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Combined and singular effects of Action Observation and Motor Imagery paradigms on resting-state sensorimotor rhythms

Aleksandar Miladinović¹, Antonella Barbaro², Eddi Valvason², Miloš Ajčević^{1,3,4},
Agostino Accardo¹, Piero Paolo Battaglini², Joanna Jarmolowska³

¹Department of Engineering and Architecture, University of Trieste, Via A. Valerio 10 34127 Trieste, Italy

²Department of Life Sciences, University of Trieste, Via Fleming 22, 34127 Trieste, Italy

³Department of Medicine Surgery and Health Sciences, University of Trieste, Trieste, Italy

⁴NEUROFARBA Department, Neuroscience Section, University of Florence, Italy

`aleksandar.miladinovic@phd.units.it`

Abstract. In the present study, 30 right-handed participants randomly performed one of three motor neurorehabilitation paradigms: action observation (AO), motor imagery (MI) and combined action observation and motor imagery (AO+MI) of the right arm and hand movement. Resting state electroencephalography (EEG) was acquired for 5 minutes before and immediately after the motor paradigms session. EEG was recorded from 10 sites over sensorimotor areas, and the average power was calculated for left (FC3, C3, C1, C5, CP3) and right (FC4, C4, C2, C6, CP4) regions in the spectral bands: delta, theta, alpha, mu, low and high beta. Our main finding demonstrates that delta, theta and mu activity decreased significantly on the contralateral regions during MI, while low beta increased significantly. Except for the mu band, the same changes were observed on the ipsilateral side, where delta and theta decreased significantly, while low beta became significantly higher. No relevant effects were observed for AO or combined AO and MI. These findings demonstrate a rapid effect of MI on cortical modulation in sensorimotor areas which is revealed by changes in resting state oscillatory activity and suggest an interesting interplay between MI and AO. The presented findings may be relevant for choosing a proper protocol for clinical motor neurorehabilitation approaches.

Keywords: Motor Imagery, Action Observation, EEG, Biomedical Signal Processing-

1 Introduction

It is known that action observation (AO) engages almost the same brain regions as action execution [1, 2]. The neurophysiological basis for this hypothesis lies in the presumed human mirror neuron system, where cortical motor regions that are active both when we execute an action and when we observe similar actions being performed by others [1, 2, 3]. Recent work has described that “action observation network” involves parietal, premotor, and occipitotemporal brain regions [2, 4]. By sharing motor circuits with action execution, AO may prime the motor system for subsequent motor practice [5, 6]. In that regards, in the last decade, AO has been recommended in the clinical environment as additional practice in neurorehabilitation settings [7, 8].

Motor imagery (MI), on the other hand, is a cognitive process during which the execution of a motor action is internally prepared without any motor output [9, 10]. Although no actual movement is made, functional magnetic resonance imaging (fMRI) and electroencephalography (EEG) studies have shown that the brain regions engaged in action execution are also activated in MI [10]. The cognitive literature proposes that the effective kinesthetic sensations, including movement, effort, heaviness, and position provide information that enables the human system to determine the position of limbs and to identify the origins and the cause of action [11]. Further, it has been proposed that there are functional equivalence and the use of common neural pathways in motor preparation/execution and motor imagery [12, 13]. Thus, because motor preparation/execution and motor imagery involve the same motor representation systems, they likely have the same neuronal substrates [1, 2, 14].

In the neurorehabilitation practice, both AO and MI have shown beneficial effects [15, 16]. Moreover, together with physical exercise, MI does not produce only beneficial effects on athletes [17] and musicians [18], but also improves behavioral outcomes on a clinical population suffering from stroke and other neurological impairments [5, 6, 19].

