Being an agent or an observer: different spectral dynamics revealed by MEG.

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ABSTRACT

Several neuroimaging studies reported that a common set of regions are recruited during action observation and execution and it has been proposed that the modulation of the $\mu$ rhythm, in terms of oscillations in the alpha and beta bands might represent the electrophysiological correlate of the underlying brain mechanisms. However, the specific functional role of these bands within the $\mu$ rhythm is still unclear. Here, we used magnetoencephalography (MEG) to analyze the spectral and temporal properties of the alpha and beta bands in healthy subjects during an action observation and execution task.

We associated the modulation of the alpha and beta power to a broad action observation network comprising several parieto-frontal areas previously detected in fMRI studies. Of note, we observed a dissociation between alpha and beta bands with a slow-down of beta oscillations
compared to alpha during action observation. We hypothesize that this segregation is linked to a different sequence of information processing and we interpret these modulations in terms of internal models (forward and inverse). In fact, these processes showed opposite temporal sequences of occurrence: anterior-posterior during action (both in alpha and beta bands) and roughly posterior-anterior during observation (in the alpha band). The observed differentiation between alpha and beta suggests that these two bands might pursue different functions in the action observation and execution processes.

**Keywords:** action observation and execution, alpha and beta rhythms, Event-Related Desynchronization (ERD), magnetoencephalography (MEG), internal models

1. INTRODUCTION

Several studies report that our sensorimotor system is activated when we observe an action performed by other people. This putative mirror-like activity in humans was found in the precentral gyrus (vPM), the inferior frontal gyrus (IFG), the inferior parietal lobule (IPL), and regions within the intraparietal sulcus (for a review see Rizzolatti and Sinigaglia, 2010). In addition to this limited number of regions, neuroimaging studies observed a broader action observation network (AON) which seems to be involved during action observation (OBS) and execution (EXE) (Avenanti et al., 2012; Buccino et al., 2004; Gazzola and Keysers, 2009). A proposed theoretical framework postulates that such AON implements forward and inverse internal models (Wolpert and Ghahramani, 2000), which should be engaged during EXE and OBS. The internal models can account both for how we link our actions to sensory consequences and how others’ actions match our own actions and sensations (Gazzola and Keysers, 2009; Iacoboni, 2005). It has been proposed that the fronto-parietal AON has a predictive nature and according to this hypothesis, during action observation the inverse and forward models are integrated to achieve a prediction of
others intentions and behavior based on simulation (Avenanti et al., 2012; Gazzola and Keysers, 2009; Press et al., 2011; Schippers and Keysers, 2010; Schutz-Bosbach and Prinz, 2007; Urgesi et al., 2010; Wilson and Knoblich, 2005). Despite this hypothesis being very attractive, a clear evidence of the electrophysiological correlates underlying the implementation of these models is still missing.

The neurophysiological signature of the putative mirror-like activity, as observed through magnetoencephalography (MEG) and electroencephalography (EEG) in humans, is thought to be a modulation (suppression) of the µ rhythm power (Hari, 2006; Pineda, 2005). Such rhythm refers to cortical oscillations in the frequency range [8-12] Hz (alpha band) and [15-25] Hz (beta band), typically recorded over somato-sensory regions during both action execution and observation (Babiloni et al., 1999; Hari et al., 1998; Hari et al., 2000; Hari et al., 1997; Pfurtscheller, 1989; Pineda et al., 2000). It has been reported that the µ rhythm waveform consists of a mixture of alpha activity and the second harmonic beta rhythm, giving rise to an arch-shaped waveform (Buzsaki, 2006). The relationship between these two bands within the µ rhythm is still under debate. In fact, this rhythm does not seem to reflect a unitary phenomenon (Pfurtscheller et al., 1996; Pineda, 2005; Stancak and Pfurtscheller, 1995), but rather a combination of different processes, potentially involved in the transformation of “seeing” into “doing”. Moreover, a complete overview of the spectro-temporal dynamics within the AON is missing, since many studies in the literature considered only the alpha component (Kilner et al., 2006; Marshall et al., 2009; Muthukumaraswamy et al., 2004; Pineda et al., 2000; Streltsova et al., 2010), or limited their attention to the amplitude modulation of the oscillatory activity (Cochin et al., 1999; Hari et al., 1998; Kilner et al., 2009; Koelewijn et al., 2008; Muthukumaraswamy and Johnson, 2004; Orgs et al., 2008), whereas studies on the temporal dynamics of brain activity during OBS and EXE focused on the sensorimotor cortex only (Babiloni et al., 2002; Caetano et al., 2007).
Thus, the novelty of this MEG study consists of exploring the neural signature of action observation and execution in the spatial and time-frequency domains over the whole cortex. Specifically, thanks to the high MEG temporal resolution, we investigated whether the two bands reflect different dynamics of action observation and execution. Moreover, we linked this dynamics to the hypothesis that information is processed according to the criteria posed by internal models.

2 MATERIALS AND METHODS:

2.1 Subjects, experimental setup and acquisition

We studied twelve healthy subjects (7 female), age range 21-31 years (mean 27 ± 3). All subjects were naïve with respect to the purpose of the experiment. They all gave their written consent to the experimental procedure according to the Code of Ethics of the World Medical Association and the standards established by the University of Chieti Institutional Review Board and Ethics Committee. The subjects were right-handed as indicated by a questionnaire adapted from Edinburgh Handedness Inventory (Oldfield, 1971). None of the participants had a history of psychiatric or neurological disease, head trauma, substance abuse or other serious medical conditions.

The experiment consisted of two conditions: the observation (OBS) and execution (EXE) of an aimless slow movement. Specifically, the used movement task is a right self-paced finger-tapping that is a partially pre-programmed action, proprioceptively but not visually feedback-controlled. Just before starting the experiment, subjects were instructed about the paradigm and they watched a single EXE block performed by the experimenter. In the observation condition, subjects were asked to observe a sequential self-paced finger-tapping video with the intention of repeating it. The movement was performed by two actors (one male and one female) and consisted in the tapping of the right thumb against the tips of the other four right fingers
alternating the sequences fore-middle-ring-little finger and the other way at a rate of 1.5 sequences every 5 seconds. In FIG.1 a frame of the stimulus video is shown in which the hand location and orientation can be appreciated. After the end of the video, a red cross on a black screen was shown for five seconds (rest period - REST) to the participants. When the red cross turned into green, subjects performed the self-paced tapping. The experimenter checked that the subject did not move the fingers (in the REST and OBS conditions) and the head through recording of EMG signals (see below).

