

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

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12 **Abbreviated title:** Different spectral dynamics of agents vs observers

13
14 **ABSTRACT**

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

22 We associated the modulation of the alpha and beta power to a broad action observation
23 network comprising several parieto-frontal areas previously detected in fMRI studies. Of note, we
24 observed a dissociation between alpha and beta bands with a slow-down of beta oscillations

25 compared to alpha during action observation. We hypothesize that this segregation is linked to a
26 different sequence of information processing and we interpret these modulations in terms of
27 internal models (forward and inverse). In fact, these processes showed opposite temporal
28 sequences of occurrence: anterior-posterior during action (both in alpha and beta bands) and
29 roughly posterior-anterior during observation (in the alpha band). The observed differentiation
30 between alpha and beta suggests that these two bands might pursue different functions in the
31 action observation and execution processes.

32

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

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36

37 1. INTRODUCTION

38 Several studies report that our sensorimotor system is activated when we observe an
39 action performed by other people. This putative mirror-like activity in humans was found in the
40 precentral gyrus (vPM), the inferior frontal gyrus (IFG), the inferior parietal lobule (IPL), and
41 regions within the intraparietal sulcus (for a review see Rizzolatti and Sinigaglia, 2010). In addition
42 to this limited number of regions, neuroimaging studies observed a broader action observation
43 network (AON) which seems to be involved during action observation (OBS) and execution (EXE)
44 (Avenanti et al., 2012; Buccino et al., 2004; Gazzola and Keysers, 2009). A proposed theoretical
45 framework postulates that such AON implements forward and inverse internal models (Wolpert
46 and Ghahramani, 2000), which should be engaged during EXE and OBS. The internal models can
47 account both for how we link our actions to sensory consequences and how others' actions match
48 our own actions and sensations (Gazzola and Keysers, 2009; Iacoboni, 2005). It has been proposed
49 that the fronto-parietal AON has a predictive nature and according to this hypothesis, during
50 action observation the inverse and forward models are integrated to achieve a prediction of

51 others intentions and behavior based on simulation (Avenanti et al., 2012; Gazzola and Keysers,
52 2009; Press et al., 2011; Schippers and Keysers, 2010; Schutz-Bosbach and Prinz, 2007; Urgesi et
53 al., 2010; Wilson and Knoblich, 2005). Despite this hypothesis being very attractive, a clear
54 evidence of the electrophysiological correlates underlying the implementation of these models is
55 still missing.

56 The neurophysiological signature of the putative mirror-like activity, as observed through
57 magnetoencephalography (MEG) and electroencephalography (EEG) in humans, is thought to be a
58 modulation (suppression) of the μ rhythm power (Hari, 2006; Pineda, 2005). Such rhythm refers to
59 cortical oscillations in the frequency range [8-12] Hz (alpha band) and [15-25] Hz (beta band),
60 typically recorded over somato-sensory regions during both action execution and observation
61 (Babiloni et al., 1999; Hari et al., 1998; Hari et al., 2000; Hari et al., 1997; Pfurtscheller, 1989;
62 Pineda et al., 2000). It has been reported that the μ rhythm waveform consists of a mixture of
63 alpha activity and the second harmonic beta rhythm, giving rise to an arch-shaped waveform
64 (Buzsaki, 2006). The relationship between these two bands within the μ rhythm is still under
65 debate. In fact, this rhythm does not seem to reflect a unitary phenomenon (Pfurtscheller et al.,
66 1996; Pineda, 2005; Stancak and Pfurtscheller, 1995), but rather a combination of different
67 processes, potentially involved in the transformation of “seeing” into “doing”. Moreover, a
68 complete overview of the spectro-temporal dynamics within the AON is missing, since many
69 studies in the literature considered only the alpha component (Kilner et al., 2006; Marshall et al.,
70 2009; Muthukumaraswamy et al., 2004; Pineda et al., 2000; Streltsova et al., 2010), or limited their
71 attention to the amplitude modulation of the oscillatory activity (Cochin et al., 1999; Hari et al.,
72 1998; Kilner et al., 2009; Koelewijn et al., 2008; Muthukumaraswamy and Johnson, 2004; Orgs et
73 al., 2008), whereas studies on the temporal dynamics of brain activity during OBS and EXE focused
74 on the sensorimotor cortex only (Babiloni et al., 2002; Caetano et al., 2007).

75 Thus, the novelty of this MEG study consists of exploring the neural signature of action
76 observation and execution in the spatial and time-frequency domains over the whole cortex.
77 Specifically, thanks to the high MEG temporal resolution, we investigated whether the two bands
78 reflect different dynamics of action observation and execution. Moreover, we linked this dynamics
79 to the hypothesis that information is processed according to the criteria posed by internal models.

80

81 **2 MATERIALS AND METHODS:**

82 *2.1 Subjects, experimental setup and acquisition*

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

91 The experiment consisted of two conditions: the observation (OBS) and execution (EXE) of
92 an aimless slow movement. Specifically, the used movement task is a right self-paced finger-
93 tapping that is a partially pre-programmed action, proprioceptively but not visually feedback-
94 controlled. Just before starting the experiment, subjects were instructed about the paradigm and
95 they watched a single EXE block performed by the experimenter. In the observation condition,
96 subjects were asked to observe a sequential self-paced finger-tapping video with the intention of
97 repeating it. The movement was performed by two actors (one male and one female) and
98 consisted in the tapping of the right thumb against the tips of the other four right fingers

99 alternating the sequences fore-middle-ring-little finger and the other way at a rate of 1.5
100 sequences every 5 seconds. In FIG.1 a frame of the stimulus video is shown in which the hand
101 location and orientation can be appreciated. After the end of the video, a red cross on a black
102 screen was shown for five seconds (rest period - REST) to the participants. When the red cross
103 turned into green, subjects performed the self-paced tapping. The experimenter checked that the
104 subject did not move the fingers (in the REST and OBS conditions) and the head through recording
105 of EMG signals (see below).

