Brain activity preceding a 2D manual catching task

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ABSTRACT

We investigated the event-related desynchronization (ERD) and synchronization (ERS) properties of cortical EEG rhythms in regions of interest (ROI) during the preparation of a 2D task for manual catching of a moving object. EEG signals were recorded through a 32-channel system in eleven healthy subjects during the interception task consisting of 2D catching with the right hand of a handle moving at constant velocity (1.5 m/s) on a predefined straight trajectory. The first session of catching movements (CATCHING_PRE) was compared with a second session after 1 h with identical characteristics (CATCHING_POST) and with other two conditions, where the subjects had to reach and grasp the handle fixed in the medium of platform (REACHING) and they looked at the object moving without catching it (GAZE TRACKING). Changes of cortical rhythms were correlated with dynamic and kinematic indexes of motor performance in both catching sessions.

Movements requiring different strategies (predictive versus prospective) are supported by specific changes of cortical EEG rhythms: in the CATCHING condition a more evident power decrease (ERD) in alpha 2 and beta band in the sensorimotor region contralateral to the catching hand was observed, while in the REACHING one a bilateral ERD in beta band was found. Motor learning and movement automatization were characterized by a significant reduction of theta ERS in the anterior cingulate cortex (ACC), a ROI linked to focused attention, and with a shift of neuronal activation in alpha 2 band from the bilateral superior parietal areas to the homologous area of the left hemisphere. Finally, our EEG findings are consistent with the role of supplementary motor (SMA), premotor and prefrontal areas in motor planning and preparation. In particular, theta ERS in left SMA significantly correlated with an improvement of motor performance, as evidenced by its correlation with the training-related reduction of interception time (IT).

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Introduction

Manual catching of a moving object is a complex task which involves programming as well as effective motor performance involving and integrating gaze, shoulder, arm and hand/fingers within a goal-directed coordination. Several studies focused the attention on ordinary tasks consisting of catching a moving ball, often used to analyze preparation to tuning motor behaviour, generally under the effect of gravity (Alderson et al., 1974; Sharp and Whiting, 1975; Georgopoulos and Massey, 1988; Lacquaniti and Maioli, 1989a,b; Lee, 1980; Zago et al., 2004). Studying how an interception and catching task is performed offers a wide scenario of research topics (Bennett et al., 2000; Mazyn et al., 2007; Marinovic et

al., 2008) ranging from limb kinematics analysis (e.g. correct positioning in a defined spatiotemporal constraints) and limb dynamics (e.g. deriving the kinetics responsible for a motion from the kinematics of the motion itself) up to motor prediction, generation of internal trajectory models in the CNS, and also compliance control during catching, particularly in the interaction with the ball (Tanaka et al. 2003). Prediction of impact parameters, basically based on visual information and cognitive interference, is regarded as a key factor of anticipatory movements in interception.

However, only few studies (Velasques et al., 2007; Machado et al., 2007) tried to analyze changes of cortical activity during preparation of intercepting and catching a moving object (i.e. ball free fall), focusing on changes of electroencephalographic (EEG) rhythms, particularly in theta and beta bands. They showed a participation of the frontal cortex in the planning of this task. Moreover, a recent magnetoencephalographic study (MEG) during a similar interception task described a fast propagation of cortical activations along the

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dorsal visual pathways to parietal areas and contralateral sensor-imotor regions (Senot et al., 2008). Finally, to our knowledge, there are no studies on the correlation between changes of EEG or MEG ongoing activity during this preparatory phase and kinematic and dynamic characteristics of motor performance.

