

## Awareness affects motor planning for goal-oriented actions

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### ABSTRACT

We studied pre-movement cortical activity related to praxic actions performed at self-paced rate and having ecological meanings and functions. Motor-related cortical potentials were recorded using 64-channels EEG in two experiments. Experiment 1 included 15 subjects performing in separate blocks two object-oriented actions: *grasping* a tea-cup and *impossible grasping* of a tea-cup (same goal but the grasp was mechanically hindered). Experiment 2 included a subset of 7 subjects from Exp. 1 and the action was *reaching* a tea-cup; this control condition had a different goal but was kinematically similar to *impossible grasping*. Different activity patterns in terms of onset, amplitude, duration and, at least in part, sources were recorded in the preparation phase (BP component) according to the specific action and to the possibility of accomplishing it. The main result is that parietal areas were involved in *grasping* preparation (called "posterior" BP) and not in *reaching* and *impossible grasping* preparation. The anterior frontal-central activity (called "anterior" BP) during preparation for *grasping* started earlier than the other two conditions. The cortical activity during preparation for *reaching* was similar to that for *impossible grasping*, except for a frontal activity only detected in the latter condition. It is concluded that the action preparation, even in its early phase, is affected by action meaning and by the awareness of being able to perform the requested action.

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### 1. Introduction

In humans, the cerebral activity preceding movements has been extensively studied with electroencephalography (EEG) starting from the sixties. In 1965, for the first time, the Bereitschaftspotential (BP) was described as a negative cortical potential beginning ca. 1.5 s prior to the onset of self-paced movements underlying the preparation for action (Kornhuber and Deecke, 1965) and 15 years later, by Shibasaki et al. (1980), it was divided into different components as the early BP, the negative slope (NS'), the motor potential (MP), and the re-afferent potential (RAP), a positive component appearing after the onset of the movement related to the somatosensory cortex activation.

Several studies on the motor-related cortical potentials (MRCPs), have investigated simple motor tasks, i.e. finger flexion or extension, foot extension or tongue protrusion, and indicated that the sources of MRCPs components are located in the frontal cortical areas during motor-planning of simple self-paced movements

(Shibasaki and Hallett, 2006). In contrast, few MRCPs studies have investigated motor preparation for praxic movements, i.e. pantomime of tool-use and intransitive actions as to say goodbye (Wheaton et al., 2005a,b). These studies showed for the first time the involvement of parietal activity preceding that of the frontal areas. However, MRCPs studies have never investigated self-paced complex actions (not-pantomimed) such as goal-oriented reaching and grasping, having ecological meanings and functions. In particular, the response timing of the parietal regions in these complex actions is still unknown.

On the other hand, there is considerable neuroimaging literature on motor preparation related to complex actions, such as object-oriented grasping and reaching (Prado et al., 2005; Cavina-Pratesi et al., 2010), showing a parieto-frontal cortical network activated in action-planning and action-execution for reaching, grasping (Connolly et al., 2003; Filimon et al., 2009; Galati et al., 2011), pantomime (Johnson-Frey et al., 2005) and as well as for simple movements, such as moving fingers with eyes closed (Filimon et al., 2007). However, none of the fMRI studies previously cited have investigated motor preparation preceding *spontaneous self-paced complex* movements, such as reaching and grasping; indeed, only a few fMRI studies have examined cortical activations for self-initiated movements, but only considered simple movements such as key-press (Cunnington et al., 2005). Additionally, due to fMRI's

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poor temporal resolution, the activation timing within the parieto-frontal network remains unknown: the activation of parietal and frontal areas is well documented, but it remains unclear if the activation is simultaneous or in sequence, and – if so – what the sequence is.

The MRCPs are particularly suitable to discriminate the brain activity associated with the preparation and execution phases. Here we used MRCPs to investigate motor preparation related to grasping and reaching movements, i.e. complex actions which require more computations than simple finger movements, such as those used in most previous MRCP studies (Shibasaki and Hallett, 2006). Indeed, finger tasks lack the transport component of the arm, which is fundamental in real-world reach-to-grasp movements. Thus, the spatial coding and the motor programming during the preparatory delay is likely not the same for simple finger and complex arm movements as reaching and grasping.

Thus, in the present study we referred to complex movements toward a real object, i.e. grasping a tea-cup, performed at self-paced rate. The aim of the present research was twofold. First, we sought to analyze the activation timing of the cortical areas involved in the praxic movements verifying the involvement of the parietal areas in this kind of actions. Second, we sought to verify whether motor preparation was modulated by the awareness of the possibility/impossibility of correctly performing the requested action.

To address this latter issue, we implemented a second condition (*impossible grasping*), in which grasping was hindered by closing the fingers with a band. The presence of the object and the interaction elicited by the instruction (“try to grasp the cup”), made this condition somewhat similar to the real grasping, distinguishing it from a pantomimed action (where the object is absent; e.g. Wheaton et al., 2005a,b). However, in the *impossible grasping*, the final goal could not be accomplished, changing the meaning of the action performed with respect to *grasping*.

Comparison between *grasping* and *impossible grasping* enables us to evaluate any modulation of motor preparation activities induced by the awareness of being able/unable to accomplish the action. Since the two conditions were kinematically different in the execution phase (*impossible grasping* movement was actually turned into reaching the cup), we set a third condition (*reaching*) to verify whether cortical activities recorded for *impossible grasping* were simply related to the action’s kinematics, i.e. to evaluate if the brain activity underlying *impossible grasping* was actually equal to that for *reaching*, or was affected by the awareness of the impossibility of accomplishing the action’s goal.

Summarizing we performed this study to find out whether the planning of complex actions (*grasping* and *reaching*) involves activity at parietal level (as expected given the neuroimaging literature on this issue) and is modulated by the awareness of being able to perform the requested action. If the possibility of accomplishing the action was irrelevant, brain activity preparing the *impossible grasping* should be similar to that preparing reaching of the same object.

## 2. Materials and methods

### 2.1. Subjects

Fifteen volunteers university students (mean age 24.7 years; SD 6.2; 8 females) with no neurological or psychiatric disease, participated in the study. All subjects were right-handed, and the manual preference was evaluated with the use of the Edinburgh Handedness Inventory (Oldfield, 1971) ( $LI > 60$ ; mean score 85). After a full explanation of the procedures, all subjects provided written informed consent. The study was approved by the local ethical committee.

### 2.2. Tasks

Participants were required to perform two tasks in separated blocks. The first task was to extend the limb to grasp a tea-cup, located in front of the subject at a convenient distance, lifting it up, as for drinking, then put it back on the table and

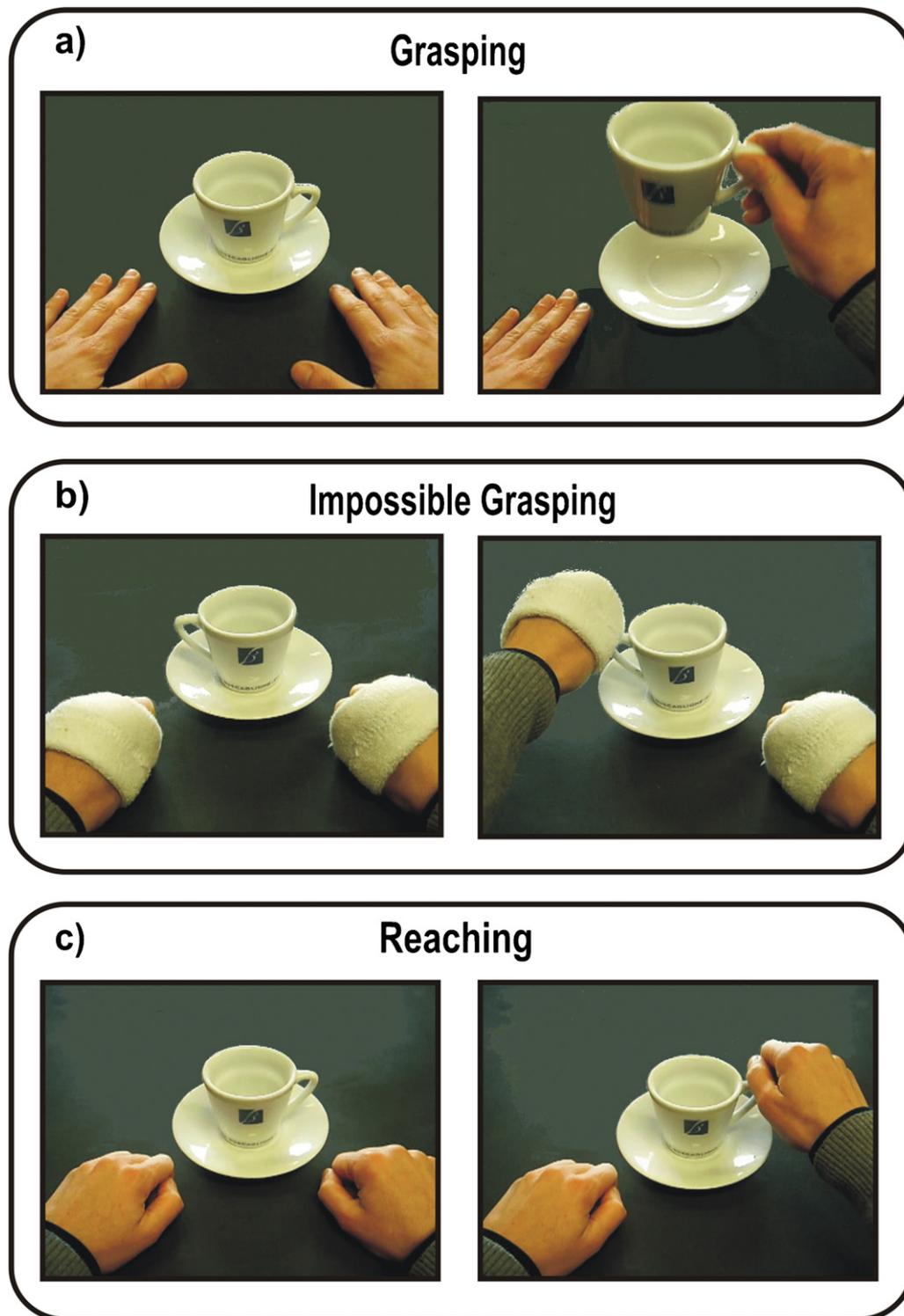
return to the resting position. The task was accomplished with the right and the left hand alternately, according to the left/right position of the cup handle. This condition is called hereafter “*grasping*”. In the second task, in order to hinder the grasping, the hands of the subjects were tied-up as fists with a band. Thus, the task was to grasp the cup but the action was actually hindered, and subjects were told they could not open their fingers. They reached, touched with the fist the cup’s handle, and felt the failure to grasp (this condition is called hereafter “*impossible grasping*”). Though the subjects were aware to be unable to cope the requested action, they were requested to perform the action as in the first condition, trying to grasp the cup, but never opening their hands (as represented in Fig. 1a and b).

