

Contents lists available at SciVerse ScienceDirect

# Clinical Neurophysiology

journal homepage: www.elsevier.com/locate/clinph



# Watching object related movements modulates mirror-like activity in parietal brain regions



S.C. Wriessnegger a,\*, R. Leeb , V. Kaiser , C. Neuper a,b, G.R. Müller-Putz a

- <sup>a</sup> Institute for Knowledge Discovery, Graz University of Technology, Inffeldgasse 13/4, 8010 Graz, Austria
- <sup>b</sup> Department of Psychology, University of Graz, Universitätsplatz II, 8010 Graz, Austria
- <sup>c</sup> Chair on Non-Invasive Brain–Machine Interface, Center for Neuroprosthetics, École Polytechnique Fédérale de Lausanne, 1015 Lausanne, Switzerland

#### ARTICLE INFO

Article history: Accepted 25 February 2013 Available online 26 March 2013

Keywords: Movement observation EEG ERD/ERS Mu rhythm Mirror neuron system

#### HIGHLIGHTS

- The observation of goal-directed movements leads to stronger event-related desynchronization (ERD) in alpha, beta and gamma frequency bands over parietal compared to central brain regions.
- Both the type of grasping and the type of object induced an ERS over sensorimotor areas in the upper alpha and lower beta band, respectively.
- Beside the often cited MNS linked mu rhythm there is further cortical rhythmicity over parietal sites, which might be part of an "extended" human MNS.

### ABSTRACT

Objective: We studied the activation of cortical motor and parietal areas during the observation of object related grasping movements. By manipulating the type of an object (realistic versus abstract) and the type of grasping (correct versus incorrect), we addressed the question how observing such object related movements influences cortical rhythmicity, especially the mu-rhythm, in the context of an "extended" human mirror neuron system (MNS).

Methods: Multichannel electroencephalogram (EEG) was recorded during the observation of different object-related grasping actions in twenty healthy subjects. Different movies were presented, showing sequences of correct or incorrect hand grasping actions related to an abstract or realistic (daily life) object.

Results: Event-related de/synchronization (ERD/ERS) analyses revealed a larger ERD in the upper alpha (10–12 Hz), beta (16–20 Hz) and gamma (36–40 Hz) frequency bands over parietal brain regions depending on the type of grasping. The type of object only influenced ERD patterns in the gamma band range (36–40 Hz) at parietal sites suggesting a strong relation of gamma band activity and cortical object representation. Abstract and realistic objects produced lower beta band synchronization at central sites only, whereas depending on the type of grasping an ERS in the upper alpha band (10–12 Hz) was observed. Conclusion: Depending on the type of the grasped object and the type of grasping stronger parietal cortical activation occurred during movement observation.

Significance: Discussing the results in terms of an "extended" human mirror neuron system (MNS), it could be concluded that beside sensorimotor areas a stronger involvement of parietal brain regions was found depending on the type of object and grasping movement observed.

© 2013 International Federation of Clinical Neurophysiology. Published by Elsevier Ireland Ltd. All rights

#### 1. Introduction

In the past years several studies employing electroencephalography (EEG) (Cochin et al., 1998; Babiloni et al., 2002;

Muthukumaraswamy et al., 2004; Oberman et al., 2007; Pfurtscheller et al., 2007; Perry and Bentin, 2009) or magnetoencephalography (MEG), (Salmelin and Hari, 1994; Hari et al., 1997, 1998; Jarvelainen, 2004) have demonstrated an attenuation of oscillatory activity during movement observation, which is similar to movement execution, primarily in the primary motor cortex regions (Neuper et al., 2009). Most of the EEG studies found a suppression of the mu rhythm (8–13 Hz) over sensorimotor regions associating this result with the mirror neuron system (MNS)

<sup>\*</sup> Corresponding author. Address: Laboratory of Brain-Computer Interfaces, Institute for Knowledge Discovery, Graz University of Technology, Inffeldgasse 13/4, A-8010 Graz, Austria. Tel.: +43 316 873 30715; fax: +43 316 873 30702.

E-mail address: s.wriessnegger@tugraz.at (S.C. Wriessnegger).

(Rizzolatti et al., 1996; Rizzolatti and Arbib, 1998) in humans (Cochin et al., 1998, 1999; Muthukumaraswamy et al., 2004; Pineda, 2005; Perry and Bentin, 2009). The so called mirror neurons fire both when an action is performed and when a similar action is observed (Rizzolatti and Craighero, 2004). Also MEG studies reported similar effects, namely an attenuation of activity in the mu (~10 Hz) and beta frequency bands (~20 Hz) during action observation (Hari et al., 1997, 1998), which have also been discussed in the context of MNS phenomena. Further support for the existence of a human analog to the MNS has been provided by a lot of functional magnetic resonance imaging (fMRI) studies (Fadiga et al., 1995; Buccino et al., 2001; Decety et al., 2002; Grezes and Decety, 2001; Grèzes et al., 2003; Iacoboni et al., 2005; Shmuelof and Zohary, 2005; Iacoboni and Wilson, 2006; Biagi et al., 2010; Newman-Norlund et al., 2010).

All the studies implied that humans possess a MNS that produces similar neuronal patterns for body movements, either observed or executed. For example Buccino et al. (2001) localized brain areas that were active during the observation of object-related and non-object-related movements of different effectors (mouth, hand, foot). Observation of both object-related and non-object-related movements determined activation of the premotor cortex, while the observation of object-related movements was additionally reflected in activation of the posterior parietal lobe. Additionally, the activation patterns in the premotor cortex were effector related and somatotopically organized. That is, the MNS in humans is not only restricted to the observation of hand actions but includes a rich repertoire of body movements (Ulloa and Pineda, 2007).

