The impact of body posture on intrinsic brain activity: The role of beta power at rest

Brunella Donno1,2,*, Daniele Migliorati1,2,3, Filippo Zappasodi1,2, Mauro Gianni Perrucci1,2, Marcello Costantini2,4*

1 Department of Neuroscience, Imaging and Clinical Sciences, University “G. d’Annunzio” of Chieti, Chieti, Italy, 2 Institute for Advanced Biomedical Technologies (ITAB), University “G. d’Annunzio” of Chieti, Chieti, Italy, 3 Center for Biomedical Brain Imaging, University of Delaware, Newark, Delaware, United States of America, 4 Department of Psychological, Health, and Territorial Sciences, ‘G. d’Annunzio’ University of Chieti-Pescara, Italy

* brunella.donno@unich.it; marcello.costantini@unich.it

Abstract

Tying the hands behind the back has detrimental effects on sensorimotor perceptual tasks. Here we provide evidence that beta band oscillatory activity in a resting state condition might play a crucial role in such detrimental effects. EEG activity at rest was measured from thirty young participants (mean age = 24.03) in two different body posture conditions. In one condition participants were required to keep their hands freely resting on the table. In the other condition, participants’ hands were tied behind their back. Increased beta power was observed in the left inferior frontal gyrus during the tied hands condition compared to the free hands condition. A control experiment ruled out alternative explanations for observed change in beta power, including muscle tension. Our findings provide new insights on how body postural manipulations impact on perceptual tasks and brain activity.

Introduction

It is well known that the physical body plays a key role in the way in which the brain encodes the environment; in fact, in everyday life cognitive processes are influenced by the sensory and motor experiences of the body. This idea, which stems from the broader theoretical framework of Embodied Cognition [1], claims that many aspects of cognition are shaped by features of the body [2]. As a consequence, if cognition derives from bodily experiences, the individuals’ physical features might play a critical role in shaping it [3]. A clear example is provided by studies on mental rotation of body parts [4–7], in which participants have to judge the laterality of pictures representing hands and feet while standing in two different postural conditions. In one condition, the subjects’ right hand is placed on the right knee and the left hand behind the back; in the other one, the hand position is reversed. For right-handed subjects, response times increase when participants judge images representing the right hands keeping their right hand behind the back. This effect is not present for images of the left hand, nor for images of the feet. Other studies show analogous results, highlighting an interference of hand posture on the ability to perform mental rotations of hand images [8]. Similarly, subjects’ body orientation...
has been shown to affect perception of both static and moving objects [9]. All these results suggest that information regarding the current positioning of body or body parts is required for the encoding of visual information. Furthermore, it has been shown that body posture affects the way in which autobiographical memories are accessed and retained by both younger and older adults [10]. Specifically, response times decrease when body position during prompted retrieval of autobiographical events is congruent or similar to the body position in the original events than when body position is incongruent [10]. Nevertheless, the impact of body posture on visual encoding of actions is still under debate. A feasible way to understand how body posture shapes visual encoding of actions is looking at the interaction between posture manipulations and intrinsic brain activity. Specifically, intrinsic brain activity is spontaneously generated by the brain and is not organized in a casual way [11]. The interaction between intrinsic brain activity and posture manipulations is better explained by a study of Thibault and colleagues [12]. In this study, prominent alterations of intrinsic brain activity over occipital and frontal regions were induced through orthostatic manipulations. Specifically, an increase of beta and gamma activity was observed while participants lied supine compared to the condition in which they either stand or sit inclined at 45 degrees. Moreover, there is converging evidence showing that intrinsic brain activity plays a key role in perceptual processes [13] involving high-frequency bands (i.e. beta and gamma) [14–16]. For instance, during tasks requiring mental simulation of actions it has been observed a decrease of oscillatory beta power over the sensorimotor regions [17]. Such a decrease reflects the engagement of the motor system corresponding to the disinhibition of motor areas [18]. Conversely, an increased beta power has been shown to reflect inhibition mechanisms related to perceptual and motor systems [19–22]. It is therefore conceivable that postural manipulations may impact visual perception by altering beta-band oscillations. Drawing from this, we investigated the effects of postural manipulations on the intrinsic brain activity, focusing on the beta frequency band. EEG activity was measured in a resting state condition from thirty healthy participants in two different body posture conditions. In one condition, participants were required to keep their hands freely resting on the table. In the other condition, participants were required to keep hands tied behind their back. Moreover, we conducted an EEG-EMG control experiment in order to rule out the presence of confounding variable (i.e. muscle tension). Specifically, subjects were asked to contract and to keep the contraction of specific muscles during the tied hands condition.

