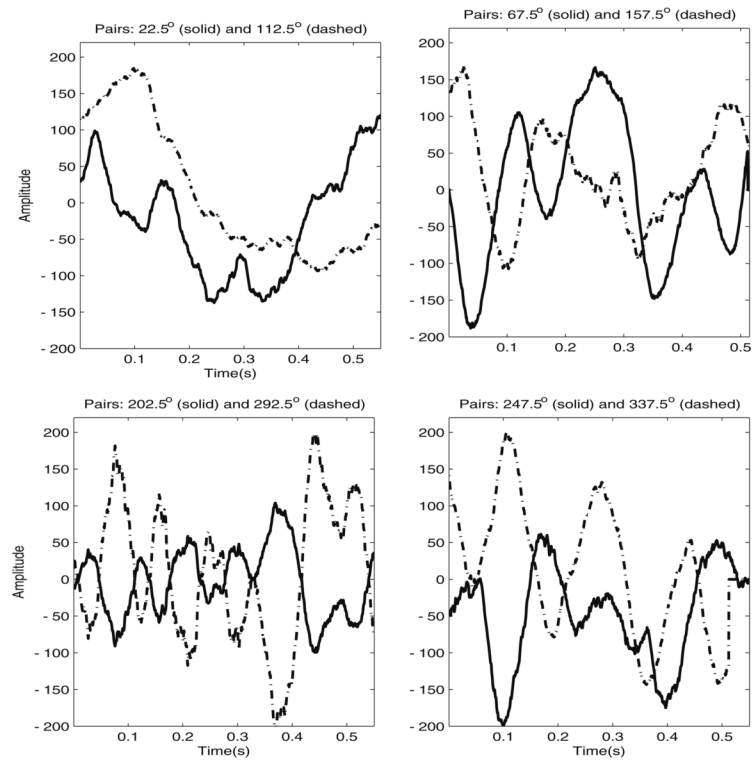
Fig. 5.
Delay (*dashed*)and movement (*solid*)LFP signals, recorded under no applied forces (*left plots*)and a clockwise force field (*right plots*). Raw signals are superimposed in *top plots*, matched-filtered signals are in *bottom plots*

Fig. 6.
Pairs of matched-filtered LFP signals, averaged over all trials and LFPs, for directions of movement at 90° to each other, recorded during movement execution. Pairs include from *top left* to *right bottom plots*, (22.5°, 112.5°), (67.5°, 157.5°), (202.5°, 292.5°) and (247.5°, 337.5°)
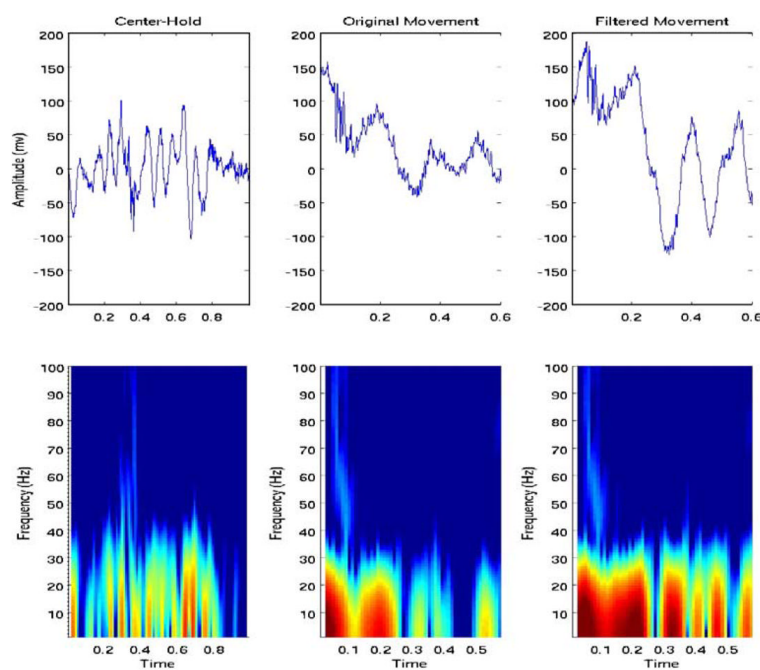
Fig. 7.
Center-hold, unfiltered movement and once matched-filtered movement LFP signals, for one direction of movement, averaged over all trials and LFPs (*top plots*)and corresponding spectra (*bottom plots*). Signals and spectra are shown in the same respective scales