The cortical activation using either AO or MI alone was studied [20], but until now, the investigations on how to combine MI with AO are quite rare. According to recent studies, combined AO and MI could enhance the activation of motor circuits by producing changes in the EEG [21, 22], suggesting that the combined use of them might be even more useful. On these bases, in order to investigate the possibility of development of new neurorehabilitation protocols, this study examines changes in resting state oscillatory activity in the sensorimotor area after AO, MI and their simultaneous application, in healthy subjects.

2 Materials and Methods

2.1 Subjects and experimental protocol

Experiments were performed on 30 right-handed (Edinburgh Handedness Inventory [23] 83.5 ± 19.3) participants (18 females, 12 males; mean \pm 1SD age: 21.66 ± 1.18 years), all with normal or corrected-to-normal vision. The subjects' motor capabilities were evaluated by Italian version of Movement Imagery Questionnaire [24, 25]. The research was conducted according to the principles of the Declaration of Helsinki. All participants released their informed consent to participate in the study after all procedures had been fully explained.

Participants were randomly assigned to one of three motor neurorehabilitation paradigms: AO, MI and combined AO+MI, thus yielding three different groups with 10 participants each. The experimental protocol consisted of: (1) pre resting-state recording, (2) one of the mentioned paradigms repeated for 40 times and (3) post resting-state recording (Fig. 1). To avoid subjects fatigue and to increase comfort, after each 10 trials in (2) a long pause was introduced. In each experimental block, participants were seated in a dark room in a front of a computer screen that was located at eye-height in front of the observer's central viewing position.

In the AO paradigm, subjects were asked to watch a video showing a right hand reaching, grasping and moving objects. The video was filmed from the subject perspective, with the aim to create an immersive effect. A male or female hand was displayed in accordance with the subject's gender. Each trial started with the warning "beep" sound followed by two seconds of black screen after which the video-clip

started to play automatically. The single video had a duration of 6.5 seconds and it was presented 40 times. In order to keep subjects attentive, two types of videos with a randomized number of precision or coarse grasp into a single block (of 10 trials) were presented and the subjects were instructed to count the number of appearances of one of them and report it after an experimental block of 10 trials.

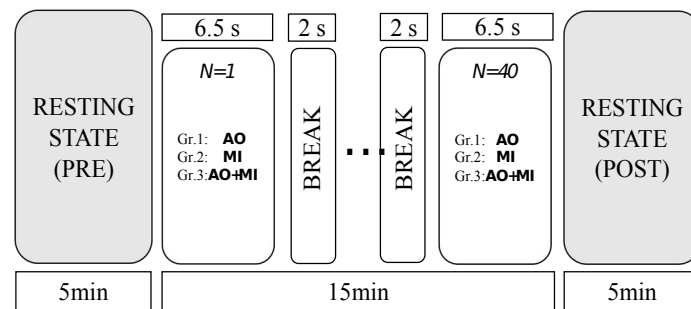


Fig. 1. A schematic diagram of the experimental protocol which begins and ends with the resting-state recordings of 5min (gray boxes) and administers (for N=40 repetitions) one of the AO, MI and AO+MI paradigms, to each 10-participant group (denoted by Gr.1-3).

In the MI paradigm, the subjects were trained on how to properly perform motor imagery, simulating their proprioception and adopting the first-person perspective (i.e. imagining the movement of their own hand). After the training, the recording session started with the "beep" warning followed by the still image of a grip (hand movement) as in AO. In this case, subjects were instructed to mentally simulate the action by trying to "experience the same feelings as during the actual execution" facilitating kinesthetic motor imagery approach. As in AO, the subjects had 6.5 seconds for MI and the process repeats for 40 times.

For the AO+MI condition, subjects observed the same videos presented in AO, but in this case, they were additionally required to perform MI corresponding to the displayed video. The paradigm was performed with the same parameters (duration and repetition) as the previous two.