Materials and method

Participants

Thirty right-handed healthy participants (12 males, mean age = 24.03; SD = 3.2; range = 20–33) were recruited to take part in the study from the student pool. The participants took part in the experiment at ITAB (Institute for Advanced Biomedical Technologies) in Chieti. Participants did not have any personal or close family history of neurological or psychiatric disorders, any brain surgery and any active medication, as self-reported. The study was approved by the local ethics committee of the province of Chieti-Pescara (ID07022013). Participants gave their informed consent before taking part in the study. The study was conducted in accordance with the ethical standards of the 1964 Declaration of Helsinki.

We calculated the power achieved in our study a posteriori. The achieved power was 87% with an α value = 0.05, two tails test.

Procedure

EEG resting-state recording and pre-processing. All participants went through two different conditions (within-subject design): i) EEG resting-state when their hands were free (free
condition) and ii) EEG resting-state when their hands were tied behind the back (tied condition). The two conditions were randomized across subjects. In the two blocks, participants had to keep their eyes open and fixate a cross in front of them placed on the computer screen. EEG activity was measured at rest for 4 minutes.

We used a 64 electrodes cap (model BrainCap, BrainAmp MR Plus amplifier, Brain Products), placed according to the 10–20 International System. We used 2 electro-oculographic channels on the right and left temple to monitor eye movement and for off-line artefact rejection. The reference electrode was positioned in correspondence of FCz electrode while the ground electrode was placed in the Inion (Iz).

The impedance was measured before each recording and was kept below 10 kΩ. All the data were processed using EEGLAB software implemented in MATLAB [23].

We acquired online data at 5 kHz, band-pass filtered from 0.016 to 250 Hz. Data were off-line filtered between 1 Hz (high-pass filtering) to 30 Hz (low-pass filtering) and downsampling at 250 Hz for the current analysis. We detected and removed bad channels using a threshold with a probability at 5% (pop rejchan). Subsequently, we rejected the continuous data using a threshold with a probability at 10% (pop rejcont).

Finally, we computed the Independent Component Analysis, using the FastICA algorithm [24] to identify and reject manually noise, ocular, cardiac, muscular artefacts and bad channels. At this point, we interpolated rejected channel and EEG signal was re-referenced to the common average reference.

To exclude that differences in the beta band power in the tied hands with respect to free hands condition is not a consequence of muscular tension during the condition of tied hands, a control experiment was done. We cross-registered EEG-EMG resting-state activity in 4 subjects (3 males, mean age = 26.75; SD = 3.6; range = 24–32) during a low-level isometric contraction of the muscles for 4 minutes, recorded along with the EMG. During the tied hands condition, we asked to participants to contract deltoids, triceps, pectorals and dorsal muscles and to keep the contraction for 4 minutes as stable as possible.

Specifically, we recorded the contraction through 8 electromyographic channels: right and left deltidoid, right and left pectoral, right and left dorsal, right and left triceps. A 32 electrodes cap (model BrainCap, BrainAmp MR Plus amplifier, Brain Products) was used. As the aim of the recording was to check the muscular artefact topography over the scalp, only ocular, cardiac and movement artefacts was rejected by ICA procedure. We computed the power spectrum density only for the beta band. The aim was to confirm a qualitative difference between the beta power spectrum scalp topography of the difference between tied versus free hands condition, obtained in the main experiment and the difference between the beta power scalp topography of the difference between contraction (tied hands condition) versus free hands condition, obtained in the control experiment. For the control experiment, for each subject we performed the beta power spectrum scalp topography of the difference between the two conditions.

**EEG cleaning: Criteria of exclusion.** In order to rule out the presence of confounding variables (i.e. muscular artefacts) and to better identify them from neural activity per sé, we applied high-pass filtering (1 Hz) EEG signals before applying FastICA [24]. It is well known that such artefacts are typically caused by muscle activity near the head, such as head movements and are characterized by high-frequency activity (> 20 Hz) [25].

It is well known that high-pass filtering EEG signals before applying ICA may improve the quality of the artefacts separation. In fact, this procedure represents a standard procedure to remove drifts prior to ICA-based artefact removal and the benefit has been demonstrated in several studies [26]. This standard procedure allowed us to isolate the EEG signal from the
EMG and finally to compare the topographies of the EEG signal of the main experiment with those of the control experiment.

EEG data analysis

Main experiment. We computed the power spectrum density for all electrodes using the periodogram Welch procedure (Hamming windowing function; window length 4 seconds; no overlap). The four classical EEG frequency bands were considered (delta: 1–4 Hz, theta: 4–8 Hz, alpha: 8–13 Hz and beta: 13–30 Hz). Delta, theta and alpha bands were used to control that the difference tied versus free hands condition was specific for the beta band.