Each OBS, REST and EXE condition lasted 5 s. The OBS and EXE conditions, each followed by REST, were alternated in a fixed sequence, i.e. OBS-REST-EXE-REST (FIG. 1). The sequence OBS-REST-EXE-REST was continuously repeated 24 times (total duration 8 min). The number of observation and execution blocks was balanced (24 trials for each condition) within a session lasting 8 min. Two consecutive sessions (SES1 and SES2) were recorded for each subject.

The stimuli were implemented by an in-house software, based on MATLAB (The MathWorks Inc., Natick, MA, USA) using Cogent 2000 (developed at FIL and ICN, UCL, London, UK) and Cogent Graphics (developed by John Romaya at the LON, Wellcome Department of Imaging Neuroscience, UCL, London, UK).

MEG data were recorded by means of a multi-channel MEG system (ATB, Pescara, Italy), consisting of 153 dc-SQUID integrated magnetometers placed over a whole head helmet surface and spaced about 3.2 cm (Della Penna, 2000). The MEG system was located inside a 4-layer magnetically shielded room, providing a magnetic shielding suitable to allow magnetometric recordings. Stimuli were delivered to the subject seated in the magnetic shielded room through an optical system and a back-projection screen. The participants were asked to avoid blinking by fixing their attention on a red cross projected during the rest, on the center of the screen during OBS and on a green cross during EXE. To account for possible eye movements and other
electromyographic artifacts, the electrooculographic (EOG) signal was recorded simultaneously with MEG signals through non-magnetic leads positioned close to the subject’s eyes. Additional pairs of electrodes were placed over the subject’s chest and right forearm, thus allowing the simultaneous recording of electrocardiogram (ECG) and electromyogram (EMG). The observation and execution trials were triggered respectively by a photo-resistive diode (sensitive to the screen colour change) whose output was recorded together with all the other MEG and electrical signals, and by electromyographic signals. Hardware recording parameters were 1025 Hz sampling rate and 0.16–250 Hz band-pass filtering. To determine the position of the subject head with respect to the sensors, the magnetic field generated by five coils placed on the scalp was recorded before and after each measurement run. A coordinate system was defined by digitizing anatomical landmarks on the subject head by the 3D digitizer 3Space Fastrak (Polhemus, Colchester, Vermont, USA). In order to provide the anatomical reference for the functional MEG data, a high-resolution structural volume was acquired with an 1.5 T scanner Magnetom Vision (Siemens, Muenchen, Germany) via a 3D MPRAGE sequence (TR = 9.7 s, echo time TE = 4 ms, alpha = 12°, inversion time = 1200 ms, voxel size = 1x1x1.25 mm³).

2.2 MEG data pre-processing

MEG recordings were digitally filtered in the band 1-80 Hz by means of a Chebychev II-type filter (40 dB attenuation with forward and backward filtering to obtain zero-phase distortion) and down-sampled to 205 Hz. To remove artifactual components from the MEG signal, Independent Component Analysis (ICA) was applied by means of the FastICA algorithm with a deflation approach (Hyvarinen, 1999; Hyvarinen and Oja, 2000).

The ICA was repeated with different initial conditions, each iteration producing a set of temporal ICs with related sensor maps. For each iteration, an automated IC classification was performed to remove the contribution of non-cerebral ICs related to cardiac, ocular and
environmental noise disturbances (Mantini et al., 2011). Cardiac, muscular and ocular components were detected by correlating the IC time courses and power time courses with the simultaneously acquired ECG, EMG and EOG signals; environmental noise was classified on the basis of its spectral characteristics, by fitting an 1/f function to the IC power spectrum density (Barbati et al., 2004).

The iteration corresponding to the largest number of ICs with the lowest artefact residual was selected for further analysis. Only non-artefact independent components (ICs) were retained for further analysis. To project the channel signals into the source space, approaches based on extended source models such as minimum-norm estimates, low-resolution tomographies, and beam-forming methods (Brookes et al., 2007; Hamalainen and Ilmoniemi, 1994; Pascual-Marqui, 2002) could be applied on the raw data after removing the artefact components. However, we preferred to use an approach already applied to the study of brain interactions at rest (de Pasquale et al., 2010; de Pasquale et al., 2012; Mantini et al., 2011), briefly described in the following.

ICs were classified into brain and non-brain components, according to their temporal and spectral contents. Specifically, in addition to the parameters described in Mantini et al. (2011) (such as the correlation of IC time course, power time course and power spectrum density with ECG/EOG reference channels, time kurtosis, goodness of fit with 1/f trend on the power spectrum density and flatness of power spectrum density), we considered also the power modulation with respect to its baseline before the trigger onset, estimated in the alpha (8–12 Hz) and beta (13–25 Hz) bands. If the relative power modulation was larger than a threshold (15% in our case, as obtained from data collected from previous experiments), then the IC was retained as a brain IC.

The brain IC channel maps (corresponding to weight distributions over channels for each IC) were projected into the source space by means of a weighted minimum-norm least square (wMNLS) approach implemented in Curry 6.0 software (Neuroscan, Hamburg, Germany). The structural
image of the subject’s head was imported and anatomical landmarks were defined on it to build a realistic BEM model of the volume conductor (Hamalainen and Ilmoniemi, 1994; Wang et al., 1992). After the wMNLS localization on a regular grid (voxel side 4 mm), each source map was transformed in a common MNI 152 space for spatial comparison across subjects. Finally, activity in each voxel \( q_i(t) = [q_{ix}(t), q_{iy}(t), q_{iz}(t)] \) was estimated by linearly combining the IC time courses using the source maps as weights (de Pasquale et al., 2010; Mantini et al., 2011).

### 2.3 Time-frequency analysis

The involvement of brain regions during the action observation (OBS) and execution (EXE) task was quantified by voxel-wise t-scored Event Related Desynchronization (ERD). The ERD reflects the active cortical processing which locally reduces synchrony of the oscillatory signals, thus reducing the resulting oscillatory power (Pfurtscheller and Lopes da Silva, 1999). Interestingly, modulation of oscillatory power has been linked to event-related potentials/fields through asymmetrical modulation of peaks of oscillations (Mazaheri and Jensen, 2008; Nikulin et al., 2007).

For each condition, subject, and voxel the power density modulation following the trigger onset was estimated through the source-space ERD-gram (Della Penna et al., 2004). This was computed on the global spectrogram \( p_j(\nu,t) \) at voxel \( j \) obtained as the sum of the spectrograms of the three activity components

\[
p_j(\nu,t) = p_{jx}(\nu,t) + p_{jy}(\nu,t) + p_{jz}(\nu,t)
\]

The spectrograms were computed using a 256 points window width (corresponding to time windows of 1280 ms, with a frequency bin of 0.78 Hz), Hamming window, and 92% overlap (corresponding to 100 ms time step).