2.2 EEG acquisition and processing

5-minutes resting state EEG for each subject were recorded before and immediately after each session. EEG signals were sampled at 256 Hz by using SAM 32FO amplifier (Micromed, Treviso, Italy) and a prewired headcap with 10 Ag/AgCl electrodes (Spes Medica, Genova, Italy) placed at standard 10-10 locations covering the sensorimotor area (FC3, FC4, C3, C4, C1, C2, C5, C6, CP3 and CP4). The reference electrode was placed in POz, while the ground electrode was placed in AFz. Electrode impedances were kept below 5 k Ω . EOG activity was recorded to identify eye-movement artifacts. EEG off-line analysis was carried out using MATLAB® (The Math-Works Inc., Natick, MA). All channels were digitally filtered with the 0.5-45 Hz 2nd order Butterworth bandpass filter. Artifacts were manually discarded after visual inspection of tracings and 60 seconds of stationary EEG signal pre and after motion paradigm epochs were selected for spectral analysis. Power spectral density (PSD) was estimated for each channel using Welch's periodogram [26] (averaged on 11 tracts of 10s each, windowed with a Hamming window, with 50% overlap). Subsequently, for each channel the relative power in each spectral band (delta: 0.5-4Hz; theta: 4-8Hz; alpha: 8-13Hz; mu: 8-10Hz; beta_{low}: 13-18Hz; beta_{high}: 18-30Hz) was calculated. For each subject and each band average power was calculated for left (FC3, C3, C1, C5 and CP3) and right (FC4, C4, C2, C6 and CP4) sensorimotor area channels. Differences between pre and post activity for each of three motion paradigms and for each power band were determined by using Wilcoxon signed-rank test. P-values < 0.05 were considered statistically significant.

3 Results

Median and range values of relative powers of the considered bands during the resting state before (PRE) and after (POST) each of the three performed paradigms are reported in Table 1. Difference between PRE and POST activity in the case of MI, showed a significant decrease of power in the delta, theta and mu bands on the left contralateral sensorimotor area, while low beta increased significantly. Except for the mu band, similar behavior was observed on right ipsilateral side, where delta and theta also decreased significantly, and low beta became significantly higher. No sig-

nificant changes were observed for AO in any of the analysed bands. In the case of AO+MI, a significant difference was found only in the theta band, which decreased in both hemispheres.

Table 1. Median (range) values of relative power in delta, theta, beta and sigma bands during the resting state right before and after each of the three paradigms (MI, AO and AO+MI). * statistically different from Pre (p-value < 0.05).