### 2.3. Procedure

Subjects comfortably seated on a chair in front of a table with an empty tea-cup on top (35 cm distance from the body). Their hands were placed on the table in a resting/starting position. Subjects were instructed to maintain, during the task, stable posture and fixation. They were instructed to choose a point over the tea cup and to fix it for the trial duration. The action was self-paced and had to be performed slowly. The action ended when the hand returned to the resting position. The action duration was ca 4 s and 1 s was the time subjects spent to arrive touching the cup in every condition. After each trial, the experimenter (seated behind the subject) turned the cup on the table switching the handle to left or right, alternating the side on each trial. The interval between each action was ca 10 s. Subjects repeated each action 240 times (120 with left hand, 120 with right hand) for each condition. Tasks were executed in separated blocks, alternating different conditions (*grasping* and *impossible grasping*); each block included 60 actions. In both conditions, the movement initiation was spontaneous and self-paced, and subjects were trained to not count or synchronize their start with the researcher cup handle switch.

### 2.4. Electrophysiological recording and data processing

Electrical brain activity was recorded during the tasks using a BrainVision™ 64-channel system (Brain Products GmbH, Munich, Germany) connected to an active sensor system (ActiCap™ by Brain Products GmbH, Munich, Germany), adopting the standard 10–10 system montage. The system included four electromyography (EMG) channels with bipolar recording located on the left and right deltoids. Eye movements were recorded. Left mastoid (M1) was used as initial reference electrode for all scalp channels. Signal was digitized at 250 Hz, with an amplifier band-pass from 0.001 to 60 Hz with 50 Hz notch filter. To further reduce high frequency noise, the time-averaged MRCPs were filtered at 8 Hz. The EMG signal was rectified and visually inspected to identify and manually mark the movement onset. EMG onset was considered as the first increased of the signal on the beneath noise. Data were segmented in epochs from 3500 ms prior to movement onset to 1000 ms after it. Only the activity related to pre-movements phase was analyzed. Semi-automatic computerized artifacts rejection was performed prior to signal averaging, in order to discard epochs contaminated with gross ocular movement or muscular contractions from further analysis; trials with amplitude exceeding  $\pm 100 \mu\text{V}$  were individually inspected and discarded if contained the aforementioned artifacts. Around 20% of the trials were rejected. Blinks were found to be the most frequent cause for rejection. The baseline was calculated from 3500 to 3000 ms before onset and used for onset and amplitude measurement. The onset of the MRCPs was calculated as the first time sample where potential exceeded the 95% confidence interval of the baseline absolute value. The period used for statistical analysis started 3000 ms prior to movement onset up to the peak of the MP. All the MRCPs components were identified on visual inspection carried out by the first author and independently confirmed by the last author. Statistical differences in the MRCPs amplitudes between *grasping* and *impossible grasping* were initially assessed with sample by sample *t*-test in all electrodes to select the locations and time windows where the differences were consistently significant. This preliminary analysis allowed us to select 10 electrodes (F7, F8, FCz, FC1, FC2, C1, C2, Pz, P3 and P4) and four time windows (–2000/1000 ms, –1000/–500 ms, –500/0 and 0/50, which also represent the main MRCP components) for further statistical analysis. On each contralateral electrode and time window, a  $2 \times 2$  repeated-measure ANOVA was carried out with task (*grasping* vs. *impossible grasping*) and hand (left vs. right) as within-subjects factors. For the MRCP onset latency and the MP peak latency a similar  $2 \times 2$  ANOVA was carried out on the electrode with the earliest activity. The LSD test was used for main effects comparisons. The overall alpha level was set at 0.05. Lateralized readiness potential (LRP) was also calculated considering the pairs of symmetrical electrodes selected by the *t*-test analysis (see above), in order to verify the lateralization of the motor preparation activity (De Jong et al., 1988; Coles, 1989). To visualize the voltage topography of the MRCPs components, spline-interpolated 3D maps were constructed using the Brain Electrical Source Analysis system (BESA, 2000 version 5.18, MEGIS Software GmbH, Gräfelting, Germany). Given that changes in electric field indicate changes of the underlying generator configuration (Lehmann and Skrandies, 1980); we measured the statistical differences among scalp topographies using a non-parametric randomization test as the topographic analysis of variance (TANOVA) at each time-point between the two conditions. For more details on TANOVA, see Murray et al. (2008). Prior to TANOVA, the MRCPs were average referenced and transformed to a global field power (GFP) of 1, which ensured that the dissimilarity was not influenced



**Fig. 1.** The left side of the figure a–c represent the starting position of the hands in the three experimental conditions (*grasping* and *impossible grasping* (a and b, Experiment 1) and *reaching* (c, control experiment)). On the right side a video-frame presenting the interaction of the hand with the object is shown.

by higher activity across the scalp in any of the conditions. Thus, this analysis provides a statistical method to determine if the brain networks underlying *grasping* differ from networks underlying *impossible grasping* and its timing.

### 2.5. Source analysis

The intracranial sources were determined using the BESA, 2000, which calculated the cerebral areas involved in the tasks and tested for possible differences in the temporal evolution of the active areas across the studied conditions. The noise-normalized minimum-norm method was employed to estimate the current

density dipoles on the cortical scalp. The minimum-norm approach is a method that is used regularly to estimate the distributed electrical current in a brain image at each time a sample; it is able to resolve the inverse problem without a priori constraints and is also able to reveal the unique constellation of current elements that models the recorded electric field distribution with the smallest amount of overall current (Hämäläinen and Ilmoniemi, 1984; Ilmoniemi, 1993). The algorithm employed minimizes the source vector current derivative from 1426 evenly distributed dipoles that are located 10% and 30% below the surface of the brain by using the approach adopted by Dale and Sereno (1993), where the correlation between  $p_i$  of the lead field for regional source  $i$  and the inverse of the data covariance matrix is computed together

with the largest singular value  $\lambda_{\max}$  of the data covariance matrix. The weighting matrix  $R$  is comprised of a diagonal matrix with weights. The equation consists of the following:  $1/(1 + \lambda_{\max} (1 - p_i))$ . To improve the minimum norm estimate (MNE), we also included depth weighting parameters across the entire source space because, as demonstrated by Lin et al. (2006), depth-weighted MNEs can improve the spatial accuracy by allowing displacement errors within 12 mm.

### 3. Results

#### 3.1. Waveform analysis

Both conditions (*grasping* and *impossible grasping*) presented the typical MRCPs components, including the slow negative potential BP (hereafter called anterior BP) slightly peaking on the contralateral fronto-central sites (FC1 and FC2), the NS' and the MP peaking more posteriorly on the contralateral central sites (C1 and C2) as shown in Fig. 2. Statistical analysis showed differences between the two conditions either in onset latency and amplitudes of these components.

LRP analysis in the  $-3000/-500$  ms time window did not show marked lateralization, but widespread distributions for both *grasping* and *impossible grasping* conditions which didn't differ each other ( $t(14) = 1.77, p = 0.1$ ).