Total spectrograms were computed for every OBS or EXE trial, in a window [-1.5, 4.3]s centered on the trigger onset, and were averaged across trials. Eventually, the ERD-gram, that is
the percentage variation of power with respect to a baseline, was estimated in the same time window in a frequency band [5 40] Hz according to the following formula:

\[
ERD_{gram_j}(\nu,t) = 100 \cdot \frac{p_j(\nu,t) - base_j(\nu)}{base_j(\nu)}
\]

in which, base(\nu), defined as the pre-stimulus power level, is the average of p(\nu,t) when \( t \in [-1.5 \text{ } - 0.5] s \) (Della Penna et al., 2004; Pfurtscheller and Lopes da Silva, 1999).

2.4 ERD maps

For each subject and condition, ERD spatial maps at the individual alpha and beta bands were obtained by averaging ERD-grams across frequencies in these rhythmical bands and across time in the [-1.5, 4.3]s window. Individual alpha and beta bands were estimated from the power spectrum densities of the ICs. The mean across the ICs time courses of the frequencies corresponding to the individual alpha peak (IAF) was used to determine the individual alpha band as IAF ± 2Hz (Klimesch et al., 1998). The mean and standard deviation across subjects of the IAF was 10.0 ± 0.7 Hz. Eventually, the individual beta band was defined from the upper limit of the alpha band to the upper corner of beta peak. The average across subjects of the beta peak was 19 ± 2 Hz, the lower beta limit was 15 ± 2 Hz and the upper one was 24 ± 2 Hz.

To obtain group-level maps, for each frequency band and condition, a random effect analysis was performed at every voxel j by means of the statistic \( t_j = \mu_j / \sigma_j \) in which \( \mu_j \) and \( \sigma_j \) are the mean and standard deviation across subjects (null hypothesis \( H_0 \): \( \mu_j = 0 \); False Discovery Rate correction for multiple comparisons) (Genovese et al., 2002). The two individual sessions were first averaged so that each subject contributed once in the random effect analysis. To identify regions involved in both observation and execution, masked conjunction maps (AND-ERD maps) were obtained as follows. For each frequency band and condition, a binary mask was built with voxels with ERD values above the related statistical threshold. At each frequency these masks were then
multiplied across conditions (logic AND operation) and this global mask was eventually multiplied by the average of the OBS and EXE ERD maps.

On these AND-ERD maps, maximally active nodes were identified as centroids of local minima, comprised in regions extracted by thresholding the ERD maps at \( p < 2\times10^{-5} \). A global set of nodes was obtained by merging the sets of maximally active nodes obtained in alpha and/or beta frequency band.

2.5 Analysis of spectral and temporal dynamics

Individual ERD-grams of the nodes selected were inspected within the individual alpha and beta bands and for each condition to obtain the most reactive frequencies (0.78 Hz resolution) corresponding to the largest ERD troughs observed in the [0 1]s post trigger time window (see FIG.S1).

In particular, three parameters were extracted from the ERD-grams separately for the individual alpha and beta bands: the most reactive frequency, the ERD latency and the largest ERD trough amplitude. For each band, these parameters were then used as input in further statistical analyses to investigate the modulation, the reacting rhythm and the processing sequence of the involved areas during OBS and EXE.

Specifically, a two-way ANOVA (Nodes x Condition) was applied to the reactive frequencies and to the peak ERD values to evaluate possible differences of band specific rhythmical activity over nodes and across conditions. The sequence of occurrence of the involved nodes was analyzed using a one-way ANOVA with Nodes as factor, separately for each condition. Duncan test was used for post-hoc comparisons on main effects and significant interactions. Here, subjective latencies were estimated with respect to the latency of peak M1 activity in each condition instead of considering their absolute values, to account for individual variability when executing the self-paced finger-tapping or when observing the same task. Additionally for each node and band, the
distribution of latencies across subjects was used for comparison with M1. A significance level of 0.05 was assumed.

2.6 Control analyses

The following analyses were run to validate the results obtained in the main experiment:

(i) to control whether the order in which the stimuli were presented affects our results we acquired additional data on a subset of participants (7 subjects) after eight months from the previous records. These were scanned when performing the same tasks described above with all the EXE blocks (24) presented in the first half of the sequence, whereas the OBS blocks (24) were presented in the second half. As in the main paradigm, each block was followed by REST.

Individual and group-level ERD maps for each frequency band (alpha and beta) and condition (EXE and OBS) were computed on MEG data. We adopted the same methodological approach used in the main experiment to generate the AND-ERD final maps. Then, to quantify the robustness of the main results, the Dice similarity coefficient (D) between AND-ERD maps for the two experimental paradigms was computed in alpha and beta bands (Dice, 1945). The Dice similarity coefficient between two samples x and y is defined as: 

\[ D = \frac{2|x \cap y|}{|x| + |y|}. \]

(ii) to control the differential effect of practice and habituation on the activation due to the repetitive motor task, the data of the first session (SES1) were split into three sub-epochs (1st, 2nd and 3rd tertile). The power of the baseline period (computed during the rest time intervals, 1.5 s before the EXE onsets) of the left and right motor regions (M1) related to the EXE blocks in the first tertile and last tertile were compared by paired two-tailed t-test in both frequencies of interest (alpha and beta). The same analysis was applied on the peak ERD values related to the first and last tertile;

(iii) a three-way repeated-measure ANOVA on reactive frequencies with condition (OBS and EXE), nodes (M1, vPM, PMd and S1), and hemisphere (left LH and right RH) as factors was performed to
check the spatial specificity of the frequency slow down effects in the beta band. For this analysis, we selected only the homologous nodes in the right hemisphere which showed an ERD above statistical threshold during EXE.

3 RESULTS:

3.1 Cortical recruitment during OBS and EXE conditions

Group level t-scored ERD maps showed specific patterns of alpha and beta modulation during both conditions, as shown in FIG.2. In particular, left parieto-frontal regions (contralateral to the hand performing the tapping) were recruited in both alpha and beta bands for the OBS [alpha t <-4.1 FDR corrected, p<.001; beta t <-4.2 FDR corrected, p<.001] (see FIG.2A) and EXE [alpha and beta t <-4.7 FDR corrected, p<.001] (see FIG.2B) conditions. In the right hemisphere, we observed a significant ERD over the occipital cortex only during OBS condition (FIG.2A) and over the sensorimotor cortex only during EXE (FIG. 2B). Now, we extracted the common areas recruited during OBS and EXE conditions through a logical AND operation (see 2.4). For the alpha and beta bands, the action observation and execution showed overlapping ERD patterns in the left hemisphere suggesting the recruitment of a similar network in the two tasks, as revealed by the related AND-ERD maps (FIG. 2C). No common regions were found in the right (ipsilateral) hemisphere. A set of voxels corresponding to centroids of local minima was extracted for alpha and beta rhythms from the AND-ERD maps (Insert Supplementary Table S1 here and FIG.S2).