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

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

115 MEG data were recorded by means of a multi-channel MEG system (ATB, Pescara, Italy),
116 consisting of 153 dc-SQUID integrated magnetometers placed over a whole head helmet surface
117 and spaced about 3.2 cm (Della Penna, 2000). The MEG system was located inside a 4-layer
118 magnetically shielded room, providing a magnetic shielding suitable to allow magnetometric
119 recordings. Stimuli were delivered to the subject seated in the magnetic shielded room through an
120 optical system and a back-projection screen. The participants were asked to avoid blinking by
121 fixing their attention on a red cross projected during the rest, on the center of the screen during
122 OBS and on a green cross during EXE. To account for possible eye movements and other

123 electromyographic artifacts, the electrooculographic (EOG) signal was recorded simultaneously
124 with MEG signals through non-magnetic leads positioned close to the subject's eyes. Additional
125 pairs of electrodes were placed over the subject's chest and right forearm, thus allowing the
126 simultaneous recording of electrocardiogram (ECG) and electromyogram (EMG). The observation
127 and execution trials were triggered respectively by a photo-resistive diode (sensitive to the screen
128 colour change) whose output was recorded together with all the other MEG and electrical signals,
129 and by electromyographic signals. Hardware recording parameters were 1025 Hz sampling rate
130 and 0.16–250 Hz band-pass filtering. To determine the position of the subject head with respect to
131 the sensors, the magnetic field generated by five coils placed on the scalp was recorded before
132 and after each measurement run. A coordinate system was defined by digitizing anatomical
133 landmarks on the subject head by the 3D digitizer 3Space Fastrak (Polhemus, Colchester, Vermont,
134 USA). In order to provide the anatomical reference for the functional MEG data, a high-resolution
135 structural volume was acquired with an 1.5 T scanner Magnetom Vision (Siemens, Muenchen,
136 Germany) via a 3D MPRAGE sequence (TR = 9.7 s, echo time TE = 4 ms, alpha = 12°, inversion time
137 = 1200 ms, voxel size = 1x1x1.25 mm³).

138 *2.2 MEG data pre-processing*

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

144 The ICA was repeated with different initial conditions, each iteration producing a set of
145 temporal ICs with related sensor maps. For each iteration, an automated IC classification was
146 performed to remove the contribution of non-cerebral ICs related to cardiac, ocular and

147 environmental noise disturbances (Mantini et al., 2011). Cardiac, muscular and ocular components
148 were detected by correlating the IC time courses and power time courses with the simultaneously
149 acquired ECG, EMG and EOG signals; environmental noise was classified on the basis of its spectral
150 characteristics, by fitting an $1/f$ function to the IC power spectrum density (Barbati et al., 2004).
151 The iteration corresponding to the largest number of ICs with the lowest artefact residual was
152 selected for further analysis. Only non-artefact independent components (ICs) were retained for
153 further analysis. To project the channel signals into the source space, approaches based on
154 extended source models such as minimum-norm estimates, low-resolution tomographies, and
155 beam-forming methods (Brookes et al., 2007; Hamalainen and Ilmoniemi, 1994; Pascual-Marqui,
156 2002) could be applied on the raw data after removing the artefact components. However, we
157 preferred to use an approach already applied to the study of brain interactions at rest (de
158 Pasquale et al., 2010; de Pasquale et al., 2012; Mantini et al., 2011), briefly described in the
159 following.

160 ICs were classified into brain and non-bran components, according to their temporal and
161 spectral contents. Specifically, in addition to the parameters described in Mantini et al. (2011)
162 (such as the correlation of IC time course, power time course and power spectrum density with
163 ECG/EOG reference channels, time kurtosis, goodness of fit with $1/f$ trend on the power spectrum
164 density and flatness of power spectrum density), we considered also the power modulation with
165 respect to its baseline before the trigger onset, estimated in the alpha (8–12 Hz) and beta (13–25
166 Hz) bands. If the relative power modulation was larger than a threshold (15% in our case, as
167 obtained from data collected from previous experiments), then the IC was retained as a brain IC.
168 The brain IC channel maps (corresponding to weight distributions over channels for each IC) were
169 projected into the source space by means of a weighted minimum-norm least square (wMNLs)
170 approach implemented in Curry 6.0 software (Neuroscan, Hamburg, Germany). The structural

171 image of the subject's head was imported and anatomical landmarks were defined on it to build a
 172 realistic BEM model of the volume conductor (Hamalainen and Ilmoniemi, 1994; Wang et al.,
 173 1992). After the wMNLS localization on a regular grid (voxel side 4 mm), each source map was
 174 transformed in a common MNI 152 space for spatial comparison across subjects. Finally, activity in
 175 each voxel $\mathbf{q}_i(t)=[q_{ix}(t), q_{iy}(t), q_{iz}(t)]$ was estimated by linearly combining the IC time courses using
 176 the source maps as weights (de Pasquale et al., 2010; Mantini et al., 2011).