Voluntary movements are accompanied by a definite pattern of changes in oscillatory firing of cortical neurons. It may play a significant role in sensory and cognitive processing and motor behaviour (Singer, 1993; Farmer, 1998; Pineda, 2005). In particular, the most and best described changes in ongoing EEG activity have been observed in beta and alpha bands. In the beta frequency range (15–30 Hz), this pattern consists of a power decrease (beta event-related desynchronization, ERD) over the central areas contralateral to the catching hand, that begins at least 1.5 s before movement onset, rapidly becoming bilateral, and is followed by an increase (beta event-related synchronization, ERS) that peaks 0.5–1 s after the end of movement (Stancak and Pfurtscheller, 1995). In the alpha band (8–12 Hz), the ERD lasts longer, and the post-movement ERS is much reduced (Stancak and Pfurtscheller, 1996). While the presence of an ERD has been linked to the activation of cortical areas related to preparation of movement, the ERS has been associated to inhibited or idling areas (Pfurtscheller and Lopes-da-Silva, 1999). Stimulus-induced movements show a similar pattern of dynamic changes, although the ERD only begins after the stimulus unless it is cyclic and therefore predictable (Alegre et al., 2003). On the other hand, reports about theta band reactivity mainly regard cognitive tasks; in particular several authors described modulation of theta oscillations in humans performing episodic and working memory tasks (Gevins et al., 1997; Klimesch, 1999). Moreover, it was previously shown that rhythmic theta activity often appears over the midfrontal region on the electroencephalogram (EEG) during various mental tasks in normal subjects (Ishihara and Yoshii, 1972; Yamaguchi, 1981; Gevins et al., 1997). Such rhythmic activity was named frontal midline theta rhythm (Ishihara and Yoshii, 1972).

On the basis of the abovementioned studies, we tried to analyze the event-related desynchronization (ERD) and synchronization (ERS) properties of cortical rhythms during the preparation of a planar task of intercepting and catching a moving object (with average velocity of 1.5 m/s) [in the following named CATCHING]. This task is chosen as it offers the opportunity of analysing human motor behaviour during rapid and ballistic movements of the upper limb without accounting for the effect of gravity. The first session of catching movements (CATCHING_PRE) was compared with a second session after 1 h with identical characteristics (CATCHING_POST) and with other two conditions, where the subjects had to reach and grasp the handle fixed in the medium of platform (REACHING) and they looked at the object moving without catching it (GAZE TRACKING).

A quantitative characterization of motor behaviour during several repetitions of the same interception and catching task was also carried out through kinematic and dynamic performance indicators. Changes of cortical rhythms during preparation of movement were correlated with the dynamic and kinematic indexes of motor performance computed for CATCHING_PRE and CATCHING_POST conditions.

Subjects and methods

Subjects

Eleven healthy volunteers (four females, seven males) with normal vision capabilities or vision that was corrected to normal, ranging in ages from 20 to 26 years (mean 24 years), participated to the experiments. All the subjects were right-handed, as assessed by the Edinburgh scale (Oldfield, 1971) with an average score of 93.92 (range 83.3–100.0), and were naïve to the purpose of the protocol which was approved by Local Ethical Committee, and gave their written informed consent.

Interception and catching platform (ICP)

A mechatronic platform (named Interception and Catching Plat-form — ICP) was designed for the controlled release of the object, in order to make the task controllable and repeatable and to allow recording and monitoring human kinematic and dynamic parameters during motion. The interception and catching apparatus is a planar device (PVC 1000×450 mm table) with a linear slider which constrains the object to a straight-line motion. The table is used as reference plane for the planar motion and is supported by two square aluminium bars (Figs. 1a, b). The system is designed to reach a slider velocity up to 2 m/s and the available stroke is 900 mm. The height of the table was adjusted according to the anthropometric dimensions of the subject. The moving object mounted on the interception and catching apparatus is a 50 mm diameter aluminium tube (handle). The diameter is chosen according to 95th percentile of the grip circumference, as reported in (Peebles and Norris, 1998). The handle was released with the same initial acceleration through a spring preload mechanism. The use of electric motors was avoided, in order to eliminate possible causes of electromagnetic interference with the sensory and acquisition systems integrated with the ICP.

For this study a specific sensory system is used which provides information on the motion kinematics and the forces at the impact with the object. Briefly, it is basically composed of a force module for dynamometric measures in the interception and catching (6-axis load cell, JR3 Inc.), and a magneto-inertial module (Xsens MTx) for measuring limb kinematic parameters during the execution of the motor task.

The ICP was placed on the table and the PVC support was regulated at middle sternum height. The subject was constrained to the chair by belts to avoid trunk rotation during catching movements and the chair was positioned so that the subject chest was about 50 mm far from the PVC table edge (Fig. 1a). The subject was wearing the bracelet with the magneto-inertial module at the level of ulnar/radial styloid processes. The wrist was positioned on a marker designed on the PVC table and wrist joint rotations were avoided by a rigid orthosis. The left arm was leant on the left leg.