Expanding existing fMRI literature on activation of cortical areas during OBS and EXE (Buccino et al., 2004; Gazzola and Keysers, 2009; Grezes et al., 2003), we associated alpha and beta rhythms modulation following OBS and EXE to a broad cortical network, compatible with the putative mirror system, i.e. ventral premotor area (vPM), the inferior parietal lobule (IPL) (FIG.2C and S2) and the inferior frontal gyrus (IFG), but also additional cortical regions in both frequency bands.
Specifically, the alpha AND-ERD map showed a large ERD trough possibly in the left middle frontal gyrus (MFG), the primary somatosensory region (S1), the superior parietal lobule (SPL), the precuneus (PrC) and the angular gyrus (AG). In the beta AND-ERD map we found local troughs over the primary motor cortex (M1), the dorsal premotor cortex (dPM) and the intraparietal sulcus (IPS) (all \( p<10^{-4} \); FIG.2C, S2 and Insert Supplementary Table S1 here). To exclude the possibility that these findings were induced by a build-up effect due to fact the OBS blocks always preceded EXE blocks in the sequence, we performed a control experiment adopting a different order of stimulation (FIG.S3). The AND-ERD maps (FIG.3) and the spatial correlation index support the hypothesis that our findings are not influenced by the sequence of stimuli as revealed by the Dice similarity coefficient \( (D) \) on the t-scored ERD maps obtained for the two sequences (alpha \( d=0.50 \); beta \( d=0.72 \)). In particular, when this coefficient was computed exclusively on the left hemisphere the results slightly improved, namely \( d=0.60 \) in alpha and \( d=0.73 \) in beta.

Moreover, our results cannot be ascribed to potential practice or habituation effects due to extensive repetition of the motor task during the recordings (see Supplementary FIG.S4), because we did not observe any significant change of the power in the baseline and of the peak ERD values over time. It can be noted that the tertile analysis described in section 2.6 represents also an important control on the level activity (in the alpha and the beta band, respectively) at rest. In fact, the absence of significant differences between the 1st and 3rd tertile supports the hypothesis of uniform activity during the different rest periods.

### 3.2 Voxel-wise analysis of rhythmical activity

The rhythmical activity of the voxels identified from the AND-ERD maps (Insert Supplementary Table S1 here) showed a specific spectral content and temporal dynamics as revealed by the following three parameters: the most reactive frequency, the ERD peak latency and the ERD peak value (see FIG.S1). The spectral content of rhythmical activity in the beta band
was differently modulated for EXE and OBS conditions, with a general slow-down during OBS with respect to EXE, whereas the alpha frequency was less affected by condition. A typical time-frequency pattern is shown in FIG.4A for a representative subject in node (M1), where the ERD during EXE (left panel) and OBS (right panel) are different over time. Typically, the ERD starts before the trigger onset (obtained from the subject’s EMG) during EXE, consistently with a the computation of a voluntary act (Buzsaki, 2006; Pfurtscheller and Lopes da Silva, 1999). The dissociation of rhythmical responses is also revealed at the group level by a two-way (Node x Condition) analysis of variance (ANOVA) on the reactive frequencies (FIG.4B). Specifically, the beta rhythm exhibited a general slow-down of the most reactive frequency during OBS (dashed line, FIG.4B, right) compared to EXE (solid line), as demonstrated by the main effect Condition (F(10,110) = 13.4, p<.004). In particular, this downward shift for beta was statistically significant in IFG, vPM, dPM, M1 (**=p<.001) and also in IPL and AG (*=p<.05), as suggested by a statistically significant interaction (F(10,110)=1.9, p<.05). Conversely, similar rhythmical dynamics were observed in the alpha band during EXE and OBS conditions, as suggested by the lack of a significant effect of Condition (F(1,11) = 1.2, p<.29) on the most reactive frequencies (FIG.4B left), except for dPM, S1 and SPL (*=p<.05, interaction effect F(10,110) = 1.97, p<.043), which showed a slow-down of the reactive frequency. Notably, this effect in the beta band was specific for left hemisphere nodes (controlateral to the moving hand) (**=p<.05), as revealed by a control analysis on a subset of homologous somatomotor nodes in both hemispheres (M1, dPM, vPM and S1) (see Supplementary FIG.S5).

To test the hypothesis that the processing sequence follows the internal models criteria, we analyzed the timing of ERD occurrence to provide the sequence of involvement of the regions obtained from the AND-ERD maps. This temporal information may also elucidate the observed modulation of the spectral content of the beta rhythm during OBS with respect to EXE. In what
follows, each node latency will be re-aligned to M1 and it will be tested against it using the node latency distribution across subjects. Moreover, to group similar node latencies an one-way ANOVA will performed with node as factor. We observed for EXE a quite similar sequential occurrence in the alpha (FIG.5A) and beta bands (FIG.5B) as confirmed by the ANOVA results on ERD peak latency across nodes (F(9)=11.6, p<10^{-7} for alpha; F(9)=15, p<10^{-7} for beta) (FIG.5C). In particular, the ERD in left prefrontal regions including vPM and IFG (cyan and blue cluster in alpha and beta, respectively) peaked earlier than in the other regions (p <.05, Duncan post hoc test). In alpha, the cyan cluster included also M1 (see Tab.1 for relative latency and statistical significance). In beta, the blue cluster included also dPM and peaked from 130 ms to 105 ms before M1 (see Tab.1). This early engagement suggests that these areas might be involved in the transformation of the go signal into motor commands. The subsequent processing step (green cluster) involved mainly dPM (at 45 ms after M1) for alpha, the sensorimotor regions (S1 at about 42 ms for alpha, M1 and S1 simultaneously for beta) through sensory re-afferences and the SPL (about 60 ms) significantly before (p <.05, Duncan post-hoc) than the other parietal regions (orange cluster - IPL, PrC and IPS from about 130ms to about 180ms, including AG for beta). Parietal regions including IPL have been reported to be early involved in higher order motor functions, such as movement initiation, as revealed by studies analyzing the preparation potential (BP - Bereitschaftspotential) (Ball et al., 1999). Here, since the analysis is based on ERD, we are sensitive to mechanisms different from the BP (Shibasaki and Hallett, 2006), revealing further aspect of the execution of a motor action. We propose that the later recruitment of parietal regions could suggest the generation of a sensory representation of the body action or the prediction of what the intended action would feel or look (Gazzola and Keysers, 2009; Miall, 2003; Wolpert and Ghahramani, 2000). Finally, ERD peaked possibly over MFG (and AG for alpha, red cluster - p<.05, latency about 240 ms). Overall, this
anterior-posterior pattern of engagement is consistent with the predictive nature of the forward model (Gazzola and Keysers, 2009; Wolpert and Ghahramani, 2000).