177 2.3 Time-frequency analysis

178 The involvement of brain regions during the action observation (OBS) and execution (EXE)
 179 task was quantified by voxel-wise t-scored Event Related Desynchronization (ERD). The ERD
 180 reflects the active cortical processing which locally reduces synchrony of the oscillatory signals,
 181 thus reducing the resulting oscillatory power (Pfurtscheller and Lopes da Silva, 1999). Interestingly,
 182 modulation of oscillatory power has been linked to event-related potentials/fields through
 183 asymmetrical modulation of peaks of oscillations (Mazaheri and Jensen, 2008; Nikulin et al., 2007).
 184 For each condition, subject, and voxel the power density modulation following the trigger onset
 185 was estimated through the source-space ERD-gram (Della Penna et al., 2004). This was computed
 186 on the global spectrogram $p_j(\mathbf{v},t)$ at voxel j obtained as the sum of the spectrograms of the three
 187 activity components

$$188 \quad p_j(\mathbf{v},t) = p_{jx}(\mathbf{v},t) + p_{jy}(\mathbf{v},t) + p_{jz}(\mathbf{v},t)$$

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

192 Total spectrograms were computed for every OBS or EXE trial, in a window [-1.5, 4.3]s
 193 centered on the trigger onset, and were averaged across trials. Eventually, the ERD-gram, that is

194 the percentage variation of power with respect to a baseline, was estimated in the same time
 195 window in a frequency band [5 40] Hz according to the following formula:

$$196 \quad ERD_gram_j(\nu, t) = 100 \cdot \frac{p_j(\nu, t) - base_j(\nu)}{base_j(\nu)}$$

197 in which, $base(\nu)$, defined as the pre-stimulus power level, is the average of $p(\nu, t)$ when
 198 $t \in [-1.5 - 0.5]s$ (Della Penna et al., 2004; Pfurtscheller and Lopes da Silva, 1999).

199 2.4 ERD maps

200 For each subject and condition, ERD spatial maps at the individual alpha and beta bands
 201 were obtained by averaging ERD-grams across frequencies in these rhythmical bands and across
 202 time in the [-1.5, 4.3]s window. Individual alpha and beta bands were estimated from the power
 203 spectrum densities of the ICs. The mean across the ICs time courses of the frequencies
 204 corresponding to the individual alpha peak (IAF) was used to determine the individual alpha band
 205 as $IAF \pm 2Hz$ (Klimesch et al., 1998). The mean and standard deviation across subjects of the IAF
 206 was 10.0 ± 0.7 Hz. Eventually, the individual beta band was defined from the upper limit of the
 207 alpha band to the upper corner of beta peak. The average across subjects of the beta peak was 19
 208 ± 2 Hz, the lower beta limit was 15 ± 2 Hz and the upper one was 24 ± 2 Hz.

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

217 multiplied across conditions (logic AND operation) and this global mask was eventually multiplied
218 by the average of the OBS and EXE ERD maps.

219 On these AND-ERD maps, maximally active nodes were identified as centroids of local
220 minima, comprised in regions extracted by thresholding the ERD maps at $p < 2 * 10^{-5}$. A global set of
221 nodes was obtained by merging the sets of maximally active nodes obtained in alpha and/or beta
222 frequency band.

223 *2.5 Analysis of spectral and temporal dynamics*

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

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

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

241 distribution of latencies across subjects was used for comparison with M1. A significance level of
242 0.05 was assumed.

243 *2.6 Control analyses*

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

245 (i) to control whether the order in which the stimuli were presented affects our results we
246 acquired additional data on a subset of participants (7 subjects) after eight months from the
247 previous records. These were scanned when performing the same tasks described above with all
248 the EXE blocks (24) presented in the first half of the sequence, whereas the OBS blocks (24) were
249 presented in the second half. As in the main paradigm, each block was followed by REST.
250 Individual and group-level ERD maps for each frequency band (alpha and beta) and condition (EXE
251 and OBS) were computed on MEG data. We adopted the same methodological approach used in
252 the main experiment to generate the AND-ERD final maps. Then, to quantify the robustness of the
253 main results, the Dice similarity coefficient (D) between AND-ERD maps for the two experimental
254 paradigms was computed in alpha and beta bands (Dice, 1945). The Dice similarity coefficient

255 between two samples x and y is defined as: $D = \frac{2|x \cap y|}{|x| + |y|}$;

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

263 (iii) a three-way repeated-measure ANOVA on reactive frequencies with condition (OBS and EXE),
264 nodes (M1, vPM, PMd and S1), and hemisphere (left LH and right RH) as factors was performed to

265 check the spatial specificity of the frequency slow down effects in the beta band. For this analysis,
266 we selected only the homologous nodes in the right hemisphere which showed an ERD above
267 statistical threshold during EXE.

268

269 **3 RESULTS:**

270 *3.1 Cortical recruitment during OBS and EXE conditions*

271 Group level t-scored ERD maps showed specific patterns of alpha and beta modulation
272 during both conditions, as shown in FIG.2. In particular, left parieto-frontal regions (contralateral
273 to the hand performing the tapping) were recruited in both alpha and beta bands for the OBS
274 [alpha $t < -4.1$ FDR corrected, $p < .001$; beta $t < -4.2$ FDR corrected, $p < .001$] (see FIG.2A) and EXE
275 [alpha and beta $t < -4.7$ FDR corrected, $p < .001$] (see FIG.2B) conditions. In the right hemisphere,
276 we observed a significant ERD over the occipital cortex only during OBS condition (FIG.2A) and
277 over the sensorimotor cortex only during EXE (FIG. 2B). Now, we extracted the common areas
278 recruited during OBS and EXE conditions through a logical AND operation (see 2.4). For the alpha
279 and beta bands, the action observation and execution showed overlapping ERD patterns in the left
280 hemisphere suggesting the recruitment of a similar network in the two tasks, as revealed by the
281 related AND-ERD maps (FIG. 2C). No common regions were found in the right (ipsilateral)
282 hemisphere. A set of voxels corresponding to centroids of local minima was extracted for alpha
283 and beta rhythms from the AND-ERD maps (Insert Supplementary Table S1 here and FIG.S2).
284 Expanding existing fMRI literature on activation of cortical areas during OBS and EXE (Buccino et
285 al., 2004; Gazzola and Keysers, 2009; Grezes et al., 2003), we associated alpha and beta rhythms
286 modulation following OBS and EXE to a broad cortical network, compatible with the putative
287 mirror system, i.e. ventral premotor area (vPM), the inferior parietal lobule (IPL) (FIG.2C and S2)
288 and the inferior frontal gyrus (IFG), but also additional cortical regions in both frequency bands.