The anterior BP component initiated about 800 ms earlier in the *grasping* (at  $-1910$  ms) than in the *impossible grasping* (at  $-1097$  ms) condition ( $F(1,14) = 4.62, p = 0.049$ ). The amplitude of this component ( $-1000/-500$  ms on FCz) was affected by the task and it was larger in the *grasping* ( $-2.0 \mu\text{V}$ ) than in the *impossible grasping* ( $-1.1 \mu\text{V}$ ) condition ( $F(1,14) = 4.86, p = 0.044$ ). Similar to BP, also the NS' component ( $-500/0$  ms on C1/2) was affected by the task, and it was larger for the *grasping* ( $-4.8 \mu\text{V}$ ) than the *impossible grasping* ( $-3.0 \mu\text{V}$ ) condition ( $F(1,14) = 6.60, p = 0.022$ ).

Since the EMG signal always precedes movement onset, the MP component was delayed with respect to the time 0, defined by EMG (see Fig. 2). The task effect was significant for the MP component which was larger in the *grasping* ( $-7.8 \mu\text{V}$ ) than the *impossible grasping* ( $-5.1 \mu\text{V}$ ) condition ( $F(1,14) = 7.04, p = 0.019$ ). ANOVA on the MP latency was not significant ( $F(1,14) = 0.08$  ns). LRP analysis showed that both NS' and MP were strongly lateralized in both conditions, which did not differ each other ( $t(14) = 1.47, p = 0.16$ ). In all the ANOVAs neither hand effect nor interaction effect were significant.

Note that in the *grasping* condition, partially overlapping to the anterior BP, it was possible to distinguish a large negative activity peaking on contralateral parietal sites P4 and P3 for left and right hand, respectively. This parietal activity, hereafter called posterior BP, started at  $-2835$  ms for left hand and at  $-2490$  for right hand lasting up to about  $-500$  ms from movement onset. Comparing the latency onset for the anterior and posterior BP in the *grasping* condition, the analysis showed such a difference as significant ( $t(1,14) = 14.73, p = 0.001$ ). Notably, the posterior BP was absent in the *impossible grasping*, as shown on the bottom panels of Fig. 2. Statistical analysis on the posterior BP amplitude ( $-2000/-1000$  ms on Pz) showed a significant effect of task ( $F(1,14) = 7.53, p = 0.015$ ), and interaction ( $F(1,14) = 4.84, p = 0.045$ ). Main effect analysis showed larger amplitude of the component ( $p < 0.02$ ) in the *grasping* ( $-3.0 \mu\text{V}$ ) than in the *impossible grasping* ( $-1.9 \mu\text{V}$ ). Further, in the *grasping* only, the left hand showed larger amplitudes ( $-3.3 \mu\text{V}$ ) than right hand movements ( $-2.7 \mu\text{V}$ ), though it was not significant.

Finally, the *impossible grasping* condition showed a contralateral pre-frontal positivity, starting from  $-2600$  ms to  $-480$  ms and peaking at  $-1450$  ms on F8 and F7 sensors (for left and right hand, respectively). This activity was not present in the *grasping* condition (top panels of Fig. 2) as revealed by statistical comparisons ( $-2000/-1000$  ms on F7/8) which showed a significant effect of

task ( $F(1,14) = 6.25, p = 0.022$ ). The hand effect and the interaction effect were not significant.

#### 3.2. Scalp topography and source localization

The topography of the BP component (Fig. 3) showed in all conditions the typical anterior (slightly contralateral) fronto-central negative focus ( $-1000$  ms maps). However, limited to the *grasping* condition, a posterior bilateral parietal focus was present. This activity was slightly more intense on contralateral hemisphere and more widespread for the left hand action, including also medial parietal sites 1–2 s before movement onset.

Voltage distributions of the NS' and the MP components were quite similar between conditions; the NS' focused on contralateral fronto-central scalp at  $-500$  ms and the MP more posterior on contralateral central sites ( $+50$  ms maps). The positivity, present in the *impossible grasping* condition, was strongly lateralized, focused on contralateral pre-frontal scalp and extended to anterior temporal sites ( $-1500$  ms maps).

Looking at the maps, it seems that the larger anterior BP amplitude recorded in the *grasping* condition may be explained by the volume conductance from the posterior BP. Furthermore, the presence of the prefrontal positivity in the *impossible grasping* condition (being partially overlapped in time to the anterior BP) might have additionally reduced the anterior BP.

Source localization obtained by minimum-norm analysis showed that the posterior BP (*grasping* condition) might originate in the superior parietal lobe, where the peak activity was detected. The pre-frontal positivity (*impossible grasping* condition) was localized within the contralateral middle frontal gyrus (Fig. 4a).

TANOVA comparison of motor preparation for *grasping* and *impossible grasping* showed that the two topographies were statistically different ( $p < 0.021$ ) mainly between  $-2000$  and  $-1000$  ms (Fig. 4b).

### 4. Control experiment

The *grasping* and the *impossible grasping* conditions mainly differed in terms of parietal activity (only present in the *grasping* action) and in terms of prefrontal activity (only present in the *impossible grasping* condition). An interpretation of these results is that the *impossible grasping* actually reflects preparation processes underlying a reaching movement, because at a kinematic level the two actions were similar. To test this interpretation, a control experiment employing a standard *reaching* condition was set. Note that the *reaching* condition is also interesting per se, since there are not MRCPs data for spontaneous self-paced reaching.

#### 4.1. Materials and methods

##### 4.1.1. Subjects

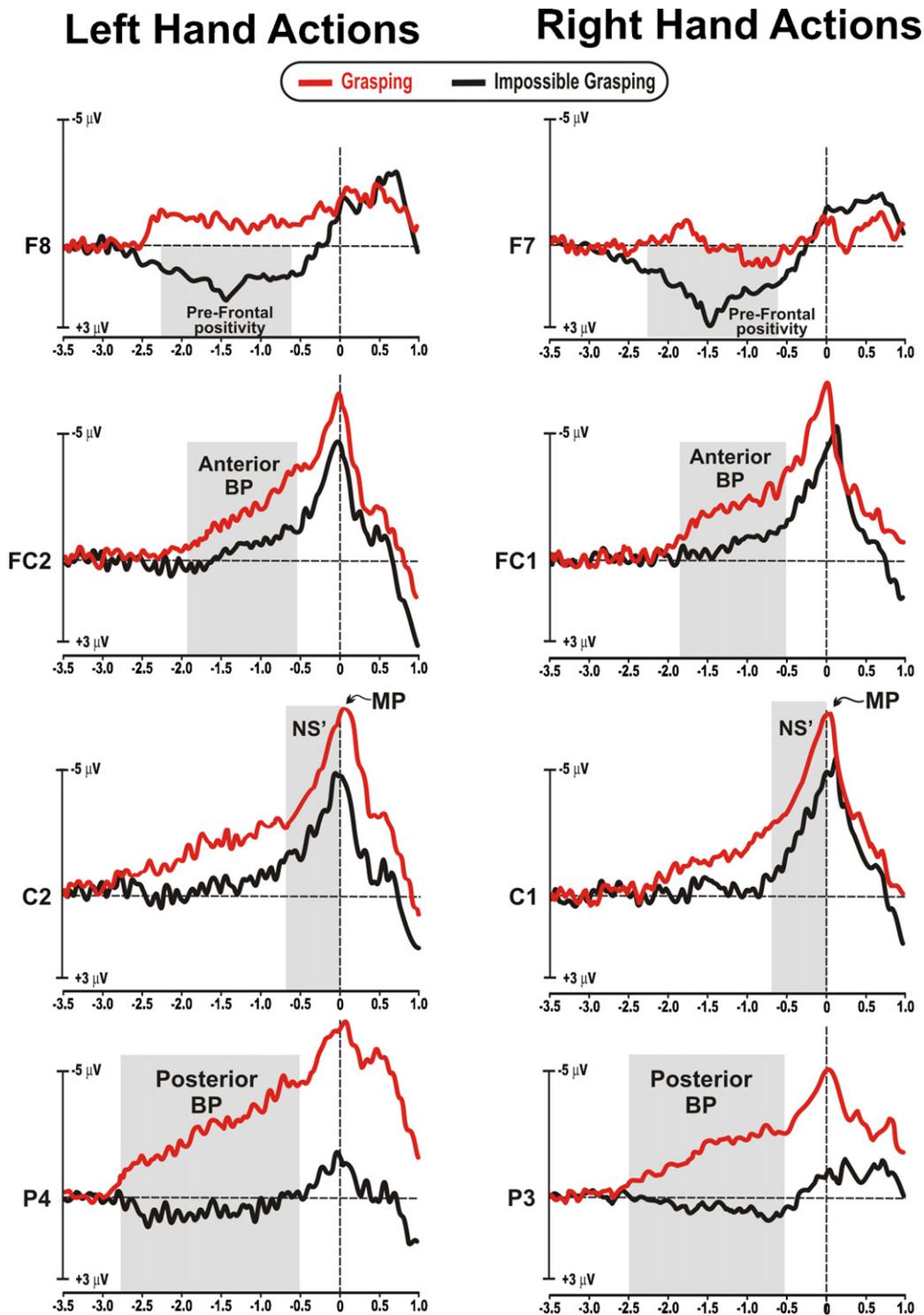
A subgroup from the previous sample (seven right-handed subjects, mean age 24.3 years, 5 females) participated to the control experiment. All subjects provided written informed consent after full explanation of the procedures.