Focusing on the investigation of the MNS through analyses of EEG so far there is agreement that in particular the mu frequency band oscillation is linked to frontal mirror neuron activity (Pineda, 2005). The mu rhythm is an 8-13 Hz oscillation generated primarily in the sensorimotor cortex and it reaches its maximum in resting situation (Gastaut and Bert, 1954). In case of movement execution, imagination or observation of movements, neurons in this area fire asynchronously, resulting in reduced mu rhythm amplitudes (Pfurtscheller and Neuper, 1997; Pineda et al., 2000). Moreover, it is known that EEG desynchronization resulting from thalamocortical stimulation is a reliable correlate of activated cortical areas (Goldman et al., 2002), while EEG synchronization is a correlate of deactivated cortex (Pfurtscheller et al., 1996). In particular, event-related desynchronization (ERD) reflects cortical activation and event-related-synchronization (ERS) has been assumed to reflect deactivation, inhibition or a so called "idling" state of the network (Neuper and Pfurtscheller, 2001). For example, Muthukumaraswamy et al. (2004) found that the mu rhythm is suppressed during observation of object-directed actions compared to the observation of a flat-hand extension, supporting the idea that the mu rhythm reflects a kind of downward premotor cortex modulation of primary sensorimotor areas (Muthukumaraswamy et al., 2004).

Further support for a link between mu suppression and the human MNS comes from Perry and Bentin (2009). In their EEG study they used the same stimuli as used in the fMRI study performed by Shmuelof and Zohary (2005), investigating the differences in mu suppression following the observation of different grasping of objects. They found larger mu suppression in the contralateral hemisphere and also a larger suppression when the hands grasped different objects in different ways than when the movement was repetitive. Additionally no suppression was found while participants observed still objects. A recent EEG study performed by Avanzini and colleagues (2012) could also show that observation of different types of hand movements (target directed, non-target directed, cyclic and non-cyclic) elicits desynchronization of rhythms from cortical central regions. Furthermore, movement-

related event-related desynchronization (ERD) in the alpha band is usually observed not only over primary sensorimotor areas (mu ERD), but also over the posterior parietal cortex (Neuper and Pfurtscheller, 1996; Andrew and Pfurtscheller, 1997; Pfurtscheller and Neuper, 1997; Babiloni et al., 1999). For example, Babiloni et al. (2002) demonstrated a stronger alpha ERD during movement observation over parietal-occipital areas than over central areas (Neuper et al., 2009). Also Buccino et al. (2001, 2004) reported beside prefrontal activation also parietal activation during action observation. These data suggest that the mirror-like properties occurring in parietal areas are indeed part of an extended mirror neuron system (Pineda, 2008). Furthermore, it has also been suggested that only observation of actions belonging to the motor repertoire can be mapped onto the observer's motor system (Buccino et al., 2004). Johnson-Frey et al. (2003) tested whether mirror cells respond selectively to hand-object interactions captured in static pictures of the same objects being grasped or touched. Results of their event-related fMRI investigation demonstrated that left and right precentral and inferior frontal (pars triangularis and pars opercularis) gyri are selectively activated when subjects passively observe realized goals of hand-object interactions. Another fMRI study (Costantini et al., 2005), tried to determine the pattern of neural activity evoked by observation of biomechanically impossible, articulated finger movements. They found that while premotor areas code human actions regardless of whether they are biologically possible or impossible, sensorimotor parietal regions may be important for coding the plausibility of actions. Additionally, other studies focusing on the importance of the MNS in processing the "intentionality" behind actions with a recognizable goal (Biagi et al., 2010; Newman-Norlund et al., 2010; Enticott et al., 2011).

Summarizing the literature there is strong evidence that actions are organized along different parameters selecting specific motor sequences on the basis of a desired outcome. That is motor representations following action observation are not limited to simple kinematic configurations but are organized according to the purpose they will fulfill. Furthermore, most of the actions which were performed are associated with a specific goal and therefore it is not surprising that motor activation maps are stored in parallel with their corresponding action goals (Ocampo and Kritikos, 2011). Moreover, the overlapping neural sources of the extended MNS in sensorimotor frontoparietal networks support the argument that it is related and involved in linking perception to action. The goal of the present study was to investigate event-related de/synchronization (ERD/ERS) patterns during the observation of different types of object-related movements. More concretely, to disentangle the effects of the presence of an object and its "affordance" and goal-directed successful grasping versus non successful grasping we implemented two main conditions: first, the "object condition", where grasping actions with realistic objects, (i.e. everyday life objects with high affordance, see Gibson, 1977; Norman, 1988) versus abstract objects (without implicit affordance) were presented. Since affordances provide strong clues to the operations of things, primarily to those fundamental properties that determine just how the thing could possibly be used (Norman, 1988) we expected different brain patterns depending on the type of object observed. Second, the "grasping condition", where correct (i.e. successful) object directed grasping versus incorrect (i.e. non successful: meaning either in a not correct way or not reaching the object) grasping actions was presented. By implementing these conditions in the action-observation process we wanted to address the question in which way and where the type of grasping (correct/ incorrect/beside) and the type of object (realistic/abstract) influences cortical rhythmicity (ERD/ERS) in the context of an extended MNS.

#### 2. Materials and methods

#### 2.1. Subjects

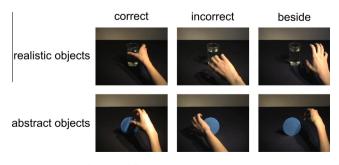
Twenty healthy individuals, 14 females and 6 males, aged 20 to 28 years (mean age:  $24 \pm 2.4$ ), with no history of neurological disorders, were recruited from a database of volunteers. All participants were naive to the purpose of the study and were paid for their participation. Subjects had normal or corrected-to-normal vision and were right-handed, except two subjects, who were left handed. Participants gave written informed consent prior to the experiment. The study was in accordance with the declaration of Helsinki and had the approval of the local ethics committee. Due to some technical problems and artefacts three subjects were excluded from analysis, resulting in a sample of seventeen participants (mean age:  $24.4 \pm 2.5$  years).