Then we extracted the power of delta, theta, alpha and beta bands calculating the mean values of the power spectrum for all frequency bands and for the two conditions (free and tied) described above. The mean values were transformed into decibel scale ($10 \times \log_{10} [\mu \text{V}^2]$) in order to normalize the data [27].

To establish whether there were significant differences in power for all frequency bands between two conditions, a non-parametric cluster-based permutation test was performed using FieldTrip toolbox in MATLAB [28]. To investigate cortical generators of electrophysiological oscillations, we computed signal source analyses on the basis of the results obtained at the scalp level.

The exact low resolution brain electromagnetic tomography (eLORETA) method in frequency domain was used to compute the cortical three-dimensional distribution of current density [29]. Computations are made in a realistic head model [30] using the Montreal Neurological Institute (MNI) Colin27 T2 template obtained from BrainWeb, (http://www.bic.mni.mcgill.ca/brainweb/).

Starting from estimated cortical distribution of generators of beta electrophysiological oscillations, the analysis of differences between free and tied hands condition showed a specific modulation whose significant neural source is localized in a specific cortical area.

EEG results

Main experiment. To test our hypothesis, we performed a non-parametric cluster-based permutation test for the power of all frequency bands between the two conditions (free and tied).

For each sample, a dependent-sample $t$-value was computed. All samples were selected for which this $t$-value exceeded an a priori threshold (uncorrected $p < 0.05$) and these were subsequently spatially clustered. The sum of the $t$ values within a cluster was used as the cluster-level statistic. A reference distribution of cluster $t$-values was obtained by randomization of data across the two conditions for 5000 times and was used to evaluate the statistic of the actual data.

The non-parametric cluster-based permutation test revealed a significant difference between free and tied condition only in the beta band power ($p_s = 0.02$). The analysis revealed increased beta power in tied hands condition compared to free hands condition and the difference between these two conditions was most pronounced over left inferior frontal electrodes (Table 1 and Fig 1).

The non-parametric cluster-based permutation test did not reveal any significant differences between free and tied condition in the other frequency bands (all $p_s > 0.05$).

As regards signal source localization, the comparison between electrophysiological activity for beta power between free and tied hands conditions showed that the main signal source was in the left inferior frontal gyrus (l-IFG) (MNI: $x = -35, y = 10, z = 15; t = 7.21$) (Fig 2).
Control experiment. To exclude that differences in the beta band power in the tied hands with respect to free hands condition is not a consequence of muscular tension during the condition of tied hands, we compared the scalp distributions of average beta power relating to the difference between tied versus free hands condition, obtained in the main experiment and the scalp distributions of average beta power relating to the difference between contraction (tied hands condition) versus free hands condition, obtained in the control experiment. For each subject, we performed the beta power spectrum scalp topography of the difference between contraction (tied hands condition) versus free hands condition.

From each scalp topography, the maximum of the muscular artefact was located in the temporal, fronto-polar and parietal regions. In particular, muscular contamination was not present over the EEG channels where a significant difference between tied and free hands condition was found in the main experiment (F3, C3, F7, FC1, C1, FC3, F5, FT7) (Fig 3).

Moreover, a similar topography was not found by visual inspection of beta band topographies of single subjects before the ICA algorithm application for artefact removal.

Discussion

Our physical body plays a key role in the way in which the brain encodes stimuli from the environment; in fact, in everyday life cognitive processes are deeply influenced by the sensory and

| Electrodes | Free Condition | Tied Condition |
|------------|----------------|---------------|
|            | Mean | SD  | Mean | SD  |
| F3         | -14.44 | 3.16 | -13.63 | 4.25 |
| C3         | -15.89 | 2.94 | -15.04 | 3.96 |
| F7         | -14.50 | 2.72 | -13.60 | 3.87 |
| FC1        | -15.30 | 3.26 | -14.48 | 3.86 |
| C1         | -16.72 | 3.07 | -15.95 | 3.75 |
| FC3        | -15.58 | 3.13 | -14.68 | 3.68 |
| F5         | -14.18 | 2.57 | -13.13 | 3.30 |
| FT7        | -13.74 | 2.86 | -13.15 | 3.28 |

Fig 1. Scalp distributions of average beta power (decibel: $10 \times \log_{10}(\mu V^2)$) in the free condition (Panel A) and tied condition (Panel B). Panel C represents the differences in beta power between the two conditions. Red dots represent electrodes in the significant cluster ($p = 0.02$).
motor experiences of our body. This theory of cognition, known under the general topic of Embodied Cognition [1], claims that many aspects of cognition are shaped by body features [2]. This theoretical framework implies that if knowledge is obtained through bodily experiences, it is constrained not only by the experiences and situations encountered, but also by the physical features of the individuals [3]. In the present study, resting state EEG activity was measured from thirty healthy participants in two different body posture conditions. In the free hands condition, participants were required to keep their hands freely resting on the table; in the tied hands condition, participants were required to keep hands tied behind their back. Power spectrum analysis revealed an increased beta power in the tied hands condition compared to the free hands condition. This difference was most pronounced over left frontal electrodes.