SM Area	BAND	Paradigm	PRE	POST	p-value
Left contralateral	delta	AO	0.413 (0.275-0.478)	0.437 (0.330-0.565)	0.148
		MI	0.429 (0.226-0.517)	0.377 (0.154-0.545)	0.049 *
		AO+MI	0.412 (0.279-0.671)	0.342 (0.263-0.770)	0.82
	theta	AO	0.120 (0.084-0.198)	0.121 (0.092-0.158)	0.461
		MI	0.110 (0.081-0.198)	0.085 (0.059-0.170)	0.004 *
		AO+MI	0.118 (0.075-0.171)	0.085 (0.073-0.168)	0.027 *
	alpha	AO	0.085 (0.068-0.193)	0.082 (0.062-0.254)	0.844
		MI	0.082 (0.071-0.135)	0.078 (0.054-0.135)	0.557
		AO+MI	0.089 (0.045-0.132)	0.072 (0.038-0.128)	0.203
	mu	AO	0.038 (0.029-0.093)	0.034 (0.020-0.064)	0.109
		MI	0.035 (0.027-0.065)	0.029 (0.021-0.045)	0.048 *
		AO+MI	0.037 (0.026-0.058)	0.031 (0.017-0.045)	0.164
	beta _{low}	AO	0.098 (0.048-0.394)	0.135 (0.064-0.211)	0.945
		MI	0.127 (0.055-0.342)	0.203 (0.077-0.498)	0.01 *
		AO+MI	0.111 (0.060-0.326)	0.142 (0.039-0.349)	0.25
	beta _{high}	AO	0.147 (0.116-0.227)	0.132 (0.073-0.176)	0.195
		MI	0.154 (0.062-0.392)	0.137 (0.068-0.408)	0.77
		AO+MI	0.165 (0.041-0.287)	0.118 (0.042-0.304)	0.95
Right ipsilateral	delta	AO	0.383 (0.276-0.571)	0.384 (0.283-0.527)	0.94
		MI	0.444 (0.211-0.526)	0.351 (0.128-0.544)	0.037 *
		AO+MI	0.497 (0.263-0.664)	0.375 (0.285-0.688)	0.426
	theta	AO	0.120 (0.084-0.191)	0.113 (0.090-0.170)	0.461
		MI	0.106 (0.072-0.202)	0.086 (0.057-0.174)	0.02 *
		AO+MI	0.124 (0.088-0.166)	0.101 (0.060-0.146)	0.008 *
	alpha	AO	0.099 (0.069-0.193)	0.095 (0.050-0.234)	0.742
		MI	0.079 (0.061-0.106)	0.076 (0.045-0.136)	0.846
		AO+MI	0.086 (0.042-0.134)	0.073 (0.048-0.132)	0.652
	mu	AO	0.040 (0.031-0.082)	0.040 (0.020-0.057)	0.312
		MI	0.035 (0.024-0.051)	0.032 (0.014-0.041)	0.105
		AO+MI	0.035 (0.018-0.063)	0.032 (0.016-0.050)	0.301
	beta _{low}	AO	0.128 (0.042-0.427)	0.172 (0.093-0.280)	0.25
		MI	0.123 (0.057-0.363)	0.163 (0.097-0.533)	0.004 *
		AO+MI	0.096 (0.065-0.232)	0.154 (0.062-0.350)	0.25
	beta _{high}	AO	0.150 (0.096-0.195)	0.141 (0.101-0.188)	0.945
		MI	0.127 (0.062-0.433)	0.153 (0.060-0.435)	0.922
		AO+MI	0.133 (0.069-0.209)	0.099 (0.059-0.290)	0.652

4 Discussion

The main finding of our study is that motor imagination induces higher activation of motor cortex with respect to action observation or their combination, inducing significant changes of resting-state EEG in mu and low beta bands, also known as sensorimotor (SMR) bands, and in the slower oscillatory bands, in particular delta and theta.

The effect of MI on mu rhythms could be explained by the specific repetitive motor event-related synchronization (ERS) and desynchronization (ERD) occurring during imagination. During ERS/EDR the strongest activity is present on the contralateral hemisphere with respect to the imagined arm [27, 28, 29], which can lead to effective changes of the resting-state EEG even after the MI session has been completed.

On the other hand, the significant increase in the lower beta band, in MI in comparison to AO and AO+MI, could be interpreted as a result of repeated motor specific beta rebounds (ERS) occurring immediately after every imagination on both contralateral and ipsilateral hemisphere, and are physiologically related to sustained muscle contraction or voluntary movement [29].

The participants in the present study were explicitly asked to use motor imagery in order to simulate a movement. Therefore, we speculate, that motor imagery can assist in the creation of a vivid simulation of the same feelings as during the actual execution [30, 31], activating in this way, the common neural pathways in motor preparation/execution and motor imagery [12, 13]. Our results suggest that motor imagery induce most efficiently changes of resting-state of SMR.

Regarding the effects of AO on the resting-state, in our case, no significant change was observed. The possible lack of attention during the task has to be disregarded as an explanation for the results, since all subjects had excellent performance on the side-task (counting the repetition of hand movements) that controlled their focus on task. As a matter of fact, the inefficacy of AO to induce significant corticomotor variation in SMR is probably due to a lower activation causing no significant variation of resting-state activity with respect to MI.