#### 2.2. Procedure

The subjects were seated in a comfortable armchair in a sound-proof, air-conditioned and dimmed cabin. The distance between the subjects and the monitor presenting the experimental paradigm was approximately 110 cm. A webcam was posed above the monitor to observe subjects' behavior from outside the cabin during the experiment.

The event-related design was performed with six different video sequences (1st person view) to address the influence of action and object type (Fig. 1). The movies showed two different conditions concerning objects (realistic/abstract) and three different conditions concerning grasping types (correct/incorrect/ beside). In total 6 conditions (correct grasping: realistic versus abstract objects; incorrect grasping: realistic versus abstract objects; beside grasping: realistic versus abstract objects) were presented in randomized order. The presented movies showed twenty different realistic objects (banana, glass, small bottle, phone, key, big bottle, cup, apple, book, plate, mobile phone, shoe, clock, radio, candle, scissors, bag, cap, milk carton, glove, chocolate) and ten different abstract objects (triangle, square, circle, trapezoid, cylinder, ring, pyramid, rectangle, cone, bar) which were grasped correctly, incorrectly or beside. In the incorrect condition the grasping hand was rotated whereas in the beside condition the grasping movement was correct but the hand did not grasp the object (see Fig. 1).

The task of the participants was to observe carefully the presented grasping sequence. To maintain attention through the whole experiment we instructed them to count the presented objects (realistic/abstract) during each block. This task had no experimental relevance but only served to keep subjects attention at a high level during the session.



**Fig. 1.** Illustration of the six different conditions: The columns show the type of object (realistic, abstract) and the rows show the type of grasping (correct, incorrect, beside). The combination of each resulted in 6 conditions.

The timing of one trial is shown in Fig. 2. Each trial (one movie) lasted about 9 s, and consisted of a static scene with the object, a moving scene with the grasping sequence and finally a fixed scene with the table without or with the object (in condition beside grasping the object remained in the scene). To ensure a smooth transition between the different movies sequences a fade in and fade out was used. One run consisted of 42 movies (21 abstract objects: 7 correct, 7 incorrect, 7 beside grasping and 21 realistic objects: 7 correct, 7 incorrect, 7 beside grasping) presented in randomized order and in total 4 runs (168 trials) were performed. In each run one object was presented three times, once for each grasping condition (e.g. the key was grasped correctly, incorrectly and beside).

At the beginning of the experiment, an artifact recording of approximately 5 min was performed to estimate the electrooculogram (EOG) influence and to calculate the correction coefficients (Schlögl et al., 2007). The recording was divided into four sections (15 s artifacts with 5 s resting in between) and the subjects were instructed via written text on the monitor to perform either eye blinking, rolling, up-down or left-right movements. At the beginning and at the end of each task a low and high warning tone, respectively, were presented.

#### 2.3. EEG signal recording and processing

#### 2.3.1. Data acquisition

EEG signals were acquired from 58 active EEG electrodes (acti-CAP, Brainproducts, Gilching, Germany) placed accordingly to the 10/20 system. The EOG was recorded by means of 3 electrodes: two placed either side of the eyes and one at the glabella. The reference electrode was placed on the left and ground electrode on the right ear. See Fig. 3 for detailed electrode locations. All data were recorded using two BrainAmp amplifiers (Brainproducts, Gilching, Germany) with a sampling rate of 500 Hz, a band pass filter between 0.5 and 70 Hz and activated notch filter. The BrainVision Reorder (Brainproducts, Gilching, Germany) stored the raw biosignal data together with the digital trigger signals coming from the stimulation video presentation which was implemented in MAT-LAB (Mathworks, Natick, US).

#### 2.3.2. Pre-processing

First, a regression analysis was used to reduce the influence of eye movements on the EEG (Schlögl et al., 2007). Furthermore, a Laplacian spatial filter (Hjorth, 1975) was applied to the data in order to highlight the activity of the local sources. Thereby, the weighted average of the surrounding four electrodes (or a reduced set in case of border electrodes) was removed from the target electrode. Generally, the surface Laplacian is a common, reference-independent EEG method that improves spatial resolution (Tenke and Kayser, 2012) by reducing the impact of volume conduction (Hjorth, 1975; Nunez et al., 1994) and increases the signal-to-noise ratio (SNR) while reducing the noise, i.e. non-specific activity (McFarland et al., 1997). Finally all EEG trials were visually controlled for artefacts and contaminated trials were discarded from further analysis.

#### 2.3.3. Feature extraction and ERD/ERS analysis

Time–frequency information based on ERD/ERS values (Pfurtscheller and Lopes da Silva, 1999, 2005) was computed for each participant and task. The resulting ERD/ERS values represent significant ERD (relative band power decrease) and ERS (relative band power increase) in narrow bands within a given frequency range. Since evoked potentials can mask the induced activity, the mean of the signal was subtracted first, then the samples were

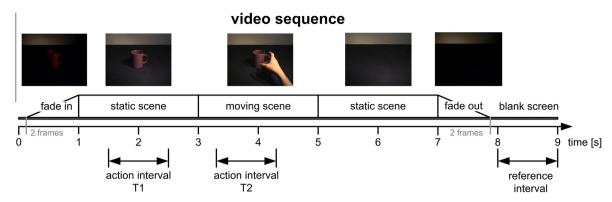


Fig. 2. Timing sequence of one trial. From second 0 to 1 the object faded in, followed by a clearly visible static scene (sec 1–3), the action interval T1. From second 3 to 5 the moving scene (action interval T2) showed the grasping action with the disappearance of the object from second 5 to 7. Then the scene faded out resulting in a blank screen for 2 s before the next trial started.