Task and experimental protocol

The subjects were seated in front of the platform, equipped with the magneto-inertial module (properly calibrated) and accommodated in the rest position (Fig. 1a). Preliminarily, subjects received general instructions and familiarized with the setup by performing some trials of interception and catching not included in the data analysis. Sensors were synchronized at the beginning of each experimental session.

In the CATCHING session the subjects performed 40 trials of 2-D catching a moving object (handle) with an average velocity of 1.5 m/s. In each trial, an alert auditory signal was provided 1 s before releasing the object. The subject moved as fast as possible from the initial rest position in order to intercept and catch the object, by avoiding anticipatory actions verified via EMG recordings from upper limb muscles. After grasping the handle, he/she came back to the rest position. Between two consecutive trials, subjects kept a free relaxed posture for about 12 s. The total duration of each trial was about 15 s.

The first catching session (CATCHING_PRE) was compared with three conditions: 1) REACHING, where subjects were required to reach and grasp the object fixed in the middle of the platform (the movement of the upper limb was triggered by an auditory cue; 40 trials); 2) GAZE TRACKING, where subjects looked at the object moving without catching it (40 trials); 3) CATCHING_POST, where subjects were required to perform a second session of 40 dynamic trials (after 1 h from the first session) with characteristics identical to those of the CATCHING_PRE session. The main purpose of this second session was to track any evidence of motor learning in executing the motor task, with respect to the first session of trials.
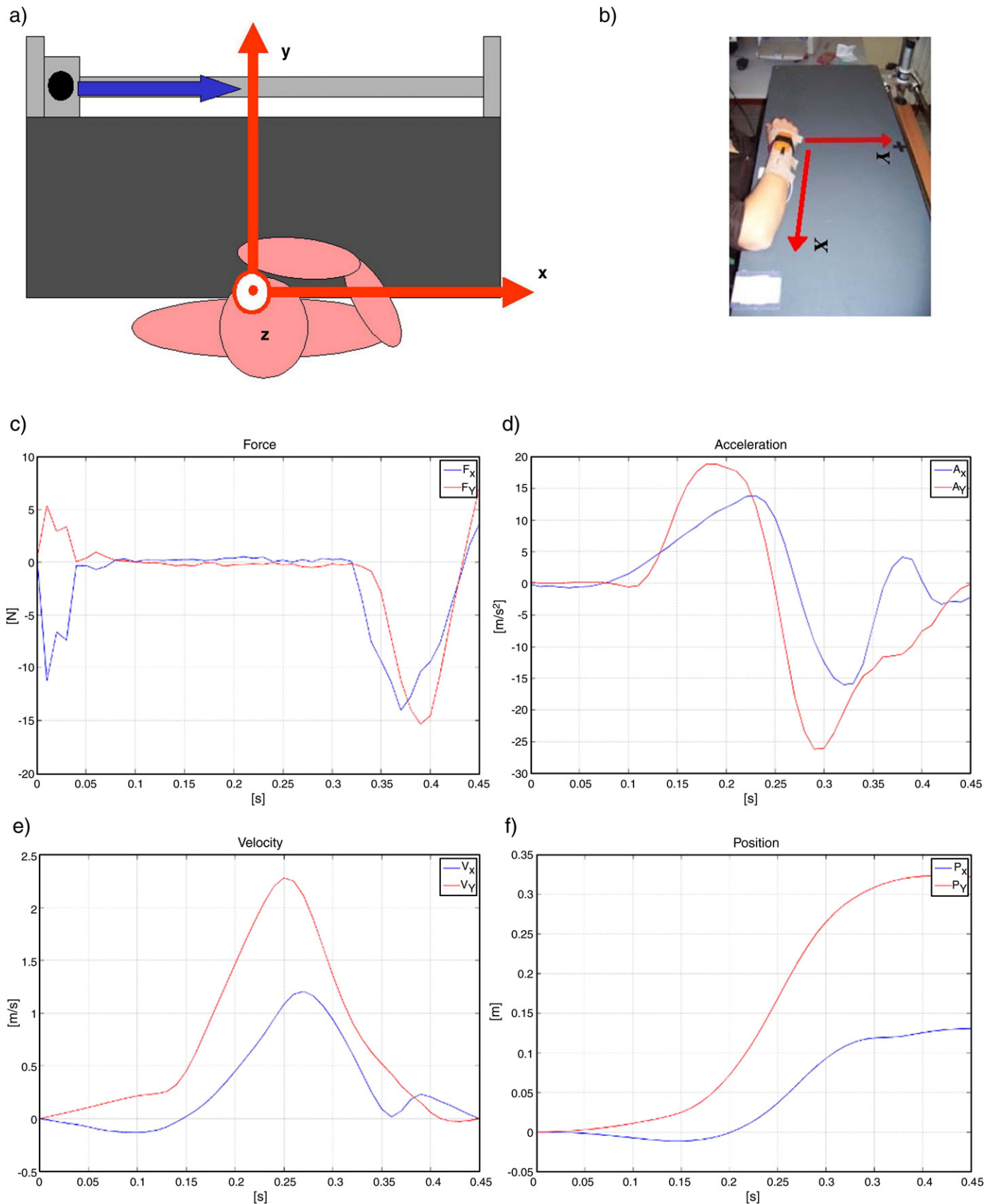
Fig. 1. The experimental setup: (a) ICP reference frame; (b) subject equipment and rest position. Motion indexes analysis for one representative subject: *x* and *y* components of force (c) and wrist acceleration (d) wrist velocity (e) and position (f) extracted from acceleration during an experimental trial of interception and catching.