Concerning the effects of combined action observation and motor imagery on the resting-state of SMR, in our case, no significant change was founded. Therefore, we must recognize that brain activity during motor imagery with action observation was not simply the sum of these two tasks. It should be noted that in such dual task, the cognitive load requested to the participants was very high and this could have an impact on its efficiency.

Clearly, our results support the idea that MI, AO and AO+MI all cause different changes of SMR. In fact, despite apparent similarity, suggesting a common substrate underlying MI and AO [32], the present results show important differences between them, that could be explained from a different theoretical point of view.

MI is an explicit covert mental state during which participants internally simulate a movement without actually performing it [33]. As during real execution, mental simulation of movement involves anticipations about sensory and motor effects of that action. Precisely, the framework of internal models suggests that, during both actual and imagined actions, the future sensorimotor state is predicted by the given efferent copy of the motor command and the current state of the body [33]. It has been proposed that such kinesthetic feeling related to the limb is typically processed through the parietal region that modulates, in turn, motor cortex facilitation during MI [34].

In contrast, during AO, the visual inputs of the movement performed by the others would not have immediate access to the observer's motor system [33]. In this context, our results are not in contrast with previous findings, which have suggested the existence of a common neural substrate for MI and AO. We believe that both AO and MI activate the motor network but exploit different sensory-motor processes. AO is based on the processing of visual information involved in the movement, indirectly activating the motor cortex [33]. This is a type of bottom-up processing, in which attention is mainly focused on sensory input that is external to the body. On the other hand, MI is related to top-down internal processing. This is the main difference, which in our opinion, can explain why in a short session of only 15 minutes, MI, but not AO, activated the motor system rapidly, causing a change in the oscillatory activity in the following resting state.

In other words, we suggest that mental simulation of movement, which involves anticipations about sensory and motor effects of that action, induces higher activation of motor cortex with respect to action observation.

We also found that theta power band decreased bilaterally in MI and in AO+MI and that the delta power band decreased contralaterally in MI. The role of the theta band is usually related to memory formation, information processing [35], working memory [36] and sensorimotor integration [37]. It was also reported that the theta band plays a role in tasks of motor imagery [38]. There is some evidence supporting the idea that frontal theta EEG activity correlates negatively with the default mode network in resting state [39]. Another study reports that amplitude increase in low frequency oscillations (e.g. delta, theta) are related to a decrease of BOLD signal. Based on theoretical considerations, it is suggested that higher energy dispersal, and therefore a higher BOLD signal, is related to a relative shift in neuronal activity from lower to higher frequencies [40]. This would result in, for instance, reduced delta and theta and increased beta amplitudes. For this reason, we suggest that default mode network of brain regions could be deactivated during attention-demanding cognitive tasks required by both MI and AO+MI paradigm. Thus, the delta and theta decrease may be considered to reflect the participant's sensory-motor integration and attention load.

In conclusion, our results demonstrate a direct and rapid effect of cortical modulation induced by MI on the EEG resting-state. Moreover, they show important differences between MI and AO. Such information may be used to improve clinical protocols of AO and MI in therapeutic approaches that can include also BCI neurofeedback protocols.

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Conflict of interest

The authors have no conflict of interest to declare.