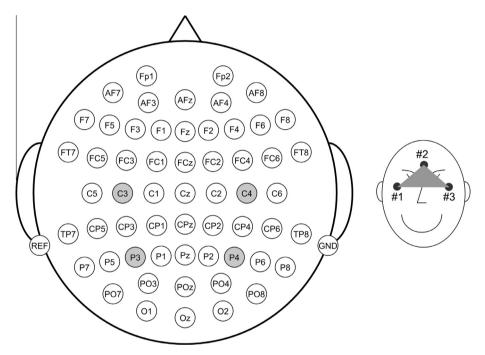


Fig. 3. Placement of the recorded 58 EEG electrodes according to the 10/20 system and location of the 3 EOG electrodes. The 4 Laplacian EEG channels which are used for the statistical analysis are highlighted in grey.

squared to compute the signal power and averaged over the trials resulting in  $Act_j$  (with j being the sample or time index) (Graimann et al., 2002). The power changes for each sample j relative to the reference interval Ref were then calculated by:

$$ERD/ERS_j = \left(\frac{Act_j}{Ref} - 1\right) \cdot 100\%$$

We extracted the ERD/ERS values on the following frequency bands: 8–10, 10–12, 16–20, 20–24 and 36–40 Hz, whereby the reference interval was always taken between second 8 and 9 (see Fig. 2). Furthermore, we defined two activation intervals of interest: time T1 from second 1.5–2.5 (static scene) and time T2 from second 3.3–4.3 (moving scene). The ERD/ERS values were averaged over the corresponding time intervals.

For the statistical analyses we restricted ourselves to the estimates at four sites (C3, C4, P3 and P4), where task-related activation patterns were expected (e.g. Avanzini et al., 2012; Babiloni et al., 2002). Fig. 3 illustrates the analyzed channels (grey) in the context of the complete 58-channel montage.

#### 2.4. Statistical analysis

In order to analyze the potential influence of the observed type of grasping and type of objects on the ERD/ERS patterns we performed a  $3 \times 2 \times 2 \times 2$  repeated measures analyses of variance (ANOVA). The ANOVA included the factors grasping "GRASP" ("correct"/"incorrect"/"beside"), "OBJECT" ("real"/"abstract"), region of interest "ROI" ("central"/"parietal") and hemisphere "HEM" ("left"/"right"), as within-subject variables for five frequency bands (alpha: 8-10 and 10-12 Hz; beta: 16-20 and 20-24 Hz; gamma band: 36-40 Hz) separately. For statistical analyses we only reported the analyses of timing period T2 (from second 3.3-4.3: moving scene), since for T1 no relevant activation patterns were obtained. Normal distribution of the data was tested and confirmed with a Kolmogorov-Smirnov test for normal distribution and whenever the sphericity assumption was violated Greenhouse-Geisser corrected values were used for further analysis. The probability of a type I error was maintained at 0.05. The ANO-VA was performed twice: first including all 17 subjects (right and left handed) and second without the two left-handed subjects, looking for possible influences on ERD/ERS patterns over motor cortical areas. Since no differences were found, the whole 17 subjects run into analyses.

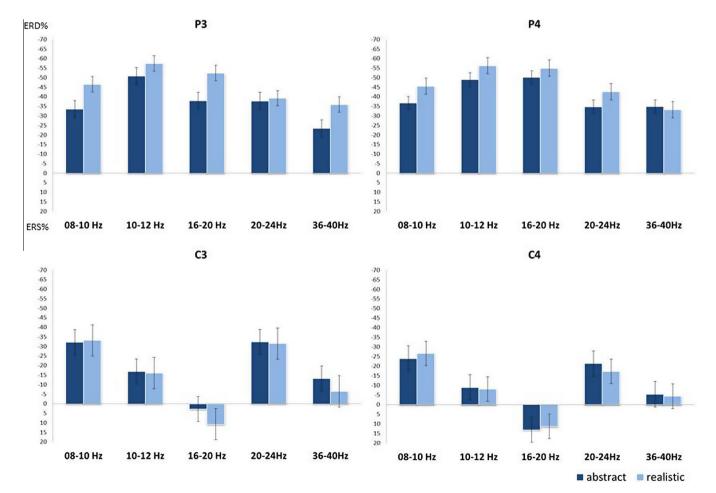
#### 3. Results

The results of the  $3 \times 2 \times 2 \times 2$  ANOVA according to the analyzed frequency bands are described below. Fig. 4 illustrates the mean ERD/ERS values (%) of both conditions, type of grasping (Fig. 4a) and type of object (Fig. 4b), over central (C3, C4) and parietal (P3, P4) sites of all 17 participants.