289 Specifically, the alpha AND-ERD map showed a large ERD trough possibly in the left middle frontal
290 gyrus (MFG), the primary somatosensory region (S1), the superior parietal lobule (SPL), the
291 precuneus (PrC) and the angular gyrus (AG). In the beta AND-ERD map we found local troughs over
292 the primary motor cortex (M1), the dorsal premotor cortex (dPM) and the intraparietal sulcus (IPS)
293 (all $p < 10^{-4}$; FIG.2C, S2 and Insert Supplementary Table S1 here). To exclude the possibility that
294 these findings were induced by a build-up effect due to fact the OBS blocks always preceded EXE
295 blocks in the sequence, we performed a control experiment adopting a different order of
296 stimulation (FIG.S3). The AND-ERD maps (FIG.3) and the spatial correlation index support the
297 hypothesis that our findings are not influenced by the sequence of stimuli as revealed by the Dice
298 similarity coefficient (D) on the t-scored ERD maps obtained for the two sequences (alpha $d=0.50$;
299 beta $d=0.72$). In particular, when this coefficient was computed exclusively on the left hemisphere
300 the results slightly improved, namely $d=0.60$ in alpha and $d=0.73$ in beta.

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

308 3.2 Voxel-wise analysis of rhythmical activity

309 The rhythmical activity of the voxels identified from the AND-ERD maps (Insert
310 Supplementary Table S1 here) showed a specific spectral content and temporal dynamics as
311 revealed by the following three parameters: the most reactive frequency, the ERD peak latency
312 and the ERD peak value (see FIG.S1). The spectral content of rhythmical activity in the beta band

313 was differently modulated for EXE and OBS conditions, with a general slow-down during OBS with
314 respect to EXE, whereas the alpha frequency was less affected by condition. A typical time-
315 frequency pattern is shown in FIG.4A for a representative subject in node (M1), where the ERD
316 during EXE (left panel) and OBS (right panel) are different over time. Typically, the ERD starts
317 before the trigger onset (obtained from the subject's EMG) during EXE, consistently with a the
318 computation of a voluntary act (Buzsaki, 2006; Pfurtscheller and Lopes da Silva, 1999). The
319 dissociation of rhythmical responses is also revealed at the group level by a two-way (Node x
320 Condition) analysis of variance (ANOVA) on the reactive frequencies (FIG.4B). Specifically, the beta
321 rhythm exhibited a general slow-down of the most reactive frequency during OBS (dashed line,
322 FIG.4B, right) compared to EXE (solid line), as demonstrated by the main effect Condition
323 ($F(10,110) = 13.4, p < .004$). In particular, this downward shift for beta was statistically significant in
324 IFG, vPM, dPM, M1 ($**=p < .001$) and also in IPL and AG ($*=p < .05$), as suggested by a statistically
325 significant interaction ($F(10,110)=1.9, p < .05$). Conversely, similar rhythmical dynamics were
326 observed in the alpha band during EXE and OBS conditions, as suggested by the lack of a
327 significant effect of Condition ($F(1,11) = 1.2, p < .29$) on the most reactive frequencies (FIG.4B left),
328 except for dPM, S1 and SPL ($*=p < .05$, interaction effect $F(10,110) = 1.97, p < .043$), which showed a
329 slow-down of the reactive frequency. Notably, this effect in the beta band was specific for left
330 hemisphere nodes (contralateral to the moving hand) ($*=p < .05$), as revealed by a control analysis
331 on a subset of homologous somatomotor nodes in both hemispheres (M1, dPM, vPM and S1) (see
332 Supplementary FIG.S5).

333 To test the hypothesis that the processing sequence follows the internal models criteria,
334 we analyzed the timing of ERD occurrence to provide the sequence of involvement of the regions
335 obtained from the AND-ERD maps. This temporal information may also elucidate the observed
336 modulation of the spectral content of the beta rhythm during OBS with respect to EXE. In what

337 follows, each node latency will be re-aligned to M1 and it will be tested against it using the node
338 latency distribution across subjects. Moreover, to group similar node latencies an one-way ANOVA
339 will performed with node as factor. We observed for EXE a quite similar sequential occurrence in
340 the alpha (FIG.5A) and beta bands (FIG.5B) as confirmed by the ANOVA results on ERD peak
341 latency across nodes ($F(9)=11.6$, $p<10^{-7}$ for alpha; $F(9)=15$, $p<10^{-7}$ for beta) (FIG.5C). In particular,
342 the ERD in left prefrontal regions including vPM and IFG (cyan and blue cluster in alpha and beta,
343 respectively) peaked earlier than in the other regions ($p <.05$, Duncan post hoc test). In alpha, the
344 cyan cluster included also M1 (see Tab.1 for relative latency and statistical significance). In beta,
345 the blue cluster included also dPM and peaked from 130 ms to 105 ms before M1 (see Tab.1). This
346 early engagement suggests that these areas might be involved in the transformation of the go
347 signal into motor commands. The subsequent processing step (green cluster) involved mainly dPM
348 (at 45 ms after M1) for alpha, the sensorimotor regions (S1 at about 42 ms for alpha, M1 and S1
349 simultaneously for beta) through sensory re-afferences and the SPL (about 60 ms) significantly
350 before ($p <.05$, Duncan post-hoc) than the other parietal regions (orange cluster - IPL, PrC and IPS
351 from about 130ms to about 180ms, including AG for beta). Parietal regions including IPL have been
352 reported to be early involved in higher order motor functions, such as movement initiation, as
353 revealed by studies analyzing the preparation potential (BP - Bereitschaftspotential) (Ball et al.,
354 1999). Here, since the analysis is based on ERD, we are sensitive to mechanisms different from the
355 BP (Shibasaki and Hallett, 2006), revealing further aspect of the execution of a motor action. We
356 propose that the later recruitment of parietal regions could suggest the generation of a sensory
357 representation of the body action or the prediction of what the intended action would feel or look
358 (Gazzola and Keysers, 2009; Miall, 2003; Wolpert and Ghahramani, 2000). Finally, ERD peaked
359 possibly over MFG (and AG for alpha, red cluster - $p<.05$, latency about 240 ms). Overall, this

360 anterior-posterior pattern of engagement is consistent with the predictive nature of the forward
361 model (Gazzola and Keysers, 2009; Wolpert and Ghahramani, 2000).