The way in which body posture manipulations modulate sensorimotor perceptual tasks is well known, as well as the involvement of beta power in the inhibition and disinhibition of motor mechanisms; however, the impact of the body posture on beta band oscillatory activity in a resting state condition is still unknown. Our results suggest that an increased beta power in the tied hands condition, compared to free hands condition, which might also explain the constrained hands effect commonly observed when participants perform perceptual action-related tasks.

However, does beta power activity in sensorimotor regions effectively play a role in processing such stimuli? And to which extent is it involved in their processing? Previous studies have
shown that observation of graspable objects, which is known to recruit sensorimotor resources [30] and to be affected by postural manipulations, is associated with a decrease in beta band power. Similarly, suppression of oscillatory activity within the mu (8–13 Hz) and beta (13–30 Hz) frequency bands over sensorimotor regions has been associated with action execution, as well as action observation [31–35]. Moreover, it has been found that also passive observation of manipulatable objects elicits neural responses similar to the ones elicited during passive observation of others’ actions [36–39].

Hence, increasing evidence suggests that the power of beta rhythm typically decreases during the preparation and the execution of a movement [40]; it increases in the motor cortex during active immobilization [41], postural maintenance [42], proactive inhibition [43], as well as when a movement have to be withheld or voluntary suppressed [44], but also before an expected postural challenge [45]. Moreover, strong pieces of evidence have demonstrated that beta power enhancement with transcranial alternating cortical stimulation has been shown to induce motor inhibition [46].

Similar results have been found when rhythmic activity is induced in the motor cortex of healthy participants using transcranial current stimulation. Specifically, the stimulation in the beta band frequency range, reflecting an increased beta power, is particularly effective in slowing movements and increasing the threshold of inducing a motor response [47–49].

Moreover, the role played by the beta band in inhibition/disinhibition of neural motor system is supported also by studies on clinical populations. Specifically, the functional relevance of the beta band rhythm in the disinhibition of neuronal populations becomes particularly clear in Parkinson’s disease (PD), where pathological high beta band activity severely compromises movement initiation and execution [50, 51]. Taken together, these findings support the idea that the beta band power maintains the functioning of the sensorimotor cortex. Our data also support the hypothesis that beta band activity may signal the tendency of the sensorimotor

Fig 3. Scalp distributions of average beta power (decibel: $10 \times \log_{10}(\mu V^2)$) of difference between tied versus free condition (Panel A) and 4 scalp distributions of average beta power (decibel: $10 \times \log_{10}(\mu V^2)$) of difference between contraction (tied hands condition) versus free condition for each subject (Panel B).
system to maintain the status quo [52]. An interesting hypothesis is that beta band activity may allow the more efficient processing of feedback (e.g. proprioceptive signals) which is required for monitoring the status quo and recalibrating the sensorimotor system [52].

Furthermore, in order to investigate cortical generators of electrophysiological oscillations of beta frequency band, we performed signal source localization for beta power spectral data. The comparison between electrophysiological activity in the free hands and tied hands condition showed that the main signal source was localised in the left inferior frontal gyrus (l-IFG). The involvement of the l-IFG in processing action related stimuli has been shown by a large amount of studies. For instance, it has been shown that this cortex is critically involved not only in planning and executing object-related hand actions [53, 54], but also in processing both others’ object-related actions and action-related features of objects. Moreover, a large number of studies have demonstrated that viewing another’s object related action recruits the left ventral premotor cortex (PMv) as if the viewer were performing that action herself [55–60]. Finally, this area has been shown to be involved in response inhibition in a Go/NoGo task, demonstrating how the integrity of this area is critical for successful implementation of inhibitory control over motor responses [61], as well as it is crucially involved in processing visual features of objects in terms of the actions they might afford [62–65]. In this context, it has been demonstrated how l-IFG and PMv are significantly activated during gesture planning and tool use actions [66].