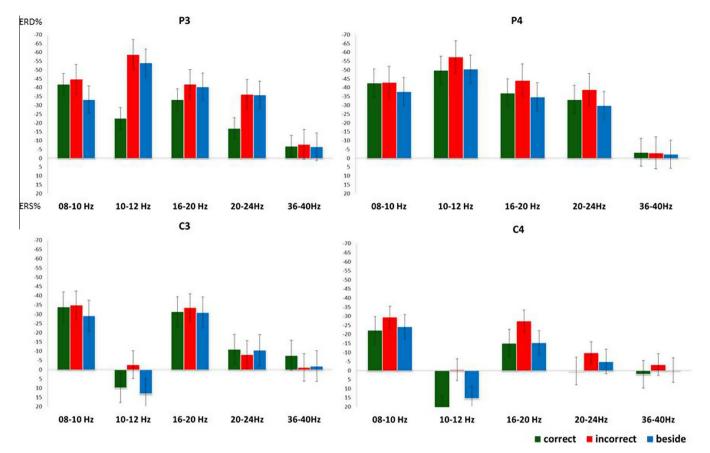
- (a) Alpha bands: No significant effects were found in the lower alpha band (8–10 Hz). In the upper alpha band (10–12 Hz) we found a significant main effect of "GRASP" (F(2,32) = 5.26; p = 0.01), indicating a stronger ERD for incorrect grasping ( $-29.85 \pm 28.00$ ) compared to correct ( $-18.29 \pm 26.70$ ) and beside ( $-19.00 \pm 24.89$ ). Furthermore, a significant main effect of ROI (F(1,16) = 22.33; p = 0.0002) was obtained with an ERS ( $9.43 \pm 45.54$ ) only at central sites and a parietal ERD ( $-54.19 \pm 26.40$ ).
- (b) Beta bands: For the lower beta band (16–20 Hz) three significant main effects (GRASP, ROI, HEM) were found. The significant main effect of GRASP (F(2,32) = 5.50; p = 0.009) indicated a stronger ERD for incorrect grasping ( $-36.75 \pm 16.85$ ) compared to correct ( $-31.43 \pm 17.16$ ) and beside ( $-30.41 \pm 20.42$ ) grasping. The main effect of ROI (F(1,16) = 10.41; p = 0.005) showed that

ERD was lower at central sites ( $-25.63\pm20.13$ ) compared to parietal ( $-40.09\pm19.52$ ) and the significant main effect of HEM (F(1,16) = 6.14; p = 0.03) indicated a stronger ERD in the left hemisphere ( $-36.73\pm18.47$ ) as in the right hemisphere ( $-28.99\pm18.91$ ). The significant interaction ROI × HEM (F(1,16) = 4.61; p = 0.047) substantiates the hemispheric differences, where a stronger ERD was only found at central sites in the left hemisphere ( $-31.95\pm21.55$ ). There was no difference in parietal ROI between left ( $-41.51\pm19.82$ ) and right hemisphere ( $-38.66\pm21.51$ ). In the upper beta band (20-24 Hz) a significant main effect of ROI (F(1,16) = 12.43; p = 0.003) was obtained with a smaller ERD at central sites ( $-7.38\pm27.95$ ) compared to parietal ( $-34.57\pm16.15$ ).

(c) Gamma band (36–40 Hz): In the gamma band a significant main effect of hemisphere was found (F(1,16) = 5.49; p = 0.03) with a stronger left hemispheric ERD pattern ( $-5.31\pm5.73$ ). Furthermore, a significant interaction of OBJECT × ROI (F(1,16) = 5.41; p = 0.03) was found. The results of the LSD (least significant difference) post hoc test showed a strong ERD for real objects only in parietal ROI (-6.66) but not in central ROI (0.76) and for abstract objects no difference between ROIs (all have ERD, central: -4.90; parietal: -3.27) was obtained. Additionally a significant interaction of OBJECT × HEM (F(1,16) = 10.26; p = 0.006) was found indicating a smaller ERD for real objects ( $-2.10\pm9.51$ ) in the left hemisphere as for abstract objects ( $-8.52\pm8.47$ ). In right hemisphere no significant difference between real (-3.80) and abstract objects (0.35) were found. For abstract objects only ERD in the left



**Fig. 4a.** Mean ERD/ERS values (%) of all 17 subjects for all frequency bands and grasping conditions (correct [in green color], incorrect [in red], beside [in blue]) over central (C3/C4) and parietal (P3/P4) sites. The upper row shows the ERD/ERS values for parietal electrode positions, P3 (left) and P4 (right) and the lower row shows the ERD/ERS values for central positions C3 (left) and C4 (right). On the *x*-axis the five frequency bands are plotted separately. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 4b.** Mean ERD/ERS values (%) of all 17 subjects for all frequency bands and object conditions (realistic [in light blue color] vs. abstract [in dark blue]) over central (C3/C4) and parietal (P3/P4) sites. The upper row shows the ERD/ERS values for parietal electrode positions, P3 (left) and P4 (right) and the lower row shows the ERD/ERS values for central positions C3 (left) and C4 (right). On the *x*-axis the five frequency bands are plotted separately. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

HEM  $(-8.52 \pm 8.47)$ , and no ERD in the right HEM  $(0.35 \pm 7.26)$  was found. For real objects there was no significant difference between the hemispheres.

For convenience reasons we present in Fig. 5a–e a topographical view of the grand average time–frequency representation of significant ERD/ERS values for each frequency band separately. All figures illustrate the activation from all 58 channels for all 6 conditions. Each head represents the grand average time–frequency representation of one condition within the timing period T2 (second 3.3–4.3).