Compared to the execution task, a different temporal dynamics between the alpha (FIG.5D) and beta bands (FIG.5E) occurred during the OBS condition, suggesting a functional dissociation between the two rhythms. Specifically, in the alpha band, the ERD peak sequence was reversed with respect to the EXE condition, showing a posterior-anterior information flow (F(9)=5.9, p<10\(^{-6}\), FIG. 5D and 5F). After the early engagement of the region including AG (blue cluster - latency = ~ - 150ms, p<.005), the sequence included parietal regions (yellow cluster - SPL and IPS, p<0.033) significantly before (60 ms) M1 (p <.03, see Tab.1), presumably for high order visual processes.

Next, the ERD peaked in frontal regions including IFG, MFG, vPM and dPM, and in parietal regions including S1, IPL and PrC, all of them showing no significant difference in latency with respect to M1 (red cluster). In summary, we suggest that this posterior-anterior information flow in the alpha band might represent the visuo-motor transformation of the observed movement into a suitable motor program or command. Thus, the sequence of alpha might be considered as the neural signature of the implementation of the inverse model, as hypothesized by Gazzola and coll. (2009).

Importantly, the sequence of ERD occurrence for the beta band (F(9)=2.5, p<.012) largely differed from the one observed for the alpha band (FIG.5E and 5F). A simultaneous early ERD occurred in posterior parietal (cyan cluster including S1, SPL, IPS, PrC, AG and IPL) and frontal (including IFG, dPM and MFG) regions, followed by the region including vPM (red cluster - p<.01 Duncan post-hoc with respect to SPL and IPS). In addition, most of the nodes (except vPM) were recruited significantly before M1 (latency = ~160-40ms, p<.03 in the worst case), whereas in the alpha band, the latencies of the majority of nodes, except AG, SPL and IPS were close to M1.

The dissociation between the alpha and beta rhythms during action observation was bolstered by an ANOVA on the ERD peak values in the two conditions, conducted separately for
each frequency (FIG.6). In the alpha band, most nodes exhibited a different modulation during OBS vs EXE, (condition factor tending to be significant, signalling the trend of the ERD values in all nodes to be smaller during the OBS with respect to EXE (F(1,11)=4.32, p<0.06); significant interaction (Node x Condition) (F(10,110)=5.35, p<2*10^-6). Conversely, the ERD values in the beta band were similar for the two conditions across nodes, excluding AG (p<.05), and showed a similar activation pattern (significant interaction Node x Condition- F(10,110)=2.38, p<0.014). Taken together, our data suggest that alpha and beta bands represent the neural correlate of different and specific aspects of action observation and execution.

4 DISCUSSION

In this MEG study we report on the electrophysiological correlates and spectro-temporal dynamics of action observation and execution. Whereas previous MEG studies focused on signals at the channel level (Babiloni et al., 2002; Cochin et al., 1999; Kilner et al., 2006, 2009; Muthukumaraswamy and Johnson, 2004; Muthukumaraswamy et al., 2004; Streltsova et al., 2010), our results were reported in the source space and revealed specific spatial and temporal features underlying the execution and observation of a motor task. Specifically, we have shown that action observation and execution share a common set of areas exhibiting the µ rhythm. These regions include several parieto-frontal regions which may be part of an action observation network (AON) (Avenanti et al., 2012; Buccino et al., 2001; Gazzola and Keysers, 2009). Importantly, our time-frequency analyses on the rhythmical activity of this network revealed a dissociation of the alpha and beta band within the µ rhythm.

4.1 Methodological Remarks
To investigate the dynamics of MEG rhythms during movement execution, two possible paradigms can be adopted: an event-related one (with a baseline preceding each event, as in Babiloni et al., 2002) or a block (task-related) design (see Hummel et al., 2002). Here, we focused on the latter paradigm and we selected the finger tapping as the type of movement. Two types of aimless movement can be differentiated: brisk vs slow. In brisk movements, the motor commands are prepared as a unity and then sent off in one package, whereas slow movements, like the finger tapping, involve sustained control during their execution. An interesting discussion can be found in Desmedt (1983) and Stancak and Pfurtscheller (1996) where the μ rhythm changes induced by brisk and slow movements are compared. In particular, it has been reported that the desynchronization of this rhythm does not differentiate between brisk and slow movements (Stancak and Pfurtscheller, 1996). Here we adopted a slow movement since it can be more easily controlled during the experiment than a brisk one, and allows to minimize the variability in movement execution across different task periods of the same subject, e.g. in terms of frequency content. Eventually, the choice of a finger tapping movement necessarily implies a block design paradigm.

As far as it regards our methodology, here we adopted an approach based on ICA followed by a weighted minimum norm estimate (wMNE) localization (Mantini et al., 2011), which has been designed to study large scale connectivity at rest (Betti et al., 2013; de Pasquale et al., 2010; de Pasquale et al., 2012; Marzetti et al., 2013). Here, we discuss the limitations of this approach, mainly related to the spatial dispersion of identified active areas. Several approaches assuming extended source models have been adopted to estimate brain activity at source level (Brookes et al., 2007; Dale et al., 2000; Hamalainen and Ilmoniemi, 1994; Pascual-Marqui, 2002) and an interesting review of their pros and cons can be found in (Hauk et al., 2011; Zhang et al., 2013 for a comparison among methods). In general, the selection of the inverse approach is usually driven by
the specific requirements of the study. Here, we expect a set of highly coupled distinct sources active within a relatively short time interval. A meta-analysis of the fMRI literature (see caption of Table S1 for a list of related references) suggests that some of these sources are relatively close, in the order of few centimeters. In this respect, beamforming approaches, which are more focused than minimum norm estimates (Sekihara et al., 2005) might be eligible to localize these sources. However, their performance on correlated sources is sub-optimal. Conversely, minimum-norm based operators present an opposite behaviour: i.e. less focused but no limitation due to the presence of correlated sources. Now, since we expect a network of possibly correlated sources to be involved during processing of OBS and EXE conditions, we selected a weighted MNE compensated for different source depths (wMNE- Fuchs et al., 1999) to project the IC sensor maps into the source space, with a consequent improvement of the spatial dispersion with respect to the standard MNE approach.

To minimize spatial dispersion, in our approach we apply an ICA to MEG data not only to identify and reject artefacts components, but also to separate brain activity into independent components that feature a more sparse source characteristics (Tsai et al., 2006). In fact, we first apply wMNE to single ICs, and then we linearly recombine the source spaces, which has been proven to be a more effective strategy then the reverse order (linear recombination followed by wMNE) (Mantini et al., 2011). A possible reason might be that source estimates of single or double sources could be more reliable than multiple simultaneously active sources (Darvas et al., 2004; Wagner et al., 2004; Wipf et al., 2010). Additionally, we adopted an individual regularization parameter in the wMNE to improve the localization outcomes.