Trials in which the subjects did not succeed in catching the object, or succeeded but with clear anticipatory movements, were considered invalid and not included in the data analysis.

Kinematic and dynamic measures

Data analysis was addressed to extract indexes of motor behaviour during the catching task.

The magneto-inertial module on the bracelet provided global wrist acceleration (including gravity) and its orientation (in terms of rotation matrix) with respect to a fixed reference frame, defined during sensor calibration. The rotation matrix allowed calculating the gravity contribution to be subtracted to the global wrist acceleration in order to have x and y components of wrist acceleration. Raw data were numerically low-pass filtered to eliminate impact artefacts. Numerical integration on the time interval of each trial via the trapezoidal method with 0.01 s spacing was used to calculate wrist velocity and position. This estimation was based on the assumption that the bias offset drift exhibited in the acceleration signal and deteriorated with time by integration was constant and that its compensation was possible, by using the available information on initial and final values of acceleration and velocity. As the error increases with the square power of the time, this assumption holds in very small time intervals, as for the considered task (where the total duration of the movement is maximum 500 ms).

In summary, the following data were extracted from the available sensors: (i) wrist acceleration in the xy plane; (ii) planar trajectories and velocity profile by means of the x, y coordinates extracted from the acceleration; (iii) x and y force components. They were used to calculate a set of indexes able to evaluate motor performance and provide a quantitative characterization of motor improvement due to several repetitions of the task. The proposed indexes were partly derived from previous works on human motor planning and control in healthy subjects (Hogan, 1984; Papaxanthis et al., 2005; Zago et al., 2005) and partly purposely defined for this task. They are:

- *Interception Time* (IT): it is defined as the time interval between the release and the interception of the handle. It is calculated as the time interval between two force peaks at the handle release and at the handle interception, respectively.
- *Time to Contact* (TTC): as in (Lee et al., 1983; Zago et al., 2004; Zago et al., 2005), it is the time of occurrence of the positive peak acceleration relative to the interception time. It is calculated from the acceleration profile over time.
- *Interception Position* (IP): it is defined as (x,y) coordinates (in the fixed reference frame) of the wrist position at the interception time. It is extracted from the reconstructed wrist trajectory signal.
- *Peak Velocity* (PV): it is the peak of x (PVx) and y (PVy) components of wrist velocity.
- *Interception Force* (IF): it is defined as the peak of x (IFx) and y (IFy) force components at the interception time.
- *Jerk index* (JI): in this work, it is measured through the mean of the jerk magnitude (Rohrer et al., 2002) (i.e. the derivative of the acceleration); hence, this corresponds to a measure of rate of variation of the acceleration during motion.