#### 4. Discussion

The present study investigated whether the observation of an object-related movement with different grasping manipulations, i.e. grasping the object correctly or incorrectly, and different types of objects, namely abstract versus realistic objects, are processed differently over parietal and central brain regions. We generally found stronger ERD over parietal regions for alpha, beta and gamma frequency bands and an ERS in the upper alpha and lower beta band only over central brain regions which is a very striking result compared to the results of the current EEG literature on movement observation. In detail, we found significant ERS patterns in the upper alpha band (10–12 Hz) at electrode positions, C3 and C4 indicating no suppression of the mu-rhythm during movement observation, contrary to the results reported by other authors (Muthukumaraswamy et al., 2004; Ulloa and Pineda, 2007; Oberman et al., 2007). One explanation could be, that the men-

tioned studies used broader frequency bands (e.g. 8-13 or 8-15 Hz) for analyses compared to our study, where we divided the alpha band in two narrow bands (8-10 and 10-12 Hz) which has also been suggested by Pfurtscheller and colleagues (2000). In their study ERD was analyzed in two alpha bands, 8-10 and 10-12 Hz, during self-paced, voluntary finger, and foot movements. The lower frequency component showed a widespread movement-type non-specific ERD, whereas the upper frequency component showed a more focused and movement-type specific pattern. The different reactivity patterns provide evidence for the existence of at least two different subtypes of mu rhythms, a somatotopically non-specific lower frequency mu and a somatotopically specific mu characteristically found in the upper alpha frequency band. The underlying idea is that activation of mirror neurons by executed, imagined or observed motor actions produces asynchronous firing and, therefore, is associated with a concomitant suppression or desynchronization of the mu rhythm (Lopes da Silva, 2006).

While there is consent about the strong linking of the mu rhythm to the MNS there is also evidence for the involvement of other brain regions like areas in the parietal cortex (Buccino et al., 2001; Buccino et al., 2004). These studies suggested that the prefrontal mirror neuron system may in fact be part of a broader network, one responsible for biological motion perception (Fagg and Arbib, 1998). For example Costantini et al. (2005) compared the results of observing biologically possible and impossible movements. They found bilateral activation of the premotor cortex during the observation of both, possible and impossible hand movements and a stronger activation of the posterior parietal

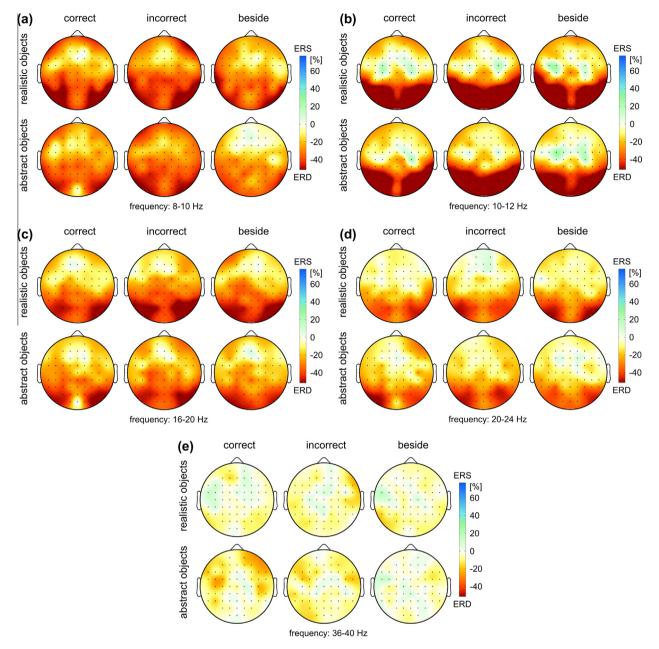


Fig. 5. (a–e) Topographical grand average time–frequency representation of significant ERD/ERS values of all 6 grasping conditions for (a) 8–10 Hz (b) 10–12 Hz (c) 16–20 Hz (d) 20–24 Hz (e) 36–40 Hz, frequency bands, covering the action interval T2 from second 3.3–4.3.

cortex (PPC) during observation of impossible than possible movements. This could be supported by our results where the manipulation of the type of grasping revealed a larger ERD in the upper alpha (10–12 Hz) and beta (16–20 Hz) frequency bands over parietal brain regions for erroneous grasping movements.

In contrast to the results where the "type of movement" is of interest, there is also strong parietal activation if the "type of object" is of importance. Like in the study performed by Neuper and colleagues (2009) there is no significant difference in the alpha and beta frequency bands between the observation of grasping realistic compared to abstract objects. Again, an overall stronger parietal desynchronization was obtained (Manthey et al., 2003; Pineda, 2005). This could be explained by the fact that observation of an object related movement includes spatial patterns, which are primarily processed in the parietal cortex (Kesner, 2009). Further support comes from Avanzini et al., 2012) who found a greater

modulation in parietal regions in the beta band during action observation.

Compared to other studies we additionally found ERD in the gamma band over parietal sites depending on the type of object, namely for real objects. For abstract objects no difference between ROIs was obtained. This significant interaction of "OBJECT" × "ROI" only in the gamma band suggested a strong relation of gamma band activity and cortical object representation as already found in previous studies (Tallon-Baudry and Bertrand, 1999; Lachaux et al., 2005; Martinovic et al., 2008).

## 5. Conclusion

In the present study we found ERD over central and parietal sites in the upper alpha, beta and gamma frequency bands during several types of movement observation. Whereas stronger parietal

ERD changes were found in alpha and beta frequency bands for incorrect grasping movements, the type of object (real/abstract) only influences ERD patterns in the gamma frequency band. Watching movements with real objects elicited stronger parietal gamma band activity. Beside that we also obtained significant ERS patterns but only at central cites. Concretely in the upper alpha band we found an ERS for correct and beside grasping movements and in the lower beta band for abstract and realistic objects. The strong involvement of the parietal cortex could be explained by the fact that it receives visual information from the occipital cortex, somatosensory information from primary sensorimotor cortex and motor information from primary motor cortex, supplementary motor area and premotor cortex. That is, during movement observation changes in the alpha and beta band in parietal regions might facilitate the processing of different object and space information with motor related memories. It could be suggested that beside the often cited MNS linked mu rhythm there is further cortical rhythmicity, namely ERD in the alpha, beta and gamma band over parietal sites, which might be part of an "extended" human MNS.