In a previous work we have discussed the influence of the spatial distance on the temporal correlation between neighbouring voxels (de Pasquale et al., 2010; de Pasquale et al., 2012). We showed that for neighbouring voxels distant at least 3.2 cm the relative dependence is highly
reduced. This corresponds to assume a spatial dispersion of 1.6 cm, which is consistent with the literature (Hauk et al., 2011). Now, in this study we discuss regions, involved in OBS and EXE, which are closer than this distance. Such regions were selected as local troughs of AND-ERD maps identified by statistical test. In particular, the regions M1/dPM and IPL/IPS were closer than the minimum distance, and were extracted in the beta band (a trough in IPL was detected also in the alpha band), as shown in FIG.S2. In alpha (see FIG.S2), troughs were detected also possibly in other areas closer than the minimum distance, such as S1, SPL and AG. However, if the detected activations were only due to a single source spreading in the nearby locations, the dynamics estimated by reactive frequencies and ERD latencies would be very similar irrespective of the frequency band. However, this does not occur when inspecting the reactive frequencies in the beta and alpha bands of M1/dPM, IPL/IPS and AG/SPL (see FIG. 4B). Additionally, the ERD latencies of dPM and M1 were always significantly different except for alpha OBS, and the latencies of IPS vs IPL and of S1 vs SPL differ during alpha OBS. Finally, the latencies of SPL and AG are always different except for beta OBS (see FIG.5C and 5F). Notably, when analyzing other nodes which were selected in different bands and are closer than 3.2 cm, such as IPL (close to M1, S1, AG and SPL), IPS (close to AG, SPL, PrC) and M1 vs S1, we obtained distinct frequency changes and different latencies at least in one condition/band. In summary, although we acknowledge that the effect of the spatial dispersion is not negligible for some neighbouring nodes, our main finding on band-specific, different dynamics observed in the two conditions seem to be robust against this effect.

4.2 Differences and commonalities of brain activity during EXE and OBS

The modulation of oscillatory power (ERD/ERS) is linked to information processing in the involved cortical areas and has been widely used to study motor cortex functioning (Donner et al.,
We found significant ERD troughs in several areas approximately over the dorsal premotor cortex (dPM), middle frontal gyrus (MFG), superior parietal lobule (SPL), angular gyrus (AG), precuneus (PrC), primary motor (M1) and somatosensory (S1) cortices (Fig. 2) (Buccino et al., 2001; Buccino et al., 2004; Rizzolatti and Sinigaglia, 2010) but also in the ventral part of the precentral gyrus (vPM), the rostral part of the inferior parietal lobule (IPL) and the intraparietal sulcus (IPS) that are included in the putative mirror system (pMNS) (Rizzolatti and Craighero, 2004). Thus, our data is compatible with the existing fMRI literature suggesting that several common parieto-frontal areas are involved in action observation and execution (Buccino et al., 2004; Gazzola and Keysers, 2009; Grezes et al., 2003).

Furthermore, we observed a significant ERD over bilateral sensorimotor regions during action execution, as previous reported (Liepert et al., 2001; Pfurtscheller and Lopes da Silva, 1999; Salmelin et al., 1995), but not during the action observation. Left lateralization for EXE only is not unexpected since all our stimuli contain right handed actions and the participants had to perform the same movements with their right hand. This is in line with the literature (Aziz-Zadeh et al., 2006; Aziz-Zadeh et al., 2002; Cabinio et al., 2010) in which it is reported the involvement of the controlateral hemisphere to the hand movement (but see Rizzolatti and Craighero, 2004) for the involvement of bilateral sensorimotor regions during the hand action observation.

### 4.3 Different spectral signatures and dynamics of EXE and OBS

Differently from previous MEG/EEG studies, typically recording consistent alpha and beta modulations on action observation and execution (Babiloni et al., 2002; Caetano et al., 2007; Cochin et al., 1998; Kilner et al., 2009; Muthukumaraswamy and Singh, 2008; Orgs et al., 2008), for
the first time to our knowledge, we observed a dissociation between alpha and beta oscillations within the \( \mu \) rhythm during action observation with respect to execution.

The \( \mu \) rhythm consist of two components with a nearly harmonic relationship. The two components, 10 Hz and 20 Hz, can occur either separately or simultaneously, suggesting that the beta component (20 Hz) activity can be phase-locked to the alpha component (10 Hz) when starting from the same neural generator or be completely independent in some other moments (Hari et al., 1997 for a review). Notably, the beta oscillations appear to be at a frequency which is twice the alpha components, thus producing the arch-shaped \( \mu \) rhythm. This is in line with a concomitant modulation of the alpha and beta bands recorded over somato-sensory regions during both EXE and OBS (Babiloni et al., 1999; Hari et al., 1998; Hari et al., 2000; Hari et al., 1997; Pfurtscheller, 1989; Pineda et al., 2000). Nevertheless, it is commonly accepted that the alpha and beta bands differ in terms of their functional role. On one hand, the alpha band activity has been related to several processes, spanning from the disengagement of task irrelevant brain areas to memory, attention, and consciousness (Jensen et al., 2002; Palva et al., 2005; Palva and Palva, 2007; Pfurtscheller, 2003). On the other hand, the beta band oscillations have been linked to motor functions such as steady contractions, voluntary movements and motor imagery (de Lange et al., 2008; Sanes and Donoghue, 1993). Recently, Engel and Fries (2010), based on previous work by (Baker, 2007; Gilbertson et al., 2005), proposed that beta band oscillations is not purely an “idling” rhythm, but bolster an active process that promotes the ongoing motor set and other processes beyond the domain of motor control.

Action execution and action observation implement a translation of action into perception and vice versa. These processes involve alpha and beta generators in the somatomotor domain (\( \mu \) rhythm), but also in other domains (visual, motor control, attention, etc.). These domains typically exhibit synchronized and desynchronized activity in a locally independent manner. However,
during the translation of “doing” into “seeing” or viceversa, they are globally engaged (Pineda, 2005).

In our study, we show that when translating “doing” into “seeing” alpha and beta seem to reflect similar processes, in all the domains (including the μ rhythm). Conversely, when translating “seeing” into “doing”, we found a dissociation between the alpha and beta bands in all domains, suggesting independent functions of these two bands. These different dynamics reveal that these two bands might pursue different functions.