##### 4.1.2. Task

Subjects were required to perform reaching-to-touch task with the right and the left hand alternately. The task was performed with the hand closed (in fist position), but without hand bands to replicate the position of the hand in the *impossible grasping* condition of the main experiment (see Fig. 1c).

##### 4.1.3. Procedure

Procedure was very similar to that of the main experiment, except for the task: subjects executed reaching movement toward



**Fig. 2.** Experiment 1. MRCPs activities averaged across 15 subjects for both right and left hand in *grasping* (red line) and *impossible grasping* (black line) at representative contralateral electrodes. The shaded areas represent the time window with significant differences between the two conditions. The main MRCPs components are labeled (anterior BP, posterior BP, NS' and MP). In the first row, the pre-frontal positivity is shown and it was limited to the *impossible grasping*. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

the cup with the left or right hand, according to the cup handle position. They touched the cup and then returned to the resting position. As in the main experiment, at the end of each trial the experimenter changed the side of the handle (left/right). Movements were repeated 240 times (120 with the right hand, 120 with the left hand) for each condition. Tasks were executed in separated blocks including 60 movements.

#### 4.1.4. MRCPs recording and data analysis

The brain activity recording and the data analyses were the same as in the main experiment. Statistical analyses included three tasks (*grasping*, *impossible grasping* and *reaching*) and were carried out on the data of the seven subjects who underwent also to the control experiment. A  $3 \times 2$  repeated measures ANOVA was used considering task and hand as factors.

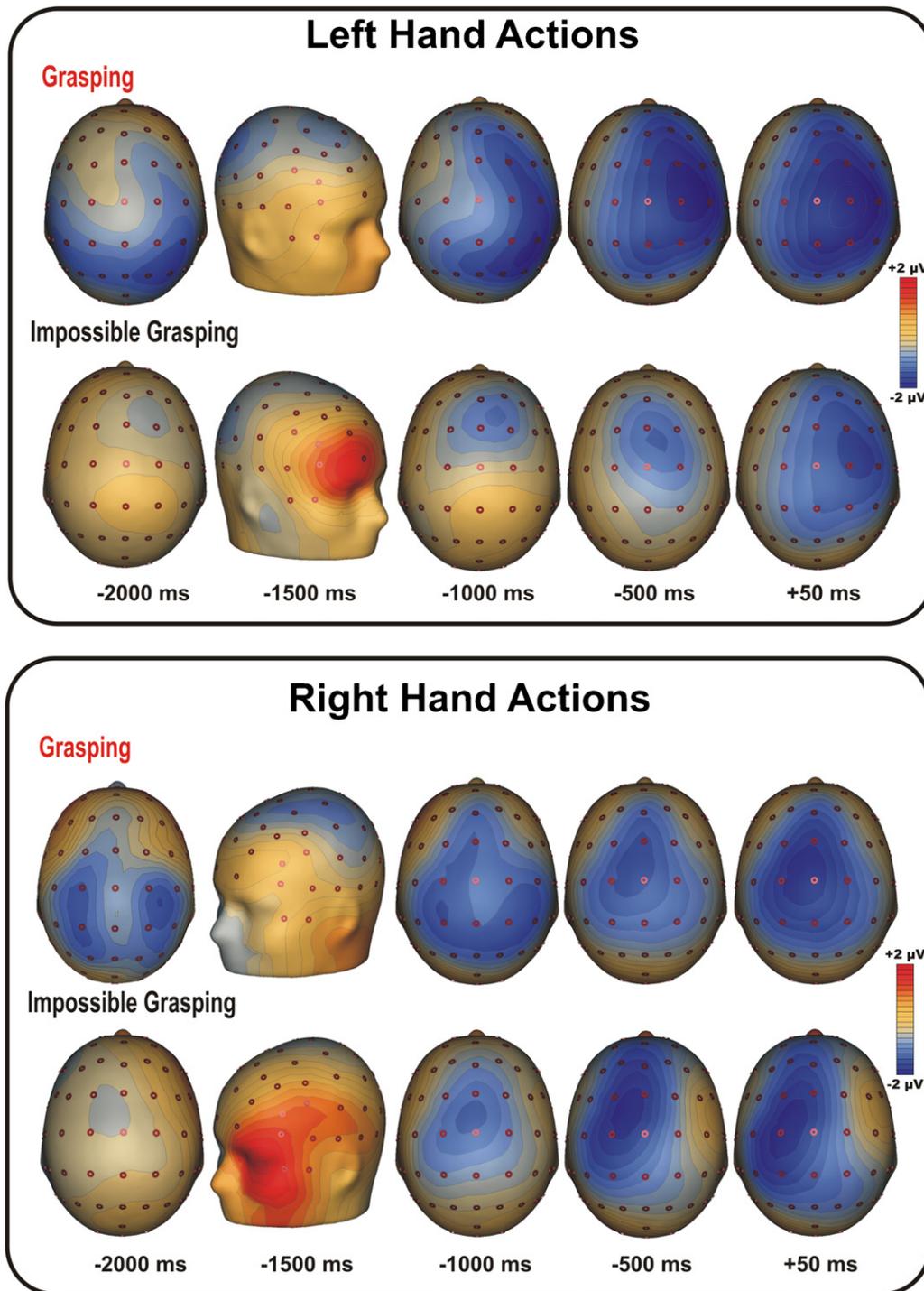


Fig. 3. Topographic 3-D maps for both left and right hand in *grasping* and *impossible grasping* conditions (in appropriate time windows) for each MRCPs component detected.