#### Acknowledgement

This work is supported by the European ICT Program Projects FP7-224631 and FP7-299566.

#### References

- Andrew C, Pfurtscheller G. On the existence of different alpha band rhythms in the hand area of man. Neurosci Lett 1997;222:103–6.
- Avanzini P, Fabbri-Destro M, Dalla Volta R, Daprati E, Rizzolatti G, Cantalupo G. The dynamics of sensorimotor cortical oscillations during the observation of hand movements: an EEG study. PLoS One 2012;7:e37534.
- Babiloni C, Carducci F, Cincotti F, Rossini PM, Neuper C, Pfurtscheller G. Human movement-related potentials vs. desynchronization of EEG alpha rhythm: a high-resolution EEG study. Neuroimage 1999;10:658–65.
- Babiloni C, Babiloni F, Carducci F, Cincotti F, Cocozza G, Del Percio C. Human cortical electroencephalography (EEG) rhythms during the observation of simple aimless movements: a high-resolution EEG study. Neuroimage 2002;17:559–72.
- Biagi L, Cioni G, Fogassi L, Guzzetta A, Tosetti M. Anterior intraparietal cortex codes complexity of observed hand movements. Brain Res Bull 2010;16:434–40.
- Buccino G, Binkofski F, Fink GR, Fadiga L, Fogassi L, Gallese V. Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. Eur J Neurosci 2001;13:400–4.
- Buccino G, Lui F, Canessa N, Pastteri I, Lagravinese G, Benuzzi F. Neural circuits involved in the recognition of actions performed by nonconspecifics: an fMRI study. J Cogn Neurosci 2004;16:114–26.
- Cochin S, Barthelemy C, Lejeun B, Roux S, Martineau J. Perception of motion and EEG activity in human adults. Electroencephalogr Clin Neurophysiol 1998;107:287–95.
- Cochin S, Barthelemy C, Roux S, Martineau J. Observation and execution of movement: similarities demonstrated by quantified electroencephalography. Eur J Neurosci 1999;11:1839–42.
- Costantini M, Galati G, Ferretti A, Caulo M, Tartaro A, Romani GL, et al. Neural systems underlying observation of humanly impossible movements: an FMRI study. Cereb Cortex 2005;15:1761–7.
- Decety J, Chaminade T, Grezes J, Meltzoff AN. A PET exploration of the neural mechanisms involved in reciprocal imitation. Neuroimage 2002;15:265–72.
- Enticott PG, Kennedy HA, Bradshaw JL, Rinehart NJ, Fitzgerald PB. Motor corticospinal excitability during the observation of interactive hand gestures. Brain Res Bull 2011;30:89–95.
- Fadiga L, Fogassi L, Pavesi G, Rizzolatti G. Motor facilitation during action observation: a magnetic stimulation study. J Neurophysiol 1995;73:2608–11.
- Fagg AH, Arbib MA. Modeling parietal-premotor interactions in primate control of grasping. Neural Netw 1998;11:1277-303.
- Gastaut HJ, Bert J. EEG changes during cinematographic presentation. Electroencephalogr Clin Neurophysiol 1954;6:433–44.
- Gibson JJ. The theory of affordances. In: Shaw R, Bransford J, editors. Perceiving, acting and knowing. Hillsdale, NJ: Erlbaum; 1977.
- Goldman RI, Stern JM, Engel J Jr, Cohen MS. Simultaneous EEG and fMRI of the alpha rhythm. Neuroreport 2002;13:2487–92.
- Graimann B, Huggins JE, Levine SP, Pfurtscheller G. Visualization of significant ERD/ ERS patterns in multichannel EEG and ECoG data. Clin Neurophysiol 2002;113:43-7.
- Grèzes J, Armony JL, Rove J, Passingham RE. Activations related to "mirror" and "canonical" neurones in the human brain: an fMRI study. Neuroimage 2003;18:928-37.