362 Compared to the execution task, a different temporal dynamics between the alpha (FIG.5D)
363 and beta bands (FIG.5E) occurred during the OBS condition, suggesting a functional dissociation
364 between the two rhythms. Specifically, in the alpha band, the ERD peak sequence was reversed
365 with respect to the EXE condition, showing a posterior-anterior information flow ($F(9)=5.9$, $p<10^{-6}$,
366 FIG. 5D and 5F). After the early engagement of the region including AG (blue cluster - latency = \sim -
367 150ms, $p<.005$), the sequence included parietal regions (yellow cluster - SPL and IPS, $p<0.033$)
368 significantly before (60 ms) M1 ($p <.03$, see Tab.1), presumably for high order visual processes.
369 Next, the ERD peaked in frontal regions including IFG, MFG, vPM and dPM, and in parietal regions
370 including S1, IPL and PrC, all of them showing no significant difference in latency with respect to
371 M1 (red cluster). In summary, we suggest that this posterior-anterior information flow in the alpha
372 band might represent the visuo-motor transformation of the observed movement into a suitable
373 motor program or command. Thus, the sequence of alpha might be considered as the neural
374 signature of the implementation of the inverse model, as hypothesized by Gazzola and coll. (2009).
375 Importantly, the sequence of ERD occurrence for the beta band ($F(9)=2.5$, $p<.012$) largely differed
376 from the one observed for the alpha band (FIG.5E and 5F). A simultaneous early ERD occurred in
377 posterior parietal (cyan cluster including S1, SPL, IPS, PrC, AG and IPL) and frontal (including IFG,
378 dPM and MFG) regions, followed by the region including vPM (red cluster - $p<.01$ Duncan post-hoc
379 with respect to SPL and IPS). In addition, most of the nodes (except vPM) were recruited
380 significantly before M1 (latency = \sim -160ms \div -40ms, $p<.03$ in the worst case), whereas in the
381 alpha band, the latencies of the majority of nodes, except AG, SPL and IPS were close to M1.

382 The dissociation between the alpha and beta rhythms during action observation was
383 bolstered by an ANOVA on the ERD peak values in the two conditions, conducted separately for

384 each frequency (FIG.S6). In the alpha band, most nodes exhibited a different modulation during
385 OBS vs EXE, (condition factor tending to be significant, signalling the trend of the ERD values in all
386 nodes to be smaller during the OBS with respect to EXE ($F(1,11)=4.32$, $p<0.06$); significant
387 interaction (Node x Condition) ($F(10,110)=5.35$, $p<2*10^{-6}$). Conversely, the ERD values in the beta
388 band were similar for the two conditions across nodes, excluding AG ($p<.05$), and showed a similar
389 activation pattern (significant interaction Node x Condition- $F(10,110)=2.38$, $p<0.014$). Taken
390 together, our data suggest that alpha and beta bands represent the neural correlate of different
391 and specific aspects of action observation and execution.

392

393 **4 DISCUSSION**

394 In this MEG study we report on the electrophysiological correlates and spectro-temporal
395 dynamics of action observation and execution. Whereas previous MEG studies focused on signals
396 at the channel level (Babiloni et al., 2002; Cochin et al., 1999; Kilner et al., 2006, 2009;
397 Muthukumaraswamy and Johnson, 2004; Muthukumaraswamy et al., 2004; Streltsova et al.,
398 2010), our results were reported in the source space and revealed specific spatial and temporal
399 features underlying the execution and observation of a motor task. Specifically, we have shown
400 that action observation and execution share a common set of areas exhibiting the μ rhythm. These
401 regions include several parieto-frontal regions which may be part of an action observation network
402 (AON) (Avenanti et al., 2012; Buccino et al., 2001; Gazzola and Keysers, 2009). Importantly, our
403 time-frequency analyses on the rhythmical activity of this network revealed a dissociation of the
404 alpha and beta band within the μ rhythm.

405

406 *4.1 Methodological Remarks*

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

422 As far as it regards our methodology, here we adopted an approach based on ICA followed
423 by a weighted minimum norm estimate (wMNE) localization (Mantini et al., 2011), which has been
424 designed to study large scale connectivity at rest (Betti et al., 2013; de Pasquale et al., 2010; de
425 Pasquale et al., 2012; Marzetti et al., 2013). Here, we discuss the limitations of this approach,
426 mainly related to the spatial dispersion of identified active areas. Several approaches assuming
427 extended source models have been adopted to estimate brain activity at source level (Brookes et
428 al., 2007; Dale et al., 2000; Hamalainen and Ilmoniemi, 1994; Pascual-Marqui, 2002) and an
429 interesting review of their pros and cons can be found in (Hauk et al., 2011; Zhang et al., 2013 for a
430 comparison among methods). In general, the selection of the inverse approach is usually driven by

431 the specific requirements of the study. Here, we expect a set of highly coupled distinct sources
432 active within a relatively short time interval. A meta-analysis of the fMRI literature (see caption of
433 Table S1 for a list of related references) suggests that some of these sources are relatively close, in
434 the order of few centimeters. In this respect, beamforming approaches, which are more focused
435 than minimum norm estimates (Sekihara et al., 2005) might be eligible to localize these sources.
436 However, their performance on correlated sources is sub-optimal. Conversely, minimum-norm
437 based operators present an opposite behaviour: i.e. less focused but no limitation due to the
438 presence of correlated sources. Now, since we expect a network of possibly correlated sources to
439 be involved during processing of OBS and EXE conditions, we selected a weighted MNE
440 compensated for different source depths (wMNE- Fuchs et al., 1999) to project the IC sensor maps
441 into the source space, with a consequent improvement of the spatial dispersion with respect to
442 the standard MNE approach.