References

1. Di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., Rizzolatti, G.: Understanding motor events: a neurophysiological study. *Exp Brain Res* 91:176-80, (1992).
2. Gallese, V., Fadiga, L., Fogassi, L., Rizzolatti, G.: Action recognition in the premotor cortex. *Brain*, 119(Pt 2):593-609 (1996).
3. Rizzolatti, G., Craighero, L.: The mirror-neuron system. *Annual Review of Neuroscience*. 27:169–192 (2004).
4. Lotze, M., Montoya, P., Erb, M., Hülsmann, E., Flor, H., Klose, U., Birbaumer, N., Grodd, W.: Activation of Cortical and Cerebellar Motor Areas during Executed and Imagined Hand Movements: An fMRI Study. *J. Cogn. Neurosci.* 11, 491–501 (1999).
5. Pomeroy, V., Aglioti, S.M., Mark, V.W., McFarland, D., Stinear, C., Wolf, S.L., Corbetta, M., Fitzpatrick, S.M.: Neurological Principles and Rehabilitation of Action Disorders. *Neurorehabil. Neural Repair*. 25, 33S-43S (2011).
6. Ertelt, D., Small, S., Solodkin, A., Dettmers, C., McNamara, A., Binkofski, F., Buccino, G.: Action observation has a positive impact on rehabilitation of motor deficits after stroke. *Neuroimage*. 36, T164–T173 (2007).
7. Buccino, G.: Action observation treatment: a novel tool in neurorehabilitation. *Philos. Trans. R. Soc. B Biol. Sci.* 369, 20130185–20130185 (2014).
8. Ste-Marie, D.M., Law, B., Rymal, A.M., Jenny, O., Hall, C., McCullagh, P.: Observation interventions for motor skill learning and performance: an applied model for the use of observation. *Int. Rev. Sport Exerc. Psychol.* 5, 145–176 (2012).
9. Jeannerod, M.: Neural Simulation of Action: A Unifying Mechanism for Motor Cognition. *Neuroimage*. 14, S103–S109 (2001).
10. Sharma, N., Baron, J.-C.: Does motor imagery share neural networks with executed movement: a multivariate fMRI analysis. *Front. Hum. Neurosci.* 7, 564–570 (2013).
11. Enoka, R. M.: *Neuromechanical basis of kinesiology* (2nd ed.). Champaign, IL: Human Kinetics (1994).
12. Decety, J.: Neural mechanisms subserving the perception of human actions. *Trends Cogn. Sci.* 3, 172–178 (1999).
13. Jeannerod, M.: The 25th Bartlett Lecture: To Act or Not to Act: Perspectives on the Representation of Actions. *Q. J. Exp. Psychol. Sect. A*. 52, 1–29 (1999).
14. Porro, C.A., Cettolo, V., Francescato, M.P., Baraldi, P.: Ipsilateral involvement of primary motor cortex during motor imagery. *Eur. J. Neurosci.* 12, 3059–3063 (2000).
15. Schuster, C., Hilfiker, R., Amft, O., Scheidhauer, A., Andrews, B., Butler, J., Kischka, U., Ettlin, T.: Best practice for motor imagery: a systematic literature review on motor imagery training elements in five different disciplines. *BMC Med.* 9, 75 (2011).