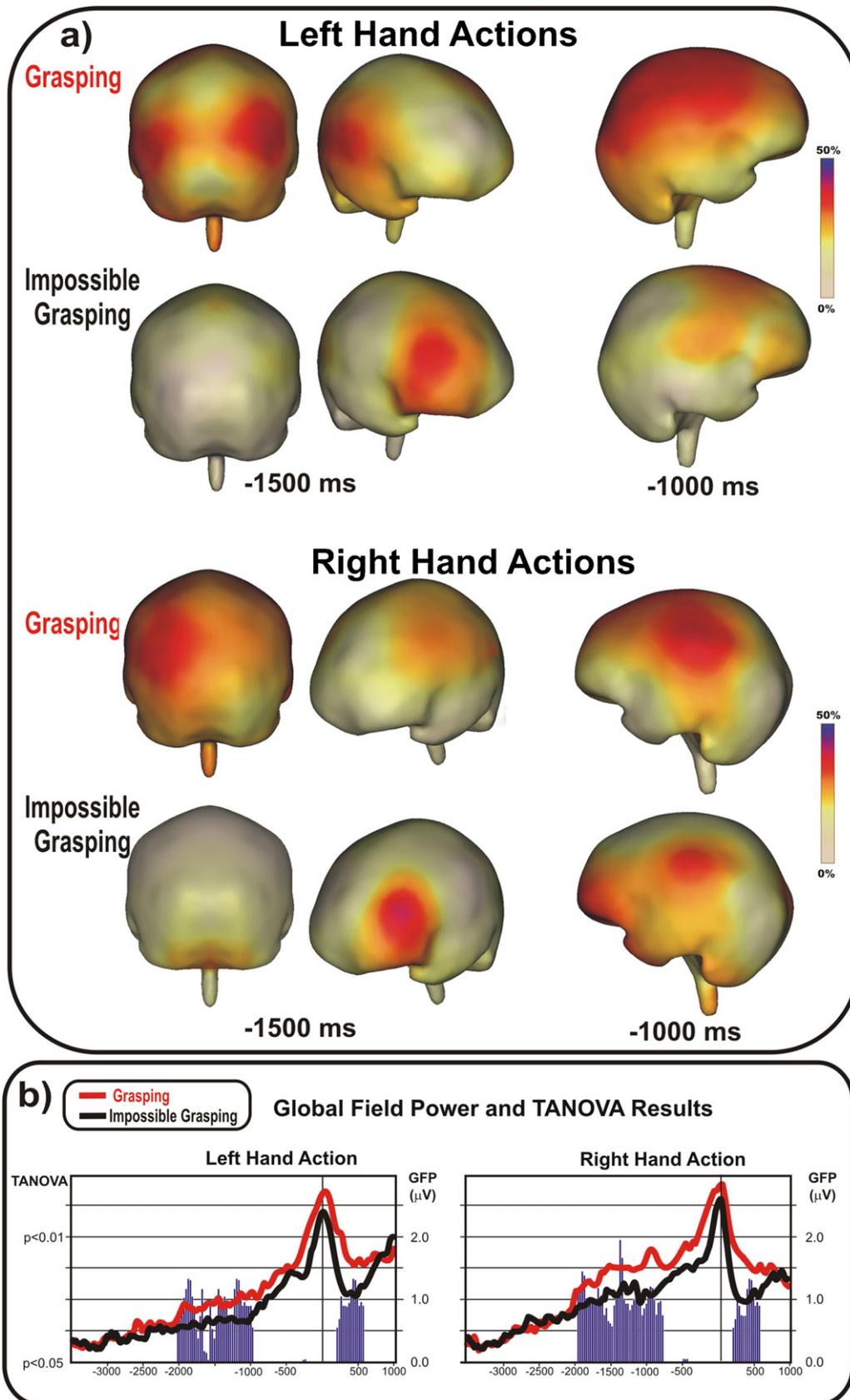
## 5. Results

### 5.1. Waveform analysis

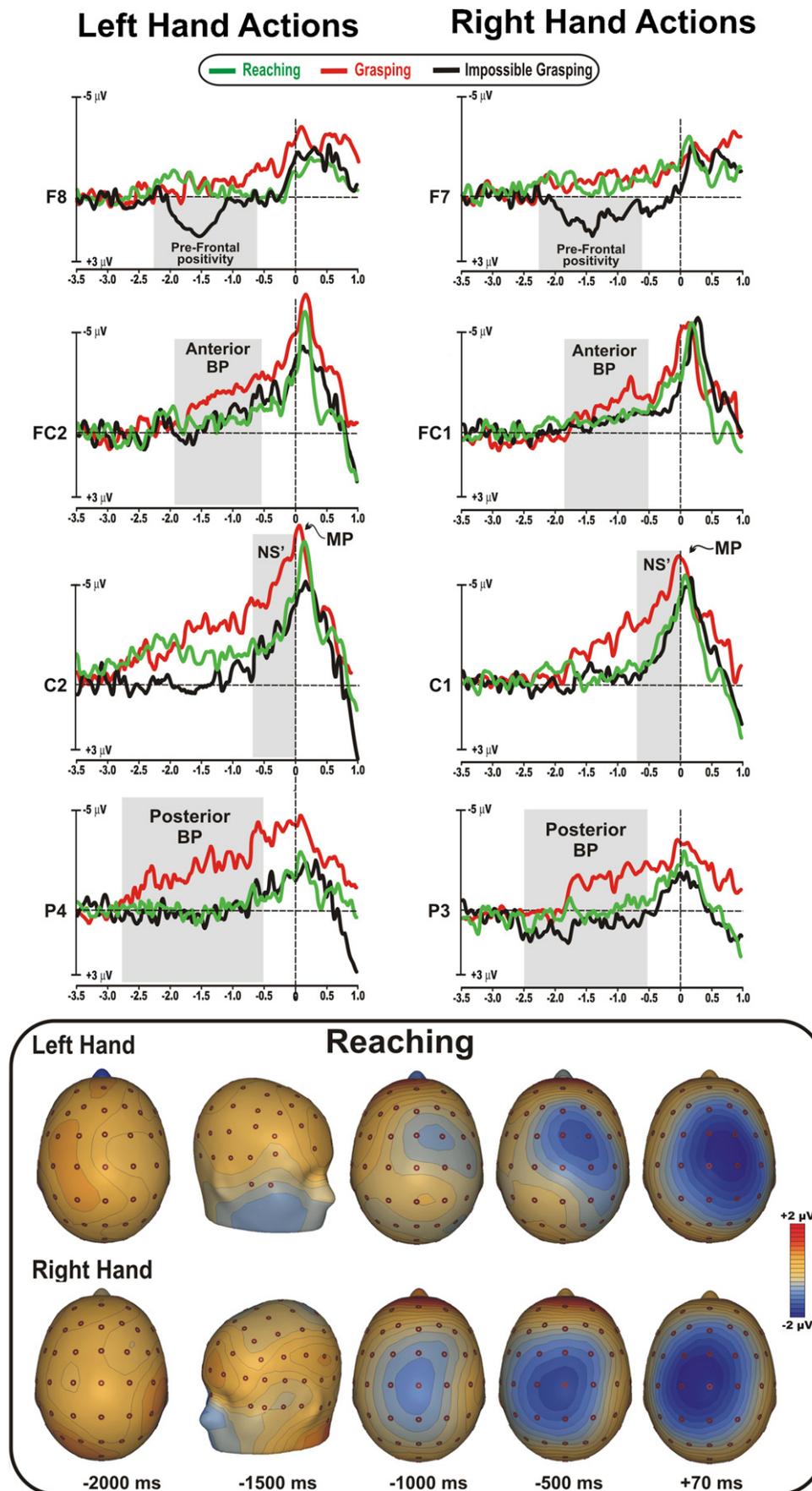
The BP component of *reaching* started at 1450 ms before movement onset in the fronto-central areas, followed by the NS'; the MP peaked at about 70 ms after movement onset on contralateral central sites. No other activities were detected related to motor preparation. Differences between right and left hand were observed, mainly related to the components latencies: left hand components were delayed by about 40 ms. LRP analysis of the

early BP component did not show a strong lateralization over the fronto-central electrodes for *reaching*, as well as in the other two conditions ( $F(2,12)=2.66$ ,  $p=0.11$ , FC1/2).

Comparing the MRCPs waveforms for the *reaching* with the *grasping* and *impossible grasping* conditions, significant differences were found for latency onset ( $F(2,12)=7.69$ ,  $p=0.007$ ), showing an earlier activity for *grasping* (2440 ms,  $p<0.001$ ) condition but no difference between *reaching* and *impossible grasping* onset (1200 and 1450 ms, respectively). Also amplitudes of the anterior ( $F(2,12)=4.29$ ,  $p=0.039$  on FC1/2) and posterior ( $F(2,12)=9.91$ ,  $p=0.002$  on Pz) BP, the NS' ( $F(2,12)=7.44$ ,  $p=0.008$  on C1/2) and



**Fig. 4.** (a) Noise-normalized minimum norm source estimation at relevant latencies in *grasping* and *impossible grasping* condition for left and right hand action; (b) global field power time course and TANOVA results (vertical bars) for *grasping* and *impossible grasping* for left and right hand action.



**Fig. 5.** Control experiment: Top: MRCPs activities averaged across seven subjects for both right and left hand in the three studied conditions. The same electrodes as in Fig. 2 are shown. The gray area highlights the time windows with the differences between cortical activities in the three conditions tested with ANOVA on the seven subjects (see text for details). Bottom: topographic 3D maps for both left and right hand in *reaching* at relevant latencies for each MRCPs component considered.

the MP components ( $F(2,12) = 4.19, p = 0.042$ ) showed a main effect of the task were the *grasping* condition was larger than the other two conditions, which did not differ each other (Fig. 5). LRP analysis showed that both the NS' and MP were markedly lateralized in all the three conditions, but did not differ between conditions ( $F(2,12) = 0.58, p = 0.57$  C1/2). No differences were detected between *reaching* and *impossible grasping* except for the contralateral frontal positivity ( $-2000/-1000$  on F7/8) only present in the *impossible grasping* ( $F(2,12) = 4.19, p = 0.041$ ) (top panels of Fig. 5). In all the previous analysis, either hand and interaction effects were not significant.

## 5.2. Scalp topography

Fig. 5 shows the scalp topography of motor preparation for *reaching*. The BP component started 1 s before the movement onset, and showed, for both right and left movements, the anterior fronto-central negativity, slightly contralateral. Approximately 500 ms before movement the NS' topography focused on the contralateral central sites. The MP peaked around 70 ms after movement onset on contralateral central sites. No other activities were recorded before  $-1$  s, either on the parietal or frontal areas.

## 6. Discussion

In the present study, we described the time sequence of cortical activities underlying motor preparation for three complex actions: *grasping*, *impossible grasping* and *reaching*, with particular focus on the grasping action in an ecologically valid context (grasping a tea cup on the table at reaching distance).

### 6.1. Spatiotemporal pattern of grasping

The first aim of the study was to analyze the cortical activity underlying grasping programming, and its response timing, verifying in particular the involvement of the parietal areas. Results showed that motor preparation for *grasping* started earlier (about 2.5 s before movement onset), and presented a wider and more complex range of components than those previously described in other MRCPs studies (see Shibasaki and Hallett, 2006). The earliest activity in the parietal cortex, posterior BP, was followed by classic MRCPs frontal components. The parietal activity detected, was present only for *grasping* condition and was localized in the superior parietal lobe (SPL) as indicated by the Minimum-Norm analysis. This activity was bilateral, even though it was more evident in the hemisphere contralateral to the hand used. These results are consistent with previous fMRI (see Castiello, 2005) and single-cells studies (Matelli and Luppino, 2001; Andersen and Buneo, 2002) which showed SPL involvement in grasping movements.