Furthermore, regardless of the origin of the observed effect (muscle tension during the tying hands), we have shown how the neural outcome, namely the increase in beta power in the tied hands with respect to free hands condition, cannot be considered as a consequence of muscular tension during the condition of tied hands. In this regard, we compared the scalp topography of beta power distribution of the control experiment and the main experiment. To confirm that the data obtained were not caused by muscular tension, we compared the scalp topography of beta power distribution relating to the difference between contraction (tied hands condition) versus free hands condition for each subject obtained during the control experiment and the topography of the average beta power distribution relating to the difference between tied versus free hands condition obtained during the main experiment.

To this aim, we conducted an EEG-EMG control experiment. The two conditions were the same as the main experiment (free and tied hands). Specifically, during the tied hands condition we asked participants to contract deltoids, triceps, pectorals and dorsal muscles and to keep the contraction as stable as possible. EEG activity in a resting state condition and EMG muscle activity in a resting state condition were measured from four participants. Results showed that muscular contamination was not present over the EEG channels where a significant difference between tied and free hands condition was found in the main experiment. To sum up, we have shown the effect of tying the hands on intrinsic brain activity and how this manipulation can change the activity in the beta frequency band in a resting state condition. Our result might contribute to explain the constrained hand effect commonly observed when participants perform perceptual action-related tasks.

**Limitations and future perspectives**

In the control experiment, a main limitation could be represented by the small-size of sample which could make the results inaccurate because the data collected is not enough: in fact, we recruited only 4 participants for EMG-EEG study. Indeed, it would be appropriate to increase the sample size of the EMG-EEG study to make the two samples of the main experiment and of the control experiment comparable.
Author Contributions

Conceptualization: Marcello Costantini.

Data curation: Daniele Migliorati.

Formal analysis: Filippo Zappasodi.

Methodology: Mauro Gianni Perrucci.

Writing – original draft: Brunella Donno.

References

1. Shapiro L. Embodied cognition: Routledge; 2010.

2. Rowlands M. The new science of the mind: From extended mind to embodied phenomenology: Mit Press; 2010.

3. Wilson RA, Foglia L. Embodied cognition. 2011.

4. Bondi E, Petrides M, Frey S, EvANs A. Neural correlates of mental transformations of the body-in-space. Proceedings of the National Academy of Sciences. 1995; 92(24):11180–4.

5. Cohen RG, Rosenbaum DA. Prospective and retrospective effects in human motor control: planning grasps for object rotation and translation. Psychological Research. 2011; 75(4):341–9. https://doi.org/10.1007/s00426-010-0311-6 PMID: 20941504

6. Ionta S, Perruchoud D, Draganski B, Blanke O. Body context and posture affect mental imagery of hands. PloS one. 2012; 7(3):e34382. https://doi.org/10.1371/journal.pone.0034382 PMID: 22479618

7. Overney LS, Michel CM, Harris IM, Pegna AJ. Cerebral processes in mental transformations of body parts: recognition prior to rotation. Cognitive brain research. 2005; 25(3):722–34. https://doi.org/10.1016/j.cogbrainres.2005.09.024 PMID: 16288855

8. Ionta S, Blanke O. Differential influence of hands posture on mental rotation of hands and feet in left and right handers. Experimental brain research. 2009; 195(2):207–17. https://doi.org/10.1007/s00221-009-1770-0 PMID: 19326106

9. Lopez C, Bachofner C, Mercier M, Blanke O. Gravity and observer’s body orientation influence the visual perception of human body postures. Journal of vision. 2009; 9(5):1–.

10. Dijkstra K, Kaschak MP, Zwaan RA. Body posture facilitates retrieval of autobiographical memories. Cognition. 2007; 102(1):139–49. https://doi.org/10.1016/j.cognition.2005.12.009 PMID: 16472850

11. Fox MD, Snyder AZ, Vincent JL, Corbetta M, Van Essen DC, Raichle ME. The human brain is intrinsically organized into dynamic, anticorrelated functional networks. Proceedings of the National Academy of Sciences. 2005; 102(27):9673–8.

12. Thibault RT, Lifshitz M, Raz A. Body position alters human resting-state: Insights from multi-postural magnetoencephalography. Brain imaging and behavior. 2016; 10(3):772–80. https://doi.org/10.1007/s11682-015-9447-8 PMID: 26409469

13. Pfurtscheller G, Aranibar A. Evaluation of event-related desynchronization (ERD) preceding and following voluntary self-paced movement. Electroencephalography and clinical neurophysiology. 1979; 46 (2):138–46. https://doi.org/10.1016/0013-4694(79)90063-4 PMID: 86421

14. Herrmann CS, Munk MH, Engel AK. Cognitive functions of gamma-band activity: memory match and utilization. Trends in cognitive sciences. 2004; 8(8):347–55. https://doi.org/10.1016/j.tics.2004.06.006 PMID: 15335461

15. Martinovic J, Busch NA. High frequency oscillations as a correlate of visual perception. International Journal of Psychophysiology. 2011; 79(1):32–8. https://doi.org/10.1016/j.ijpsycho.2010.07.004 PMID: 20654659

16. Tallon-Baudry C. The roles of gamma-band oscillatory synchrony in human visual cognition. Front Biosci. 2009; 14:321–32.