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

452 In a previous work we have discussed the influence of the spatial distance on the temporal
453 correlation between neighbouring voxels (de Pasquale et al., 2010; de Pasquale et al., 2012). We
454 showed that for neighbouring voxels distant at least 3.2 cm the relative dependence is highly

455 reduced. This corresponds to assume a spatial dispersion of 1.6 cm, which is consistent with the
456 literature (Hauk et al., 2011). Now, in this study we discuss regions, involved in OBS and EXE,
457 which are closer than this distance. Such regions were selected as local troughs of AND-ERD maps
458 identified by statistical test. In particular, the regions M1/dPM and IPL/IPS were closer than the
459 minimum distance, and were extracted in the beta band (a trough in IPL was detected also in the
460 alpha band), as shown in FIG.S2. In alpha (see FIG.S2), troughs were detected also possibly in other
461 areas closer than the minimum distance, such as S1, SPL and AG. However, if the detected
462 activations were only due to a single source spreading in the nearby locations, the dynamics
463 estimated by reactive frequencies and ERD latencies would be very similar irrespective of the
464 frequency band. However, this does not occur when inspecting the reactive frequencies in the
465 beta and alpha bands of M1/dPM, IPL/IPS and AG/SPL (see FIG. 4B). Additionally, the ERD latencies
466 of dPM and M1 were always significantly different except for alpha OBS, and the latencies of IPS vs
467 IPL and of S1 vs SPL differ during alpha OBS. Finally, the latencies of SPL and AG are always
468 different except for beta OBS (see FIG.5C and 5F). Notably, when analyzing other nodes which
469 were selected in different bands and are closer than 3.2 cm, such as IPL (close to M1, S1, AG and
470 SPL), IPS (close to AG, SPL, PrC) and M1 vs S1, we obtained distinct frequency changes and
471 different latencies at least in one condition/band. In summary, although we acknowledge that the
472 effect of the spatial dispersion is not negligible for some neighbouring nodes, our main finding on
473 band-specific, different dynamics observed in the two conditions seem to be robust against this
474 effect.

475
476 *4.2 Differences and commonalities of brain activity during EXE and OBS*

477 **The modulation of oscillatory power (ERD/ERS) is linked to information processing in the**
478 **involved cortical areas and has been widely used to study motor cortex functioning (Donner et al.,**

479 2009; Gaetz and Cheyne, 2006; Meyniel and Pessiglione, 2014; Neuper and Pfurtscheller, 2001).

480 We found significant ERD troughs in several areas approximately over the dorsal premotor cortex
481 (dPM), middle frontal gyrus (MFG), superior parietal lobule (SPL), angular gyrus (AG), precuneus
482 (PrC), primary motor (M1) and somatosensory (S1) cortices (FIG.2) (Buccino et al., 2001; Buccino et
483 al., 2004; Rizzolatti and Sinigaglia, 2010) but also in the ventral part of the precentral gyrus (vPM),
484 the rostral part of the inferior parietal lobule (IPL) and the intraparietal sulcus (IPS) that are
485 included in the putative mirror system (pMNS) (Rizzolatti and Craighero, 2004). Thus, our data is
486 compatible with the existing fMRI literature suggesting that several common parieto-frontal areas
487 are involved in action observation and execution (Buccino et al., 2004; Gazzola and Keysers, 2009;
488 Grezes et al., 2003).

489 Furthermore, we observed a significant ERD over bilateral sensorimotor regions during
490 action execution, as previous reported (Liepert et al., 2001; Pfurtscheller and Lopes da Silva, 1999;
491 Salmelin et al., 1995), but not during the action observation. Left lateralization for EXE only is not
492 unexpected since all our stimuli contain right handed actions and the participants had to perform
493 the same movements with their right hand. This is in line with the literature (Aziz-Zadeh et al.,
494 2006; Aziz-Zadeh et al., 2002; Cabinio et al., 2010) in which it is reported the involvement of the
495 contralateral hemisphere to the hand movement (but see Rizzolatti and Craighero, 2004) for the
496 involvement of bilateral sensorimotor regions during the hand action observation).

497

498 *4.3 Different spectral signatures and dynamics of EXE and OBS*

499 Differently from previous MEG/EEG studies, typically recording consistent alpha and beta
500 modulations on action observation and execution (Babiloni et al., 2002; Caetano et al., 2007;
501 Cochin et al., 1998; Kilner et al., 2009; Muthukumaraswamy and Singh, 2008; Orgs et al., 2008), for

502 the first time to our knowledge, we observed a dissociation between alpha and beta oscillations
503 within the μ rhythm during action observation with respect to execution.

504 The μ rhythm consist of two components with a nearly harmonic relationship. The two
505 components, 10 Hz and 20 Hz, can occur either separately or simultaneously, suggesting that the
506 beta component (20 Hz) activity can be phase-locked to the alpha component (10 Hz) when
507 starting from the same neural generator or be completely independent in some other moments
508 (Hari et al., 1997 for a review). Notably, the beta oscillations appear to be at a frequency which is
509 twice the alpha components, thus producing the arch-shaped μ rhythm. This is in line with a
510 concomitant modulation of the alpha and beta bands recorded over somato-sensory regions
511 during both EXE and OBS (Babiloni et al., 1999; Hari et al., 1998; Hari et al., 2000; Hari et al., 1997;
512 Pfurtscheller, 1989; Pineda et al., 2000). Nevertheless, it is commonly accepted that the alpha and
513 beta bands differ in terms of their functional role. On one hand, the alpha band activity has been
514 related to several processes, spanning from the disengagement of task irrelevant brain areas to
515 memory, attention, and consciousness (Jensen et al., 2002; Palva et al., 2005; Palva and Palva,
516 2007; Pfurtscheller, 2003). On the other hand, the beta band oscillations have been linked to
517 motor functions such as steady contractions, voluntary movements and motor imagery (de Lange
518 et al., 2008; Sanes and Donoghue, 1993). Recently, Engel and Fries (2010), based on previous work
519 by (Baker, 2007; Gilbertson et al., 2005), proposed that beta band oscillations is not purely an
520 “idling” rhythm, but bolster an active process that promotes the ongoing motor set and other
521 processes beyond the domain of motor control.