About one second after the onset of the parietal activity (1.5 s before the grasping), the classical anterior BP was recorded. Then, one second later (and lasting until action onset) the NS' was present. The anterior BP is supposed to be generated in the supplementary-motor area (SMA) and in the pre-SMA, while the NS' is generated in the pre-motor cortex (Shibasaki and Hallett, 2006); this sequence of activation is consistent also with previous fMRI studies using time-resolved event-related paradigms (Cunnington et al., 2005).

Comparing *grasping* performed with left and right hands, motor preparation differed in terms of amplitude and latency. The onset of left hand movement was faster and its amplitude was larger than the right hand, though such a difference was not significant. Anyway, in MRCPs literature, longer motor preparation and more intense activity is generally interpreted as a sign of less economic or higher metabolic (or mental) costs in action planning, and thus reflects a more complex task to be performed (Di Russo et al., 2005).

This difference supports the view that for right-handers, programming an action with the left hand is more demanding than for the right-hand (Begliomini et al., 2008).

The timing of activities of the different cortical areas here described, converges on the view that the superior parietal areas provide the frontal pre-motor areas with grasp-related information by parallel channels for sensory-motor integrations (Milner et al., 1999; Rizzolatti and Luppino, 2001). In fact, posterior BP starting ca. 2500 ms before action was too early to be considered an activity of monitoring the execution of plans generated in the premotor areas (Haggard, 2011) and would indicate an interaction between parietal and premotor areas, with the starting activity rising in the parietal area. Parietal activity was also present in the temporal window closer to the action, even though encompassed by the anterior motor areas' activities; this later parietal activity would be consistent with a monitoring function.

The view that the superior parietal areas provide the frontal pre-motor areas with grasp-related information is supported by a vast body of literature mostly based on single-cells (see Rizzolatti and Matelli, 2003), fMRI and TMS experiments (Tunik et al., 2005; Davare et al., 2010), describing parallel parieto-frontal circuits underlying visually guided grasping movements (see Castiello, 2005). Several areas along the intra-parietal sulcus in SPL are also critical for processing context and grasp-dependent information, enabling the pre-motor areas to prepare hand shaping (Davare et al., 2010) and update visually guided grasp (Tunik et al., 2005). Indeed, grasping actions require moving the arm and the hand toward an object, and also involve the processing of object shape, size and orientation to pre-shape the hand. These features of the object are mainly processed in the anterior intraparietal sulcus, in correspondence with the anterior intraparietal area (AIP), a critical node for visually guided grasping execution and planning (Culham et al., 2003, 2004; Shmuelof and Zohary, 2005). Present results are also supported by fMRI literature investigating the interaction with graspable-objects, especially tools (Creem-Regher and Proffitt, 2001, Creem-Regher and Lee, 2005).

The parietal activity observed here for grasping resembles that observed in previous MRCP studies investigating motor preparation for pantomimes of hand praxic actions (Wheaton et al., 2005b,c). However, the parietal activity for pantomimes observed by Wheaton was considerably more posterior than that observed in the present study. Likely, this might be due to differences between pantomime and grasping actions in terms of visual, motor and somatosensory aspects related to a real interaction with the object. The more anterior activity observed here for grasping, possibly related to area AIP, would be explained by a visuo-motor gradient along the posterior parietal cortex (PPC) in the posterior-anterior direction (Stark and Zohary, 2008; Beurze et al., 2009; Filimon et al., 2009; Filimon, 2010; Galati et al., 2011). According to this gradient, spatial specificity decreases and action specificity increases when gradually moving from posterior to anterior regions. This smooth gradient of selectivity, which may reflect different stages of transformation of visual signals into motor commands, might justify the more anterior grasping-related activity observed here. Moreover, Wheaton et al. found an activity mainly contralateral to the hand used whereas the results here described showed a bilateral involvement. This is likely due to the difference between the task employed here (movements toward the body midline) and that used by Wheaton and coworkers (movements confined on the left ipsilateral side).

### 6.2. Action planning and awareness

The second aim of the study was to investigate whether cortical activities underlying action planning were modulated by the possibility of accomplishing the action. Results support this view:

*impossible grasping* was planned in a different way compared to *grasping*. The posterior BP was absent, the anterior BP and NS' were reduced and a peculiar prefrontal activity was observed. To control for kinematic aspects we tested a pure reaching condition. Brain activity underlying the *impossible grasping* was very similar to that recorded for *reaching*, except for prefrontal activity only being present in the *impossible grasping* condition. This difference in activity between *impossible grasping* and *reaching* is a key result with respect to the second aim of this study. Indeed, since the two actions were similar at a kinematic level, a lack of difference between planning *impossible grasping* and *reaching* could be explained by the fact that the same motor plan was planned and executed in both cases. The different activity found at the prefrontal level between these two actions was remarkable and likely reflects a correlate of the possibility/impossibility of accomplishing the action. Source analysis roughly localized the prefrontal activity in the middle frontal gyrus, an area known to be involved in spatial working memory processes (Leung et al., 2006) and inhibitory control (de Zubizaray et al., 2000). This prefrontal activity, only present in *impossible grasping*, could be explained as an inhibition of the goal of grasping action due to the hand handicap, or as a marker of the awareness of the impossibility of performing the requested action. In any case, we can deduce that motor preparation was affected by the awareness of the impossibility of accomplishing the action.

These data opens up the possibility of considering the so-called "unconscious period" in the decision to act expressed by the BP component (Libet et al., 1983), as not entirely unconscious. Libet and many other authors investigating the volition to move have isolated the time window during which the intention to move becomes conscious (around 300 ms before movement); before this time, the medial frontal activity grows systematically, without any consciousness of "urge to move" (Libet, 1985; Haggard, 2008, 2011; Fried et al., 2011). Unlike these studies, what we refer to for awareness is not related to the volitional control of movement itself, but to the type and meaning of the movement to be performed. The awareness of not being able to accomplish the action affected the brain activity associated with the early phase of action preparation, i.e. the unconscious period.

The absence of early activity in parietal cortex (the parietal BP) in the *impossible grasping* deserves some comments. We previously interpreted the posterior BP as an activity to provide the frontal premotor cortex with grasp-related information; the lack of posterior BP in *impossible grasping* and *reaching* would be consistent with a non-grasping action: in the first case grasping was hindered, in the second case the task was only to reach. Results suggest that this early SPL activity is related to the type of interaction to be performed with the object itself. Indeed, the kinematic of the *grasping* condition is more complex than that in the *impossible grasping* and pure *reaching* conditions. Grasping an object requires a sequence of movement to be prepared/executed (grasp, lift, lowering the cup). Sequential movement is well known to elicit stronger cortical activations as compared to a single movement. Thus the parietal activation, present only in the multi-step grasping movement, might be related to planning a movement with multiple steps. Additionally, long-range grasping requires fingers pre-shaping, recruiting a large number of muscles and joints; the execution lasts longer and involves more somatosensory feedback than *reaching* and *impossible grasping*. Thus, it is likely that the general higher complexity of the *grasping* affected the type of spatial and motor coding during the preparatory delay and revealed the posterior BP at parietal level.

Interestingly, the cup with its handle was present in all cases; thus the three conditions were comparable from the point of view of the object's affordances. The graspable object should automatically activate the reach-to-grasp network (e.g. Chao and Martin, 2000; Grezes and Decety, 2002; Grezes et al., 2003a,b) in the three

conditions; in contrast, the parietal activity was modulated by the goal of the action, being posterior BP a specific feature of the *grasping* condition. In this respect note that our subjects were instructed to attempt to achieve the goal of grasping the cup also with the bound hands. Thus, in theory, the goal in the *grasping* and *impossible grasping* conditions were the same, nevertheless we observed the posterior BP only in the grasping condition. Observing the subjects in the *impossible grasping*, we noted that they did not simply extend the arm and touched the cup, as in *reaching*: their movement was more controlled and a hesitation was present when the handicapped hand was close to the cup, as if they tried, as requested, to grasp the cup. However, we cannot rule out the hypothesis that binding the hands itself did actually alter the goal of the movement, regardless of instruction.

One might contend that another possible interpretation for the lack of the posterior BP in the *impossible grasping* condition is that, in the latter case, a part of the hand was occluded from vision. It is well known that viewing the hand elicits activation in parietal areas (such as V6A, MIP and AIP), especially as related to the presence of graspable objects in the peripersonal space (e.g. Filimon et al., 2009). However note that the hand, though covered by a band, was still visible: fingers knuckle as well as part of the back of the hand appeared from the band (though this is not easily appreciable from Fig. 1c). Thus, the lack of parietal activity cannot be easily explained in terms of invisible vs. visible hand. In support of this view, note that in the *reaching* condition (where the hand was completely visible) we did not record any posterior parietal activity. Thus, we feel to exclude the possibility that results have been influenced by hand vision (or absence of vision) rather than the type of task.