This dissociation between alpha and beta might be linked to the observed different temporal dynamics and a slow-down of beta oscillations compared to alpha. Specifically, we showed that action execution recruits regions of the AON in an anterior-posterior temporal sequence (Nishitani and Hari, 2000) in both alpha and beta bands (see FIG.5A, 5B, 5C). The fronto-parietal sequence of occurrence is in accordance with the forward model hypothesis arguing that an efference copy of motor command is sent towards parietal cortices during action execution to predict sensory and proprioceptive consequences of the intended action (Wolpert and Ghahramani, 2000). Specifically, the transformation of the go signal into motor commands could explain the recruitment of the frontal regions (dPM, vPM and IFG) before (beta) or simultaneously (alpha) to M1 latency (Hari et al., 2000; Nishitani and Hari, 2000). Furthermore, the latencies of these regions did not differ significantly, possibly due to the high number of direct connections between M1 and S1 (Matelli et al., 1986) and the slow timing of the spectral power changes. In addition, posterior parietal regions (Prc, IPL, SPL and AG) are recruited after the beginning of the movement (M1 as reference), thus suggesting not only the generation of sensory representation of the action, but also the involvement of other attentional and computational processes that are common to the action observation. Conversely, during action observation, we observed a roughly posterior-anterior sequence in the alpha band (FIG.5D) and a simultaneous fronto-parietal
occurrence in beta band (FIG.5E). The reversed posterior-anterior sequence of involvement observed in the alpha band during action observation with respect to execution is consistent with the generation of an inverse model, which allows us to infer the motor program that could have caused the sensory input (Gazzola and Keysers, 2009; Wolpert and Ghahramani, 2000). In particular, it has been proposed that observing others’ actions engages the sensorimotor resources of the onlooker via a simulation mechanism. Such mechanism prompts the inverse model in order to translate other’s action into a motor command, thus allowing the representation of the observed movement in a motor format.

Accordingly, posterior parietal regions (AG, SPL and PrC) are recruited before M1, probably depending on high order visual processes. Furthermore, S1 which mediates the sensory (proprioceptive and tactile) aspects of the observed action, peaked simultaneously to M1. Similarly, no difference in latencies was observed between M1 and frontal regions that are involved in the transformation of the sensory representation of the action in motor command. On the other hand, in the beta band all nodes of interest (excluding vPM) are recruited simultaneously and significantly before of M1. This widespread pattern of engagement cannot be ascribed to the above model and is linked with a downshift of the reactive frequencies during OBS compared to EXE (see FIG.4A e B). In fact, it has been proposed that the spectral content of the oscillations is influenced by the spatial scales of the engaged neuronal pool, i.e. fast oscillations are confined to a small neuronal space, whereas slow oscillations recruit very large networks (Buzsaki and Draguhn, 2004; Steriade, 2001). This could relate the spatial spread of the engagement with the downshift towards slower frequencies.

4.4 Role of beta rhythm during EXE and OBS
While the occurrence within the alpha band fits the internal models hypothesis, the interpretation of the beta band activity is challenging and requires further investigations. In fact, beta activity is often reduced during motor control, but it has also been assigned a more cognitive role related to the maintenance of the sensorimotor or cognitive set (Engel and Fries, 2010; Jenkinson and Brown, 2011). We note that such cognitive processing may take place both during EXE and OBS. In EXE, as previously discussed, the observed suppression in a specific sequence of occurrence (linked to the forward model) might represent the necessary cognitive steps to transform action into perception. On the other hand, in OBS, we can only speculate on the functional role of the beta band in the light of recent models of the AON that suggest that activity in these regions is predictive (Avenanti et al., 2012; Press et al., 2011; Schippers and Keysers, 2010; Schutz-Bosbach and Prinz, 2007; Urgesi et al., 2010; Wilson and Knoblich, 2005). In particular, action perception might rely on forward internal models that predict the future course of others motor acts. In this vein, AON is organized as a dynamic control system where information can flow not only from visual to visuomotor nodes but also in the opposite direction. During action observation, forward and inverse model could work together. The observed action is internally simulated through the inverse model that generates a suitable motor command. The forward model can be used to predict the sensory consequences of the internally simulated action and then to assess the accuracy of this prediction by comparing it with the actual consequences (Avenanti et al., 2012).

Our results show that beta band activity does not reflect the postero-anterior processing sequence as hypothesized in the inverse model. We suppose that the simultaneous recruitment of parieto-frontal regions we found, might reflect this active role of motor activation in which motor commands are fed back in the posterior regions to anticipate the future phases of others actions. This anticipation would determine a top-down influence on action perception to modulate and
complete the sensory information. However, further investigation with specifically designed tasks are needed to assess the predictive role of beta during action observation. Indeed, we did not find strong evidence of backward anterior-posterior processing sequence but this could be due to the adopted task. Since the presented movement (finger-tapping) is very simple and has no functional meaning, it can be easily predicted what the models are doing.

Another possible explanation of the simultaneous recruitment of the fronto-parietal nodes in beta band could be linked to the mechanism that promotes the ‘self-other’ disentangling, i.e. how the same cortical circuits engaged during both action execution and observation encode the self-other distinction (Jeannerod, 2007). Our speculation links to the review of Engel and Fries (Engel and Fries, 2010), who suggest that the beta rhythm reflects the tendency of the sensory-motor system to ‘maintain’ the status quo by means of a more efficient processing of feedbacks. Moreover, recent results showed a frequency signature of the Default Mode Network in the beta band, supporting the involvement of this rhythm in self-related processes (de Pasquale et al., 2012). Thus, the observed downshift in this frequency band might promote a change of the cognitive set necessary to implement the inverse model when observing other’s actions while the concomitant widespread involvement of this network in the beta band might represent a means to achieve this aim.

In conclusion, we observed that the µ rhythm is not a unitary phenomenon, i.e. alpha and beta oscillations likely reflect different aspects involved in action observation and execution. We propose that this differentiation might subserve different cognitive operations during action observation vs action execution. Eventually, the reported functional dissociation between alpha and beta bands may have an impact in clinical applications such as the neurological rehabilitation based on the µ-rhythm neurofeedback (Pineda et al., 2008). In fact, a lack of µ suppression has been hypothesized as an electrophysiological correlate of the putative Mirror Neuron System
(pMNS) dysfunction and it might contribute to poor imitation and social skills in children with autism spectrum disorder (ASD) (Rizzolatti et al., 2009).

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REFERENCES


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TABLES

Table 1.
Latencies of ERD troughs relative to M1 latencies.