17. Brinkman L, Stolk A, Dijkerman HC, de Lange FP, Toni I. Distinct roles for alpha-and beta-band oscillations during mental simulation of goal-directed actions. Journal of Neuroscience. 2014; 34(44):14783–92. https://doi.org/10.1523/JNEUROSCI.2039-14.2014 PMID: 25355230

18. Cheyne DO. MEG studies of sensorimotor rhythms: a review. Experimental neurology. 2013; 245:27–39. https://doi.org/10.1016/j.expneurol.2012.08.030 PMID: 22981841

19. Hari R, Salmelin R. Human cortical oscillations: a neuromagnetic view through the skull. Trends in neurosciences. 1997; 20(1):44–9. https://doi.org/10.1016/S0166-2236(96)10065-5 PMID: 9004419
20. Jensen O, Goel P, Kopell N, Pohja M, Hari R, Ermentrout B. On the human sensorimotor-cortex beta rhythm: sources and modeling. Neuroimage. 2005; 26(2):347–55. https://doi.org/10.1016/j.neuroimage.2005.02.008 PMID: 15907295
21. Natraj N, Poole V, Mizelle J, Flumini A, Borghi AM, Wheaton LA. Context and hand posture modulate the neural dynamics of tool–object perception. Neuropsychologia. 2013; 51(3):506–19. https://doi.org/10.1016/j.neuropsychologia.2012.12.003 PMID: 23261936
22. Zimmermann M, Toni I, de Lange FP. Body posture modulates action perception. Journal of Neuroscience. 2013; 33(14):5930–8. https://doi.org/10.1523/JNEUROSCI.0570-12.2013 PMID: 23554475
23. Delorme A, Makeig S. EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. Journal of neuroscience methods. 2004; 134(1):9–21. https://doi.org/10.1016/j.jneumeth.2003.10.009 PMID: 15102499
24. Hyvärinen A, Oja E. Independent component analysis: algorithms and applications. Neural networks. 2000; 13(4–5):411–30. https://doi.org/10.1016/s0893-6080(00)00026-5 PMID: 10946390
25. Goncharova II, McFarland DJ, Vaughan TM, Wolpaw JR. EMG contamination of EEG: spectral and topographical characteristics. Clinical neurophysiology. 2003; 114(9):1580–93. https://doi.org/10.1016/s1388-2457(03)00093-2 PMID: 12948787
26. Zakeri Z, Assecondi S, Bagshaw A, Arvanitis T, editors. Influence of signal preprocessing on ICA-based EEG decomposition. XIII Mediterranean Conference on Medical and Biological Engineering and Computing 2013; 2014: Springer.
27. Fell J, Widman G, Rehberg B, Elger CE, Fernandez G. Human mediotemporal EEG characteristics during propofol anesthesia. Biological cybernetics. 2005; 92(2):92–100. https://doi.org/10.1007/s00422-004-0538-7 PMID: 15685392
28. Oostenveld R, Fries P, Maris E, Schoffelen J-M. FieldTrip: open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. Computational intelligence and neuroscience. 2011; 2011:1. https://doi.org/10.1155/2011/720971
29. Pascual-Marqui RD. Discrete, 3D distributed, linear imaging methods of electric neuronal activity. Part 1: exact, zero error localization. arXiv preprint arXiv:07103341. 2007.
30. Creem-Regehr SH, Lee JN. Neural representations of graspable objects: are tools special? Cognitive Brain Research. 2005; 22(3):457–69. https://doi.org/10.1016/j.cogbrainres.2004.10.006 PMID: 15722215
31. Amsel D, Cui F, Keyser C, Maurits NM, Gazzola V. μ-suppression during action observation and execution correlates with BOLD in dorsal premotor, inferior parietal, and SI cortices. Journal of Neuroscience. 2011; 31(40):14243–9. https://doi.org/10.1523/JNEUROSCI.0963-11.2011 PMID: 21976509
32. Cochin S, Barthelemy C, Lejeune B, Roux S, Martinez J. Perception of motion and gEEG activity in human adults. Electroencephalography and clinical neurophysiology. 1998; 107(4):287–95. https://doi.org/10.1016/s0013-4694(98)00071-6 PMID: 9872446
33. Frenkel-Toledo S, Bentin S, Perry A, Liebermann DG, Soroker N. Dynamics of the EEG power in the frequency and spatial domains during observation and execution of manual movements. Brain research. 2013; 1509:43–57. https://doi.org/10.1016/j.brainres.2013.03.004 PMID: 2350633
34. Hari R, Fosss N, Avikainen S, Kirveskari E, Salenius S, Rizzolatti G. Activation of human primary motor cortex during action observation: a neuromagnetic study. Proceedings of the National Academy of Sciences. 1998; 95(25):15061–5.
35. Perry A, Bentin S. Mirror activity in the human brain while observing hand movements: A comparison between EEG desynchronization in the μ-range and previous fMRI results. Brain research. 2009; 1282:126–32. https://doi.org/10.1016/j.brainres.2009.05.059 PMID: 19500557
36. Caggiano V, Fogassi L, Rizzolatti G, Thier P, Casile A. Mirror neurons differentially encode the peripersonal and extrapersonal space of monkeys. science. 2009; 324(5925):403–6. https://doi.org/10.1126/science.1166818 PMID: 19372433
37. Cisek P, Kalaska JF. Neural mechanisms for interacting with a world full of action choices. Annual review of neuroscience. 2010; 33:269–98. https://doi.org/10.1146/annurev.neuro.051508.135409 PMID: 20345247
38. Proverbio AM. Tool perception suppresses 10–12Hz μ rhythm of EEG over the somatosensory area. Biological psychology. 2012; 91(1):1–7. https://doi.org/10.1016/j.biopsycho.2012.04.003 PMID: 22543070
39. Proverbio AM, Adorni R, D’Aniello GE. 250ms to code for action affordance during observation of manipulable objects. Neuropsychologia. 2011; 49(9):2711–7. https://doi.org/10.1016/j.neuropsychologia.2011.05.019 PMID: 21664367
40. Pfurtscheller G, Da Silva FL. Event-related EEG/MEG synchronization and desynchronization: basic principles. Clinical neurophysiology. 1999; 110(11):1842–57. https://doi.org/10.1016/s1388-2457(99)00141-8 PMID: 10576479