### 6.3. Lack of parietal activity in reaching

The absence of parietal activity during *reaching* was unexpected; in fact previous studies reported the parietal involvement in reaching movements, both in monkeys (Fattori et al., 2001; Calton et al., 2002; Gail and Andersen, 2006; Ferraina et al., 2009) and in humans (Astafiev et al., 2003; Connolly et al., 2003; Prado et al., 2005; Hinkley et al., 2011; Galati et al., 2011). The present result may be due to various reasons. First, the technique used involved "back averaging" neural activity time-locked to a motor response (see Haggard, 2011); it is possible that parietal activity preceding reaching actions (unlike grasping) might not be strictly time synchronized to the movement onset (movement-related) and so hardly detectable by the MRCPs technique, whereas the aforementioned fMRI, and single-cells studies measured visual (go-signal) stimulus-related brain activity. Support for this view comes from description of a visuo-motor gradient along the PPC in the posterior-anterior direction, with posterior-reaching regions dominated by visual/attentional signals, and anterior-grasping ones under the control of the effectors that will be used in the following action (Beurze et al., 2009; Filimon et al., 2009; Galati et al., 2011). Second, in all three conditions the target was located in a central position respect to the subject. It is known that the parietal reach-circuit is constituted by cortical areas greatly dominated by contralateral responses (e.g. Astafiev et al., 2003; Hagler et al., 2007; Konen and Kastner, 2008; Galati et al., 2011). Due to the presence of the aforementioned visuo-motor gradient along the PPC, the posterior reaching-related areas, more dominated by visual signals, are likely sensitive to the lateralized position of the target. Thus, it is possible that, unlike for *grasping*, the central position of the target was not ideal to trigger the activity of parietal reach-regions. Third, we know from the neuroimaging literature that the human cortical regions underlying reaching movements are located medially in the POS (Beurze et al., 2009; Filimon et al., 2009) where monkey area V6A is located (Galletti et al., 1996) and in the IPS (Connolly et al., 2003) where monkey area MIP is located (Snyder et al., 1997). The

surface technique used in the present study might not allow the recording of such deep activities as in fMRI and single-cells recordings. Fourth, according to previous fMRI studies (Culham et al., 2003; Kròliczak et al., 2007) grasping execution produces greater activation than reaching in several regions, including the parietal areas. This smaller parietal activation for *reaching* might also occur in the preparation phase, thus giving a parietal contribution too small to be detected with EEG.

Alternatively, it is possible that this lack of parietal activity for *reaching* reflects a genuine effect related to the type of paradigm and task used here. In this respect, it is noteworthy that present results on *movement-related* brain activity preceding *self-paced complex-actions* have not a direct counterpart in the literature to be compared to. The fMRI studies investigating motor preparation in self-paced paradigms used only very simple tasks such as a key-press (Cunnington et al., 2002). To date, there are no other MRCPs or fMRI studies investigating the neural network underlying motor preparation by combining both complex task and self-paced paradigms. Indeed, previous EEG studies comparing simple versus 'complex' movements (e.g. Cui et al., 2000a,b; Lang et al., 1989; Mizelle et al., 2010) considered complexity differently than the current work. They used bimanual sequential movements (i.e. finger abduction/extension and knee movement), which are not comparable to grasping in kinematic terms. Future studies using the same combination self-paced paradigm and complex action could shed new light on the role of the parietal cortex.

## 7. Conclusions

The present study extends literature on the neural basis of action planning and contributes to the analysis of the interaction between parietal and premotor cortex. We showed the presence of parietal activity, well before the action begins, for goal-oriented actions such as grasping an object. This activity starts about two seconds prior to the action and is maximal about one second later in the areas contralateral to the used hand. Moreover, the type of action to be performed also modulates motor preparation in terms of timing and intensity of the different brain activity. Finally, the prefrontal activity in the impossible condition might be related to the awareness of being unable to perform the requested action, which is another aspect affecting action planning.

## References

- Andersen, R.A., Buneo, C.A., 2002. Intentional maps in posterior parietal cortex. *Annual Reviews. Neuroscience* 25, 189–220.
- Astafiev, S.V., Shulman, G.L., Stanley, C.M., Snyder, A.Z., Van Essen, D.C., Corbetta, M., 2003. Functional organization of human intraparietal and frontal cortex for attending, looking and pointing. *Journal of Neuroscience* 23, 4689–4699.
- Begliomini, C., Nelini, C., Caria, A., Grodd, W., Castiello, U., 2008. Cortical activation in human grasp-related areas depend on hand used and handedness. *PLoS ONE* 3, e3388.
- Beurze, S.M., de Lange, F.P., Toni, I., Medendorp, W.P., 2009. Spatial and effector processing in the human parieto-frontal network for reaches and saccades. *Journal of Neurophysiology* 101, 3053–3062.
- Calton, J.L., Dickinson, A.R., Snyder, L.H., 2002. Non-spatial, motor-specific activation in posterior parietal cortex. *Nature Neuroscience* 5, 580–588.
- Castiello, U., 2005. The neuroscience of grasping. *Nature Reviews. Neuroscience* 6, 726–736.
- Cavina-Pratesi, C., Monaco, S., Fattori, P., Galletti, C., McAdam, T.D., Quinlan, D.J., Goodale, M.A., Culham, J.C., 2010. Functional magnetic resonance imaging reveals the neural substrates of arm transport and grip formation in reach-to-grasp actions in humans. *Journal of Neuroscience* 30, 10306–10323.
- Chao, L.L., Martin, A., 2000. Representation of manipulable man-made objects in the dorsal stream. *Neuroimage* 12, 478–484.
- Coles, M.G.H., 1989. Modern mind brain reading: psychophysiology, physiology and cognition. *Psychophysiology* 26, 251–269.
- Connolly, J.D., Andersen, R.A., Goodale, M.A., 2003. fMRI evidences for a parietal reach region in the human brain. *Experimental Brain Research* 153, 140–145.
- Creem-Regher, S.H., Proffitt, D.R., 2001. Grasping objects by their handles: a necessary interaction between cognition and action. *Journal of Experimental Psychology. Human Perception and Performance* 27, 218–228.
- Creem-Regher, S.H., Lee, J.N., 2005. Neural representation of graspable objects: are tools special? *Cognitive Brain Research* 22, 457–469.
- Cui, R.Q., Egkher, A., Huter, D., Lang, W., Lindinger, G., Deecker, L., 2000a. High resolution spatiotemporal analysis of the contingent negative variation in simple or complex motor tasks and a non-motor task. *Clinical Neurophysiology* 111, 1847–1859.
- Cui, R.Q., Huter, D., Lang, W., Deecke, L., 2000b. Neuroimage of voluntary movement: topography of the Bereitschaftspotential, a 64-channel DC current source density study. *Neuroimage* 9, 124–134.
- Culham, J.C., Danckert, S.L., DeSouza, J.F.X., Gati, J.S., Menon, R.S., Goodale, M.A., 2003. Visually guided grasping produces fMRI activation in dorsal but not ventral stream. *Experimental Brain Research* 153, 180–189.
- Culham, J.D., Valyear, K.F., Stiglick, A.J., 2004. fMRI activation in grasp-related regions during naming of tools and other graspable objects. *Journal of Vision* 8, 410.
- Cunnington, R., Windischberger, C., Moser, E., 2005. Premovement activity of the pre-supplementary motor area and the readiness for action: studies of time-resolved event-related functional MRI. *Human Movement Science* 24, 644–656.
- Cunnington, R., Windischberger, C., Deecke, L., Moser, E., 2002. The preparation and execution of self-initiated and externally triggered movement: a study of event-related fMRI. *Neuroimage* 15, 373–385.
- Dale, A.M., Sereno, M.I., 1993. Improved localization of cortical activity by combining EEG and MEG with MRI cortical surface reconstruction: a linear approach. *Journal of Cognitive Neuroscience* 5, 162–176.
- Davare, M., Rothwell, J.C., Lemon, R.N., 2010. Causal connectivity between the human anterior intraparietal areas and premotor cortex during grasp. *Current Biology* 20, 176–181.
- De Jong, R., Wierda, M., Mulder, G., Mulder, L.J.M., 1988. The use of partial information on response preparation. *Experimental Psychology: Human Perception and Performance* 14, 682–692.
- de Zubicaray, G.I., Andrew, C., Zelaya, F.O., Williams, S.C., Dumanoir, C., 2000. Motor response suppression and the prepotent tendency to respond: a parametric fMRI study. *Neuropsychologia* 38, 1280–1291.
- Di Russo, F., Incoccia, C., Formisano, R., Sabatini, U., Zoccolotti, P., 2005. Abnormal motor preparation in severe traumatic brain injury with good recovery. *Journal of Neurotrauma* 22, 297–312.
- Fattori, P., Gamberini, M., Kutz, D.F., Galletti, C., 2001. 'Arm-reaching' neurons in the parietal area V6A of the macaque monkey. *European Journal of Neuroscience* 13, 2309–2313.
- Ferraina, S., Brunamonti, E., Giusti, M.A., Costa, S., Genovesio, A., Caminiti, R., 2009. Reaching in depth: hand position dominates over binocular eye position in the rostral superior parietal lobe. *Journal of Neuroscience* 29, 11461–11470.
- Filimon, F., Nelson, J.D., Hagler, D.J., Sereno, M.I., 2007. Human cortical representations for reaching: mirror neuron for execution, observation and imagery. *Neuroimage* 37, 1315–1328.
- Filimon, F., Nelson, J.D., Huang, R.S., Sereno, M.I., 2009. Multiple parietal reach regions in humans: cortical representation for visual and proprioceptive feedback during on-line reaching. *Journal of Neuroscience* 29, 2961–2971.
- Filimon, F., 2010. Human cortical control of hand movements: parietofrontal networks for reaching, grasping and pointing. *Neuroscientist* 16, 388–407.
- Fried, I., Mukamel, R., Kreiman, G., 2011. Internally generated preactivation of single neurons in human medial frontal cortex predicts volition. *Neuron* 69, 548–562.
- Gail, A., Andersen, R.A., 2006. Neural dynamics in monkey parietal reach region reflect context-specific sensorimotor transformations. *Journal of Neuroscience* 26, 9376–9384.
- Galati, G., Committeri, G., Pitzalis, S., Pelle, G., Patria, F., Fattori, P., Galletti, C., 2011. Intentional signals during saccadic and reaching delays in the human posterior parietal cortex. *European Journal of Neuroscience*, 1–15, doi:10.1111/j.1460-9568.2011.07885.x.
- Galletti, C., Fattori, P., Battaglini, P.P., Shipp, S., Zeki, S., 1996. Functional demarcation of a border between areas V6 and V6A in the superiorparietal gyrus of the macaque monkey. *European Journal of Neuroscience* 8, 30–56.
- Grezes, J., Decety, J., 2002. Does visual perception of object afford action? Evidence from a neuroimaging study. *Neuropsychologia* 40, 212–222.
- Grezes, J., Armony, J.L., Rowe, J., Passingham, R.E., 2003a. Activations related to mirror and canonical neurones in the human brain: an fMRI study. *Neuroimage* 18, 928–937.
- Grezes, J., Tucker, M., Armony, J., Ellis, R., Passingham, R.E., 2003b. Objects automatically potentiate action: an fMRI study of implicit processing. *European Journal of Neuroscience* 17, 2735–2740.
- Haggard, P., 2008. Human volition: towards a neuroscience of will. *Nature Reviews. Neuroscience* 9, 934–946.
- Haggard, P., 2011. Decision time for free will. *Neuron* 69, 404–406.
- Hagler Jr., D.J., Riecke, L., Sereno, M., 2007. Parietal and superior frontal visuospatial maps activated by pointing and saccades. *Neuroimage* 35, 1562–1577.
- Hämäläinen, M.S., Ilmoniemi, R.J., 1984. Interpreting Measured Magnetic Fields of the Brain: Minimum Norm Estimates of Current Distributions. Technical Report TTK-F-A559. Helsinki University of Technology.
- Hinkley, L.B.N., Nagarajan, S.S., Dalal, S.S., Guggisberg, A.G., Disbrow, E.A., 2011. Cortical temporal dynamics of visually guided behavior. *Cerebral Cortex* 21, 519–529.
- Ilmoniemi, R.J., 1993. Models of source currents in the brain. *Brain Topography* 5, 331–336.