522 Action execution and action observation implement a translation of action into perception
523 and viceversa. These processes involve alpha and beta generators in the somatomotor domain (μ
524 rhythm), but also in other domains (visual, motor control, attention, etc.). These domains typically
525 exhibit synchronized and desynchronized activity in a locally independent manner. However,

526 during the translation of “doing” into “seeing” or viceversa, they are globally engaged (Pineda,
527 2005).

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

533 This dissociation between alpha and beta might be linked to the observed different
534 temporal dynamics and a slow-down of beta oscillations compared to alpha. Specifically, we
535 showed that action execution recruits regions of the AON in an anterior-posterior temporal
536 sequence (Nishitani and Hari, 2000) in both alpha and beta bands (see FIG.5A, 5B, 5C). The fronto-
537 parietal sequence of occurrence is in accordance with the forward model hypothesis arguing that
538 an efference copy of motor command is sent towards parietal cortices during action execution to
539 predict sensory and proprioceptive consequences of the intended action (Wolpert and
540 Ghahramani, 2000). Specifically, the transformation of the go signal into motor commands could
541 explain the recruitment of the frontal regions (dPM, vPM and IFG) before (beta) or simultaneously
542 (alpha) to M1 latency (Hari et al., 2000; Nishitani and Hari, 2000). Furthermore, the latencies of
543 these regions did not differ significantly, possibly due to the high number of direct connections
544 between M1 and S1 (Matelli et al., 1986) and the slow timing of the spectral power changes. In
545 addition, posterior parietal regions (Prc, IPL, SPL and AG) are recruited after the beginning of the
546 movement (M1 as reference), thus suggesting not only the generation of sensory representation
547 of the action, but also the involvement of other attentional and computational processes that are
548 common to the action observation. Conversely, during action observation, we observed a roughly
549 posterior-anterior sequence in the alpha band (FIG.5D) and a simultaneous fronto-parietal

550 occurrence in beta band (FIG.5E). The reversed posterior-anterior sequence of involvement
551 observed in the alpha band during action observation with respect to execution is consistent with
552 the generation of an inverse model, which allows us to infer the motor program that could have
553 caused the sensory input (Gazzola and Keysers, 2009; Wolpert and Ghahramani, 2000). In
554 particular, it has been proposed that observing others' actions engages the sensorimotor
555 resources of the onlooker via a simulation mechanism. Such mechanism prompts the inverse
556 model in order to translate other's action into a motor command, thus allowing the
557 representation of the observed movement in a motor format.

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

571

572 *4.4 Role of beta rhythm during EXE and OBS*

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

592 Our results show that beta band activity does not reflect the postero-anterior processing
593 sequence as hypothesized in the inverse model. We suppose that the simultaneous recruitment of
594 parieto-frontal regions we found, might reflect this active role of motor activation in which motor
595 commands are fed back in the posterior regions to anticipate the future phases of others actions.
596 This anticipation would determine a top-down influence on action perception to modulate and

597 complete the sensory information. However, further investigation with specifically designed tasks
598 are needed to assess the predictive role of beta during action observation. Indeed, we did not find
599 strong evidence of backward anterior-posterior processing sequence but this could be due to the
600 adopted task. Since the presented movement (finger-tapping) is very simple and has no functional
601 meaning, it can be easily predicted what the models are doing.

602 Another possible explanation of the simultaneous recruitment of the fronto-parietal nodes
603 in beta band could be linked to the mechanism that promotes the 'self-other' disentangling, i.e.
604 how the same cortical circuits engaged during both action execution and observation encode the
605 self-other distinction (Jeannerod, 2007). Our speculation links to the review of Engel and Fries
606 (Engel and Fries, 2010), who suggest that the beta rhythm reflects the tendency of the sensory-
607 motor system to 'maintain' the *status quo* by means of a more efficient processing of feedbacks.
608 Moreover, recent results showed a frequency signature of the Default Mode Network in the beta
609 band, supporting the involvement of this rhythm in self-related processes (de Pasquale et al.,
610 2012). Thus, the observed downshift in this frequency band might promote a change of the
611 cognitive set necessary to implement the inverse model when observing other's actions while the
612 concomitant widespread involvement of this network in the beta band might represent a means
613 to achieve this aim.

614 In conclusion, we observed that the μ rhythm is not a unitary phenomenon, i.e. alpha and
615 beta oscillations likely reflect different aspects involved in action observation and execution. We
616 propose that this differentiation might subserve different cognitive operations during action
617 observation vs action execution. Eventually, the reported functional dissociation between alpha
618 and beta bands may have an impact in clinical applications such as the neurological rehabilitation
619 based on the μ -rhythm neurofeedback (Pineda et al., 2008). In fact, a lack of μ suppression has
620 been hypothesized as an electrophysiological correlate of the putative Mirror Neuron System

621 (pMNS) dysfunction and it might contribute to poor imitation and social skills in children with
622 autism spectrum disorder (ASD) (Rizzolatti et al., 2009).