41. Salmelin R, Hämäläinen M, Kajola M, Hari R. Functional segregation of movement-related rhythmic activity in the human brain. Neuroimage. 1995; 2(4):237–43. https://doi.org/10.1006/nimg.1995.1031 PMID: 9343608

42. Baker S, Olivier E, Lemon R. Coherent oscillations in monkey motor cortex and hand muscle EMG show task-dependent modulation. The Journal of physiology. 1997; 501(1):225–41.

43. Zavala B, Zaghoul K, Brown P. The subthalamic nucleus, oscillations, and conflict. Movement Disorders. 2015; 30(3):328–38. https://doi.org/10.1002/mds.26072 PMID: 25688872

44. Swann N, Tandon N, Canolty R, Ellmore TM, Droyer S, et al. Intracranial EEG reveals a time-and frequency-specific role for the right inferior frontal gyrus and primary motor cortex in stopping initiated responses. Journal of Neuroscience. 2009; 29(40):12675–85. https://doi.org/10.1523/JNEUROSCI.3359-09.2009 PMID: 19812342

45. Androulidakis AG, Doyle LM, Yarrow K, Litvak V, Gilbertson TP, Brown P. Anticipatory changes in beta synchrony in the human corticospinal system and associated improvements in task performance. European Journal of Neuroscience. 2007; 25(12):3758–65. https://doi.org/10.1111/j.1460-9568.2007.05620.x PMID: 17610595

46. Joundi RA, Jenkinson N, Britain J-S, Aziz TZ, Brown P. Driving oscillatory activity in the human cortex enhances motor performance. Current Biology. 2012; 22(5):403–7. https://doi.org/10.1016/j.cub.2012.01.024 PMID: 22305755

47. Feurra M, Bianco G, Santar encourage E, Del Testa M, Rossi A, Rossi S. Frequency-dependent tuning of the human motor system induced by transcranial oscillatory potentials. Journal of Neuroscience. 2011; 31(34):12165–70. https://doi.org/10.1523/JNEUROSCI.0978-11.2011 PMID: 21865459

48. Pogosyan A, Gaynor LD, Eusebio A, Brown P. Boosting cortical activity at beta-band frequencies slows movement in humans. Current Biology. 2009; 19(19):1637–41. https://doi.org/10.1016/j.cub.2009.07.074 PMID: 19800236