- Johnson-Frey, S., Newman-Norlund, R., Grafton, S., 2005. A distributed left hemisphere network active during planning of everyday tool use skills. *Cerebral Cortex* 15, 681–695.
- Konen, C.S., Kastner, S., 2008. Representation of eye movements and stimulus motion in topographically organized areas of human posterior parietal cortex. *Journal of Neuroscience* 28, 8361–8375.
- Kornhuber, H.H., Deecke, L., 1965. Hirnpotentialänderungen bei Willkurbewegungen und passiven Bewegungen des Menschen: Bereitschaftspotential und reafferente Potentiale. *Pflügers Archiv* 284, 1–17.
- Kròliczak, G., Cavina-Pratesi, C., Goodman, D.A., Culham, J.C., 2007. What does the brain do when you fake it? An fMRI study of pantomimed and real grasping. *Journal of Neurophysiology* 97, 2410–2422.
- Lang, W., Zilch, O., Koska, C., Lindinger, G., Deecke, L., 1989. Negative cortical DC shifts preceding and accompanying simple and complex sequential movements. *Experimental Brain Research* 74, 99–104.
- Lehmann, D., Skrandies, W., 1980. Reference-free identification of components of checkerboard-evoked multichannel potential fields. *Electroencephalography and Clinical Neurophysiology* 48, 609–621.
- Leung, H.C., Gore, J.C., Goldman-Rakic, P.S., 2006. Sustained mnemonic response in the human middle frontal gyrus during on-line storage of spatial memoranda. *Journal of Cognitive Neuroscience* 14, 659–671.
- Libet, B., 1985. Unconscious cerebral initiative and the role of conscious will in voluntary action. *The Behavioral and Brain Sciences* 8, 529–566.
- Libet, B., Gleason, C.A., Wright, E.W., Pearl, D.K., 1983. Time of conscious intention to act in relation to onset of cerebral activity (readiness-potential). The unconscious initiation of a freely voluntary act. *Brain* 106, 623–642.
- Lin, F.H., Witzel, T., Ahlfors, S.P., Stufflebeam, S.M., Belliveau, J.W., Hämäläinen, M.S., 2006. Assessing and improving the spatial accuracy in MEG source localization by depth-weighted minimum-norm estimates. *Neuroimage* 31, 160–171.
- Matelli, M., Luppino, G., 2001. Parietofrontal circuits for action and space perception in the macaque monkey. *Neuroimage* 14, S27–S32.
- Milner, A.D., Paulignan, Y., Dijkerman, H.C., Michel, F., Jeannerod, M., 1999. A paradoxical improvement of misreaching in optic ataxia: new evidence for two separate neural systems for visual localization. *Proceedings: Biological Sciences* 266, 2225–2229.
- Mizelle, J.C., Forrester, L., Hallett, M., Wheaton, L.A., 2010. Theta frequency band activity and attentional mechanism and proprioceptive demand. *Experimental Brain Research* 204, 189–197.
- Murray, M.M., Brunet, D., Michel, C.M., 2008. Topographic ERP analyses: a step-by-step tutorial review. *Brain Topography* 20, 249–264.
- Oldfield, R.C., 1971. The assessment and analysis of handedness. *The Edinburgh Inventory*. *Neuropsychologia* 9, 97–113.
- Prado, J., Clavagnier, S., Otzenberger, H., Scheiber, C., Kennedy, H., Perenin, M.T., 2005. Two cortical streams for reaching in central and peripheral vision. *Neuron* 48, 849–858.
- Rizzolatti, G., Luppino, G., 2001. The cortical motor system. *Neuron* 31, 889–901.
- Rizzolatti, G., Matelli, M., 2003. Two different streams form the dorsal visual system: anatomy and functions. *Experimental Brain Research* 153, 146–157.
- Shibasaki, H., Barrett, G., Halliday, E., Halliday, A.M., 1980. Cortical potentials following voluntary and passive finger movements. *Electroencephalography and Clinical Neurophysiology* 50, 201–213.
- Shibasaki, H., Hallett, M., 2006. What is Bereitschaftspotential? *Clinical Neurophysiology* 117, 2341–2356.
- Shmuelof, L., Zohary, E., 2005. Dissociation between ventral and dorsal fMRI activation during object and action recognition. *Neuron* 47, 457–470.
- Snyder, L.H., Batista, A.P., Andersen, R.A., 1997. Coding of intention in the posterior parietal cortex. *Nature* 386, 167–170.
- Stark, A., Zohari, E., 2008. Parietal mapping of visuomotor transformations during human tool grasping. *Cerebral Cortex* 18, 2358–2368.
- Tunik, E., Frey, S.H., Grafton, S.T., 2005. Virtual lesions of the anterior intraparietal area disrupt goal-dependent on-line adjustments of grasp. *Nature Neuroscience* 8, 505–511.
- Wheaton, L.A., Nolte, G., Bohlhalter, S., Fridman, E., Hallett, M., 2005a. Synchronization of parietal and premotor areas during preparation and execution of praxis hand movements. *Clinical Neurophysiology* 116, 1382–1390.
- Wheaton, L.A., Shibasaki, H., Hallett, M., 2005b. Temporal activation pattern of parietal and premotor areas related to praxis movements. *Clinical Neurophysiology* 116, 1201–1212.
- Wheaton, L.A., Yakota, S., Hallett, M., 2005c. Posterior parietal negativity preceding self-paced praxis movements. *Experimental Brain Research* 163, 535–539.