623

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924 **TABLES**

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

Nodes	EXE				OBS			
	ALPHA		BETA		ALPHA		BETA	
	Relative latency	p (test with respect to M1)	Relative latency	p (test with respect to M1)	Relative latency	p (test with respect to M1)	Relative latency	p (test with respect to M1)
SPL	58.33	0.05	58.33	0.09	-62.5	0.04	-160.42	5×10^{-4}
IPS	158.33	4×10^{-5}	185.42	10^{-4}	-66.67	0.03	-152.08	0.001
MFG	258.33	10^{-4}	241.62	5×10^{-4}	-12.5	0.4	-110.42	0.02
PrC	183.33	0.001	158.33	0.001	20.83	0.3	-104.17	0.01
IFG	-33.33	0.1	-112.5	0.002	-37.5	0.1	-97.92	0.002
dPM	45.83	0.03	-104.17	0.01	-20.83	0.2	-93.75	0.01
AG	208.33	9×10^{-4}	125	5×10^{-4}	-154.17	8×10^{-5}	-85.42	0.02
IPL	133.33	2×10^{-4}	137.5	3×10^{-4}	-16.67	0.2	-77.08	0.03

S1	41.67	0.07	20.83	0.3	12.5	0.2	-37.5	0.07
vPM	-12.5	0.3	-129.17	0.001	12.5	0.3	-31.25	0.2

925

926 Note: For each condition (OBS and EXE) and frequency (alpha and beta) we report the latency (ms)

927 of each node related to M1 assumed as reference. Statistical significance ($p < 0.05$) was estimated

928 through the distribution of individual latencies. Significantly different latencies are marked in red.

929 We assumed $p = 0.07$ to represent a tendency to significance.

930

931

932 **FIGURE CAPTIONS**933 **FIG.1 Main experimental timeline.**

934 In a block design, the participants were shown a red cross on a black screen for 5 seconds (Rest

935 block), after which subjects were asked to observe a video showing a right-handed finger tapping

936 movement that lasted 5 s (OBS block). At the end of the video, a rest block was presented. When

937 the red cross turned into green the subjects had to perform the same movement observed in the

938 video with their right hand for 5 s (EXE block).

939

940 **FIG. 2 ERD maps.**

941 A) Group level ERD maps (voxelwise percentage power variations with respect to a baseline

942 period, averaged over a time window after the stimulus onset) computed in the alpha (top) and

943 beta (bottom) band for the observation (OBS) condition. The represented quantity is t-score. Only

944 statistically significant values are shown ($p < .001$, FDR corrected). Recruitment of left fronto-

945 parietal areas and bilateral occipital areas occurs in both bands.

946 B) Group level ERD maps for the execution (EXE) condition. The same quantities as in A) are

947 represented. Recruitment of contralateral fronto-parietal areas and ipsilateral sensory-motor

948 areas occurs in both bands.

949 C) ERD maps averaged across the OBS and EXE conditions for the alpha (top) and beta (bottom)
 950 bands computed on voxels statistically significant in both conditions ($p < .001$, FDR corrected, logic
 951 AND operation). No significant voxels in both conditions are obtained in the right hemisphere and
 952 occipital regions. Labels of nodes corresponding to local ERD troughs are superimposed to the
 953 AND-ERD map (white; the complete list can be found in Tab. S1 “Insert Supplementary Table S1
 954 here”). The AND-ERD maps suggest the involvement of a broad action observation network (AON).
 955 Specifically, vPM, IFG, IPL, dPM, M1, MFG, AG, S1, PrC, SPL, IPS are presumably recruited in both
 956 conditions.

957

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

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

964

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

966 A) Percentage ERD time/frequency plots for the EXE (left) and OBS (right) conditions computed in
 967 the left M1 for a representative subject. In this figure the individual alpha and beta bands are
 968 respectively marked in gray and red on the frequency axis. The most reactive frequencies
 969 (corresponding to the largest ERD trough after the stimulus onset) are marked by arrows. The
 970 spectral content visibly differs between the two frequency bands: a clear slow-down of rhythmical
 971 activity is evident in the beta band between OBS and EXE (red arrows). Conversely, a tiny effect
 972 (gray arrows) is observed in the alpha band in this subject.

973 B) Reactive frequencies for the common areas involved during EXE (solid line) and OBS (dashed
974 line) in the alpha (left) and beta (right) bands. Error bars indicate standard error. A dissociation of
975 rhythmical involvement occurs between the two conditions. Specifically, while in alpha EXE and
976 OBS elicit a similar rhythmical response, in the OBS condition a slow-down is observed in the beta
977 band (main effect Condition in a two-way ANOVA, $F(10,110)=13.4$, $p<.004$) with respect to EXE.
978 Specifically, Duncan post-hoc analysis reveals a significant Node x Condition interaction in the
979 alpha ($F(10,110)=1.97$, $p<0.043$) and beta ($F(10,110)=1.9$, $p<.05$) bands. Significant nodes are
980 marked by asterisks (* $p<.05$, ** $p<.001$).

981

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

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

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

994 C) The latency of each node, is plotted in the alpha (solid line) and beta (dashed line) bands. Error
995 bars indicate standard errors. For both frequency bands a fronto-parietal involvement occurs
996 during execution.

997 D) In the alpha band the temporal dynamics during OBS is different with respect to EXE: a
998 posterior- anterior sequence of processing (Duncan post-hoc one-way ANOVA, $F(9)=5.9$, $p<10^{-6}$)
999 with some nodes grouped with M1.

1000 E) In the beta band the sequence of occurrence is different from the EXE condition and the alpha
1001 band: most of nodes in posterior parietal and frontal regions are simultaneously recruited (Duncan
1002 post-hoc one-way ANOVA, $F(9)=2.5$, $p<.012$). Moreover, they are involved significantly before M1
1003 (see Tab.1).

1004 F) The latency of each node is plotted in the alpha (solid line) and beta (dashed line) bands. Error
1005 bars indicate standard error. This analysis suggests that alpha and beta bands show a different
1006 dynamics supporting a functional segregation hypothesis.