49. Wach C, Krause V, Moliadze V, Paulus W, Schnitzler A, Pollok B. Effects of 10Hz and 20Hz transcranial alternating current stimulation (tACS) on motor functions and motor cortical excitability. Behavioural brain research. 2013; 241:1–6. https://doi.org/10.1016/j.bbr.2012.11.038 PMID: 23219965

50. Brown P. Abnormal oscillatory synchronisation in the motor system leads to impaired movement. Current opinion in neurobiology. 2007; 17(6):656–64. https://doi.org/10.1016/j.conb.2007.12.001 PMID: 18221864

51. Jenkinson N, Brown P. New insights into the relationship between dopamine, beta oscillations and motor function. Trends in neurosciences. 2011; 34(12):611–8. https://doi.org/10.1016/j.tins.2011.09.003 PMID: 22018805

52. Engel AK, Fries P. Beta-band oscillations—signalling the status quo? Current opinion in neurobiology. 2010; 20(2):156–65. https://doi.org/10.1016/j.conb.2010.02.015 PMID: 20359884

53. Jeannerod M, Arbib MA, Rizzolatti G, Sakata H. Grasping objects: the cortical mechanisms of visuomotor transformation. Trends in neurosciences. 1995; 18(7):314–20. PMID: 7571012

54. Rizzolatti G, Gentilucci M. Motor and visual-motor functions of the premotor cortex. Neurobiology of neocortex. 1988; 42:269–84.

55. Buccino G, Binkofski F, Fink GR, Fadiga L, Fogassi L, Gallese V, et al. Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. European journal of neurosciences. 2001; 13(2):400–4. PMID: 11168545

56. Calvo-Merino B, Grézès J, Glaser DE, Boysson B, Haggard P. Seeing or doing? Influence of visual and motor familiarity in action observation. Current Biology. 2006; 16(19):1905–10. https://doi.org/10.1016/j.cub.2006.07.065 PMID: 17027486

57. Galati G, Committeri G, Spiloti G, Aprile T, Di Russo F, Pitzalis S, et al. A selective representation of the meaning of actions in the auditory mirror system. Neuroimage. 2008; 40(3):1274–86. https://doi.org/10.1016/j.neuroimage.2007.12.044 PMID: 18276163

58. Grafton ST, Arbib MA, Fadiga L, Rizzolatti G. Localization of grasp representations in humans by position emission tomography. Experimental brain research. 1996; 112(1):103–11. https://doi.org/10.1007/bf0027183 PMID: 8951412

59. Ortigue S, Sinigaglia C, Rizzolatti G, Grafton ST. Understanding actions of others: the electrodynamics of the left and right hemispheres. A high-density EEG neuroimaging study. PloS one. 2010; 5(8): e12160. https://doi.org/10.1371/journal.pone.0012160 PMID: 20730095
60. Rizzolatti G, Fadiga L, Gallese V, Fogassi L. Premotor cortex and the recognition of motor actions. Cognitive brain research. 1996; 3(2):131–41. https://doi.org/10.1016/0926-6410(95)00038-0 PMID: 8713554

61. Swick D, Ashley V, Turken U. Left inferior frontal gyrus is critical for response inhibition. BMC neuroscience. 2008; 9(1):102.

62. Buccino G, Sato M, Cattaneo L, Rodà F, Riggio L. Broken affordances, broken objects: a TMS study. Neuropsychologia. 2009; 47(14):3074–8. https://doi.org/10.1016/j.neuropsychologia.2009.07.003 PMID: 19615389

63. Chao LL, Martin A. Representation of manipulable man-made objects in the dorsal stream. Neuroimage. 2000; 12(4):478–84. https://doi.org/10.1006/nimg.2000.0635 PMID: 10988041

64. Grafton ST, Fadiga L, Arbib MA, Rizzolatti G. Premotor cortex activation during observation and naming of familiar tools. Neuroimage. 1997; 6(4):231–6. https://doi.org/10.1006/nimg.1997.0293 PMID: 9417966

65. Grèzes J, Tucker M, Armony J, Ellis R, Passingham RE. Objects automatically potentiate action: an fMRI study of implicit processing. European Journal of Neuroscience. 2003; 17(12):2735–40. https://doi.org/10.1046/j.1460-9568.2003.02695.x PMID: 12823480

66. Johnson-Frey SH, Newman-Norlund R, Grafton ST. A distributed left hemisphere network active during planning of everyday tool use skills. Cerebral cortex. 2004; 15(6):681–95. https://doi.org/10.1093/cercor/bhh169 PMID: 15342430