16. Sharma, N., Pomeroy, V.M., Baron, J.-C.: Motor imagery: a backdoor to the motor system after stroke? *Stroke*. 37, 1941–1952 (2006).
17. Holmes, P., Calmels, C.: A Neuroscientific Review of Imagery and Observation Use in Sport. *J. Mot. Behav.* 40, 433–445 (2008).
18. Lotze, M., Halsband, U.: Motor imagery. *J Physiol* 99, 386–395 (2006).
19. Jackson, P.L., Lafleur, M.F., Malouin, F., Richards, C., Doyon, J.: Potential role of mental practice using motor imagery in neurologic rehabilitation. *Arch. Phys. Med. Rehabil.* 82, 1133–1141 (2001).
20. Macuga, K.L., Frey, S.H.: Neural representations involved in observed, imagined, and imitated actions are dissociable and hierarchically organized. *Neuroimage*. 59, 2798–2807 (2012).
21. Vogt, S., DiRienzo, F., Collet, C., Collins, A., Guillot, A.: Multiple roles of motor imagery during action observation. *Front Hum Neurosci* 7, 807 (2013).
22. Eaves, D. L., Riach, M., Holmes, P. S., Wright, D. J.: Motor Imagery during Action Observation: A Brief Review of Evidence, Theory and Future Research Opportunities. *Frontiers in Neuroscience* 10, 514 (2016).
23. Oldfield, R.C.: The Assessment and Analysis of Handedness: The Edinburgh Inventory. *Neuropsychologia* 9(1), 97–113 (1971).
24. Hall, C. R., Kathleen A. M.: Measuring Movement Imagery Abilities: A Revision of the Movement Imagery Questionnaire. *Journal of Mental Imagery* 21, 143–54 (2012).
25. Williams, S. E., Cumming, J., Ntoumanis, N., Nordin-Bates, S. M., Ramsey, R., Hall, C.: Further validation and development of the Movement Imagery Questionnaire. *Journal of Sport & Exercise Psychology* 34, 621-646 (2012).
26. Welch, P.: The use of fast Fourier transform for the estimation of power spectra: a method based on time averaging over short, modified periodograms. *IEEE Transactions on audio and electroacoustics* 15(2), 70-73 (1967).
27. Pfurtscheller, G., Brunner, C., Schlogl, A., Lopes da Silva, F.H.: Mu rhythm (de)synchronization and EEG single-trial classification of different motor imagery tasks. *NeuroImage* 31, 153–159 (2006).
28. Pfurtscheller, G., Aranibar, A.: Event-related cortical desynchronization detected by power measurements of scalp EEG. *Electroencephalogr Clin Neurophysiol* 42, 817–826 (1977).
29. Van Elswijk, G., Maj, F., Schoffelen J-M., Overeem, S., Stegeman, D.F., Fries, P.: Corticospinal beta-band synchronization entails rhythmic gain modulation. *J Neurosci* 30, 4481–4488 (2010).
30. Sirigu, A., Duhamel, J.R., Cohen, L., Pillon, B., Dubois, B., Agid, Y.: The mental representation of hand movements after parietal cortex damage. *Science* 273, 1564–1568 (1996).
31. Papaxanthis, C., Schieppati, M., Gentili, R., Pozzo, T.: Imagined and actual arm movements have similar durations when performed under different conditions of direction and mass. *Exp Brain Res* 143, 447–452 (2002).
32. Hardwick, R.M., Caspers, S., Eickhoff, S.B., Swinnen, S.P.: Neural Correlates of Motor Imagery, Action Observation, and Movement Execution: A Comparison Across Quantitative Meta-Analyses. *Neurosci Biobehav Rev* 94, 31-44 (2018).
33. Jeannerod, M.: Neural simulation of action: a unifying mechanism for motor cognition. *Neuroimage*. 14, S103–S109 (2001).
34. Tian, X., Poeppel, D.: Mental imagery of speech and movement implicates the dynamics of internal forward models. *Front Psychol* 1, 166 (2010).

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35. McCartney, H., Johnson, A.D., Weil, Z.M., Givens, B.: Theta reset produces optimal conditions for long-term potentiation. *Hippocampus* 14, 684–687 (2004).
36. Jensen, O., Tesche, C.D.: Frontal theta activity in humans increases with memory load in a working memory task. *Eur J Neurosci* 15, 1395–1399 (2002).
37. Cruikshank, L.C., Singhal, A., Hueppelsheuser, M., Caplan, J.B.: Theta oscillations reflect a putative neural mechanism for human sensorimotor integration. *J Neurophysiol* 107, 65–77 (2012).
38. Kahana, M.J., Seelig, D., Madsen, J.R.: Theta returns. *Curr Opin Neurobiol* 11, 739–744 (2001).
39. Scheeringa, R., Bastiaansen, M. C., Petersson, K. M., Oostenveld, R., Norris, D. G., Haagoort, P.: Frontal theta EEG activity correlates negatively with the default mode network in resting state. *International journal of psychophysiology* 67(3), 242-251 (2008).
40. Kilner, J.M., Mattout, J., Henson, R., Friston, K.J.: Hemodynamic correlates of EEG: a heuristic. *Neuroimage* 28, 280-286 (2005).