- Grezes J, Decety J. Functional anatomy of execution, mental simulation, observation and verb generation of actions: a meta-analysis. Hum Brain Mapp 2001;12:1–19.
- Hari R, Salmelin R, Makela JP, Salenius S, Helle M. Magnetoencephalographic cortical rhythms. Int J Psychophysiol 1997;26:51–62.
- Hari R, Forss N, Avikainen S, Kirveskari E, Salenius S, Rizzolatti G. Activation of human primary motor cortex during action observation: a neuromagnetic study. Proc Natl Acad Sci 1998;95:15061–5.
- Hjorth B. An on-line transformation of EEG scalp potentials into orthogonal source derivations. Electroencephalogr Clin Neurophysiol 1975;39:526–30.
- Iacoboni M, Molnar-Szakacs I, Gallese V, Buccino G, Mazziotta JC, Rizzolatti G. Grasping the intentions of others with one's own mirror neuron system. Plos Biol 2005;3:529–35.
- Iacoboni M, Wilson SM. Beyond a single area: motor control and language within a neural architecture encompassing Broca's area. Cortex 2006;42:503–6.
- Järveläinen J, Schürmann M, Hari R. Activation of the human primary motor cortex during observation of tool use. Neuroimage 2004;23:187–92.
- Johnson-Frey SH, Moloof FR, Newman-Norlund R, Farrerm C, Inati S, Grafton ST. Action or hand-object interactions? Human inferior frontal cortex and action observation. Neuron 2003;39:1053-8.
- Kesner RP. The posterior parietal cortex and long-term memory representation of spatial information. Neurobiol Learn Mem 2009;91:197–206.
- Lachaux JP, George N, Tallon-Baudry C, Martinerie J, Hugueville L, Minotti L, et al. The many faces of the gamma band response to complex visual stimuli. Neuroimage 2005;25:491–501.
- Lopes da Silva FH. Event-related neural activities what about phase? Prog Brain Res 2006;159:3–17.
- McFarland DJ, McCane LM, David SV, Wolpaw JR. Spatial filter selection for EEG-based communication. Electroencephalogr Clin Neurophysiol 1997;103: 386-94.
- Martinovic J, Gruber T, Hantsch A, Müller MM. Induced gamma-band activity is related to the time point of object identification. Brain Res 2008;1198:93–106.
- Manthey S, Schubotz RI, von Cramon DY. Premotor cortex in observing erroneous action: an fMRI study. Brain Res 2003;15:296–307.
- Muthukumaraswamy SD, Johnson BW, McNair NA. Mu rhythm modulation during observation of an object-directed grasp. Brain Res 2004;19:195–201.
- Neuper C, Pfurtscheller G. Post-movement synchronization of beta rhythmus in the EEG over the cortical foot area in man. Neurosci Lett 1996;216:17–20.
- Neuper C, Pfurtscheller G. Event-related dynamics of cortical rhythms, frequencyspecific features and functional correlates. Int | Psychophysiol 2001;43:41–58.
- Neuper C, Scherer R, Wriessnegger SC, Pfurtscheller G. Motor imagery and action observation: modulation of sensorimotor brain rhythms during mental control of a brain-computer interface. Clin Neurophysiol 2009;120:239–47.
- Newman-Norlund R, van Schie HT, van Hoek ME, Cuijpers RH, Bekkering H. The role of inferior frontal and parietal areas in differentiating meaningful and meaningless object-directed actions. Brain Res 2010;22:63–74.
- Norman DA. The design of everyday things. New York: Doubleday; 1988.
- Nunez PL, Silberstein RB, Cadiush PJ, Wijesinghe J, Westdorp AF, Srinivasan R. A theoretical and experimental study of high resolution EEG based on surface Laplacians and cortical imaging. Electroencephalogr Clin Neurophysiol 1994;90:40–57.
- Oberman LM, McCleery JP, Ramachandran VS, Pineda JA. EEG evidence for mirror neuron activity during the observation of human and robot actions: toward an analysis of the human qualities of interactive robots. Neurocomputing 2007;70:2194–203.
- Ocampo B, Kritikos A. Interpreting actions: the goal behind mirror neuron function. Brain Res Rev 2011:67:260–7.
- 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 Res 2009:1282:126–32.
- Pfurtscheller G, Stancák A Jr, Neuper C. Event-related synchronization (ERS) in the alpha band an electrophysiological correlate of cortical idling: a review. 1996; 24:39–46.
- Pfurtscheller G, Neuper C. Motor imagery activates primary sensorimotor area in humans. Neurosci Lett 1997;239:65–8.
- Pfurtscheller G, Lopes da Silva F. Event-related EEG/MEG synchronization and desynchronization: basic principles. Clin Neurophysiol 1999;110:1842–57.
- Pfurtscheller G, Neuper C, Krausz G. Functional dissociation of lower and upper frequency mu rhythms in relation to voluntary limb movement. Clin Neurophysiol 2000;111:1873–9.
- Pfurtscheller G, Lopes da Silva FH. Event-related desynchronization (ERD) and event-related synchronization (ERS). In: Niedermeyer E, Lopes da Silva FH, editors. Electroencephalography: basic principles, clinical applications and related fields. 5th ed. Philadelphia, PA: Lippincott, Williams & Wilkins; 2005. p. 1003–16.
- Pfurtscheller G, Scherer R, Lee R, Keinrath C, Neuper C, Lee F. Viewing moving objects in virtual realisticity can change the dynamics of sensorimotor EEG rhythms. Presence Teleop Virt 2007;16:111–8.
- Pineda JA. The functional significance of mu rhythms: translating seeing and hearing into doing. Brain Res 2005;50:57–68.
- Pineda JA. Sensorimotor cortex as a critical component of an "extended" mirror neuron system: does it solve the development, correspondence, and control problems with mirroring? Behav Brain Funct 2008:1–16.
- Pineda JA, Allison BZ, Vankov A. The effects of self-movement, observation, and imagination on mu rhythms and readiness potentials (RP's): toward a brain-computer interface (BCI). IEEE Trans Neural Syst Rehabil Eng 2000;8:219–22.

- Rizzolatti G, Arbib MA. Language within our grasp. Trends Neurosci 1998;21:188–94.
- Rizzolatti G, Fadiga L, Gallese V, Fogassi L. Premotor cortex and the recognition of motor actions. Cogn Brain Res 1996;3:131–41.
- Rizzolatti G, Craighero L. The mirror-neuron system. Annu Rev Neurosci 2004;27:169–92.
- Salmelin R, Hari R. Characterization of spontaneous MEG rhythms in healthy adults. Electroencephalogr Clin Neurophysiol 1994;91:237–48.
- Schlögl A, Keinrath C, Zimmermann D, Scherer R, Leeb R, Pfurtscheller G. A fully automated correction method of EOG artifacts in EEG recordings. Clin Neurophysiol 2007;118:98–104.
- Shmuelof L, Zohary E. Dissociation between ventral and dorsal fMRI activation during object and action recognition. Neuron 2005;47:457–70.
- Tallon-Baudry C, Bertrand O. Oscillatory gamma activity in humans and its role in object representation. Trends Cogn Sci 1999;3:151–62.
- Tenke CE, Kayser J. Generator localization by current source density (CSD): implications of volume conduction and field closure at intracranial and scalp resolutions. Clin Neurophysiol 2012;123:2328–45.
- Ulloa ER, Pineda JA. Recognition of point-light biological motion: mu rhythms and mirror neuron activity. Behav Brain Res 2007;183:188–94.