<table>
<thead>
<tr>
<th>Nodes</th>
<th>EXE</th>
<th>OBS</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>ALPHA</td>
<td>BETA</td>
</tr>
<tr>
<td></td>
<td>Relative latency</td>
<td>p (test with respect to M1)</td>
</tr>
<tr>
<td>SPL</td>
<td>58.33</td>
<td>0.05</td>
</tr>
<tr>
<td>IPS</td>
<td>158.33</td>
<td>4*10^-5</td>
</tr>
<tr>
<td>MFG</td>
<td>258.33</td>
<td>10^-4</td>
</tr>
<tr>
<td>PrC</td>
<td>183.33</td>
<td>0.001</td>
</tr>
<tr>
<td>IFG</td>
<td>-33.33</td>
<td>0.1</td>
</tr>
<tr>
<td>dPM</td>
<td>45.83</td>
<td>0.03</td>
</tr>
<tr>
<td>AG</td>
<td>208.33</td>
<td>9*10^-4</td>
</tr>
<tr>
<td>IPL</td>
<td>133.33</td>
<td>2*10^-4</td>
</tr>
</tbody>
</table>
Note: For each condition (OBS and EXE) and frequency (alpha and beta) we report the latency (ms) of each node related to M1 assumed as reference. Statistical significance (p<0.05) was estimated through the distribution of individual latencies. Significantly different latencies are marked in red. We assumed p=0.07 to represent a tendency to significance.

<table>
<thead>
<tr>
<th></th>
<th>41.67</th>
<th>0.07</th>
<th>20.83</th>
<th>0.3</th>
<th>12.5</th>
<th>0.2</th>
<th>-37.5</th>
<th>0.07</th>
</tr>
</thead>
<tbody>
<tr>
<td>vPM</td>
<td>12.5</td>
<td>0.3</td>
<td>-129.17</td>
<td>0.001</td>
<td>12.5</td>
<td>0.3</td>
<td>-31.25</td>
<td>0.2</td>
</tr>
</tbody>
</table>

**FIGURE CAPTIONS**

**FIG. 1** Main experimental timeline.

In a block design, the participants were shown a red cross on a black screen for 5 seconds (Rest block), after which subjects were asked to observe a video showing a right-handed finger tapping movement that lasted 5 s (OBS block). At the end of the video, a rest block was presented. When the red cross turned into green the subjects had to perform the same movement observed in the video with their right hand for 5 s (EXE block).

**FIG. 2** ERD maps.

A) Group level ERD maps (voxelwise percentage power variations with respect to a baseline period, averaged over a time window after the stimulus onset) computed in the alpha (top) and beta (bottom) band for the observation (OBS) condition. The represented quantity is t-score. Only statistically significant values are shown (p<.001, FDR corrected). Recruitment of left fronto-parietal areas and bilateral occipital areas occurs in both bands.

B) Group level ERD maps for the execution (EXE) condition. The same quantities as in A) are represented. Recruitment of controlateral fronto-parietal areas and ipsilateral sensory-motor areas occurs in both bands.
C) ERD maps averaged across the OBS and EXE conditions for the alpha (top) and beta (bottom) bands computed on voxels statistically significant in both conditions (p<.001, FDR corrected, logic AND operation). No significant voxels in both conditions are obtained in the right hemisphere and occipital regions. Labels of nodes corresponding to local ERD troughs are superimposed to the AND-ERD map (white; the complete list can be found in Tab. S1 “Insert Supplementary Table S1 here”). The AND-ERD maps suggest the involvement of a broad action observation network (AON).

Specifically, vPM, IFG, IPL, dPM, M1, MFG, AG, S1, PrC, SPL, IPS are presumably recruited in both conditions.

**FIG.3** AND-ERD maps of the control experiment.

ERD maps averaged across the EXE and OBS conditions for the alpha (top panel) and beta (bottom panel) bands computed on those voxels exceeding the statistical threshold (p<.05, FDR corrected) in both conditions (logic AND operation) (7 subjects). The represented quantity is t-score. For the left hemisphere the Dice similarity coefficient between the maps of FIG.2C and FIG.3 is 60% in alpha and 73% for beta band.

**FIG.4** Spectral dynamics of alpha and beta rhythms during action observation and execution.

A) Percentage ERD time/frequency plots for the EXE (left) and OBS (right) conditions computed in the left M1 for a representative subject. In this figure the individual alpha and beta bands are respectively marked in gray and red on the frequency axis. The most reactive frequencies (corresponding to the largest ERD trough after the stimulus onset) are marked by arrows. The spectral content visibly differs between the two frequency bands: a clear slow-down of rhythmical activity is evident in the beta band between OBS and EXE (red arrows). Conversely, a tiny effect (gray arrows) is observed in the alpha band in this subject.
B) Reactive frequencies for the common areas involved during EXE (solid line) and OBS (dashed line) in the alpha (left) and beta (right) bands. Error bars indicate standard error. A dissociation of rhythmical involvement occurs between the two conditions. Specifically, while in alpha EXE and OBS elicit a similar rhythmical response, in the OBS condition a slow-down is observed in the beta band (main effect Condition in a two-way ANOVA, F(10,110)=13.4, p<.004) with respect to EXE. Specifically, Duncan post-hoc analysis reveals a significant Node x Condition interaction in the alpha (F(10,110)=1.97, p<0.043) and beta (F(10,110)=1.9, p<.05) bands. Significant nodes are marked by asterisks (* p<.05, ** p<.001).

FIG.5 ERD temporal dynamics during action execution and observation.

A) The sequence of occurrence revealed by ERD peak latencies in alpha for the nodes responding to both EXE and OBS. Each node, superimposed on the flattened cortex, is colour-coded according to its latency (see colorbar) that is computed with respect to M1 assumed as reference (M1 latency=0). Nodes are reported in ascending order (left to right) based on their latency. Contours group nodes whose latencies are not significantly different (Duncan post-hoc one-way ANOVA with Node as factor main effect F(9)=11.6, p<10^{-7}). Four different groups were identified, showing an anterior-posterior sequence of occurrence. The average latency of the last occurring group is reported.

B) The same quantities as in A) are shown in the beta band (Duncan post-hoc one-way ANOVA with Node as factor main effect F(9)=15, p<10^{-7}). The sequence of occurrence is similar to the alpha band.

C) The latency of each node, is plotted in the alpha (solid line) and beta (dashed line) bands. Error bars indicate standard errors. For both frequency bands a fronto-parietal involvement occurs during execution.
D) In the alpha band the temporal dynamics during OBS is different with respect to EXE: a posterior-anterior sequence of processing (Duncan post-hoc one-way ANOVA, F(9)=5.9, p<10^{-6}) with some nodes grouped with M1.

E) In the beta band the sequence of occurrence is different from the EXE condition and the alpha band: most of nodes in posterior parietal and frontal regions are simultaneously recruited (Duncan post-hoc one-way ANOVA, F(9)=2.5, p<.012). Moreover, they are involved significantly before M1 (see Tab.1).

F) The latency of each node is plotted in the alpha (solid line) and beta (dashed line) bands. Error bars indicate standard error. This analysis suggests that alpha and beta bands show a different dynamics supporting a functional segregation hypothesis.