EEG and EMG recording

Thirty-two EEG channels (scalp sites defined according to the international 10–20 system as Fp1, Fp2, F3, F4, C3, C4, P3, P4, O1, O2, F7, F8, P7, P8, T7, T8, FZ, CZ, PZ, FC1, FC2, CP1, CP2, FC5, FC6, FT9, FT10, FCZ, CP5, CP6, TP9, TP10) with binaural reference were recorded with scalp electrodes mounted on an elastic cap. Impedances of all electrodes were kept below 5 kΩ. Recordings were carried out utilizing a time constant of 0.1 s. EEG data were sampled at 256 Hz (pre-sampling analogical filter 0.48–124 Hz, BrainAmp System).

In addition, vertical (vEOG) and horizontal electro-oculogram (hEOG) were recorded bipolarly. Electromyography (EMG) was recorded from the right Triceps (TRC), Extensor Digitorum Communis (EDC), Flexor Digitorum Superficialis (FDS) and Opponens Pollicis (OP) muscles with a filtering bandpass of 5–200 Hz. EMG signals were acquired by skin electrode pairs in a belly-tendon montage. Moreover, EMG activity from the Masseter muscle was recorded to detect muscle artefacts on the EEG signals (mainly at the level of temporal channels).

EEG analysis

After data visual inspection and the application of *ad hoc* developed artefact rejection procedures (Barbati et al., 2004), about 30 EEG epochs of 1 s length were considered in the period immediately preceding the onset of the EMG activity on the Triceps muscle (CATCHING and REACHING sessions) or the ocular movement (GAZE TRACKING session). This 'Pre-movement' period (from −1 s to 0, being 0 = movement onset, for both Triceps and ocular movements) was compared with a 1 s 'pre-event' Baseline period chosen about 5 s before the movement onset (from −5 to −4 s). The power spectral densities in the Pre-movement and Baseline periods were evaluated by standard FFT approach using Welch technique and Hanning windowing function. The following frequency bands were considered: theta (4–7 Hz), alpha-1 (8–10 Hz), alpha-2 (11–13 Hz), beta-1 (14–23 Hz), beta-2 (24–30 Hz).

We employed standardized low-resolution electromagnetic tomography analysis (sLORETA; Pascual-Marqui et al., 1994; Pascual-Marqui, 2002) for the source analysis of band activities. LORETA solutions consisted of voxel current density values able to predict the power on scalp electrodes. We considered sLORETA solutions in defined region of interest (ROI) for each band and for each condition, in 'Pre-movement' and 'pre-event' Baseline periods. These ROIs included: left and right frontal (prefrontal, BA 9,10,11,44,45,46,47; supplementary motor areas — SMA, BA 8; premotor — BA 6), left and right primary sensory-motor areas (BA 1,2,3,4), left and right parietal (superior parietal: BA 5,7; inferior parietal, BA 39, 40), temporal (BA 20, 21,22,37,38,41,42) and occipital (BA 17, 18, 19) regions, anterior cingulate cortex (AAC, BA 24). Values of sLORETA solution in ROI were log-transformed to better fit a Gaussian distribution.

To quantify the event-related changes of EEG in the different bands, we applied an event-related desynchronization/synchronization (ERD/ERS) procedure [Pfurtscheller and Lopes-da-Silva, 1999] to the signals obtained by sLORETA analysis. The ERD/ERS was defined as the ratio of the current density at the 'event' ('Pre-movement' period) compared to a 'pre-event' baseline.

Statistical analysis

Gaussianity of all the analyzed motion and electrophysiological variables was checked by Kolmogorov–Smirnov test.

Difference in performance indexes across subjects was evaluated comparing means of the 40 repetition of kinematic/dynamics indexes in the 2 repetitions by univariate ANOVA, with Condition (CATCHING_PRE, CATCHING_POST) as fixed factor and Subject as random factor.

To quantify the event-related changes of band activity in each ROI, we used the ERD/ERS procedure. To this aim, an ANOVA design was applied, with *Condition* (CATCHING_PRE, CATCHING_POST, GAZE TRACKING, REACHING), *Reactivity* (Pre-movement, Baseline), *ROI* and *Hemisphere* (Left, Right) as within subject factor. A reduced model for each ROI was applied in the case that a significant *ROI* Condition*Reactivity* interaction was found. The significance of the *Reactivity* factor indicated a difference between the Pre-movement and Baseline period. A negative difference (ERD) indicated a band power reduction in the time epoch preceding the movement onset, while a positive difference (ERS) indicated a band power increase.
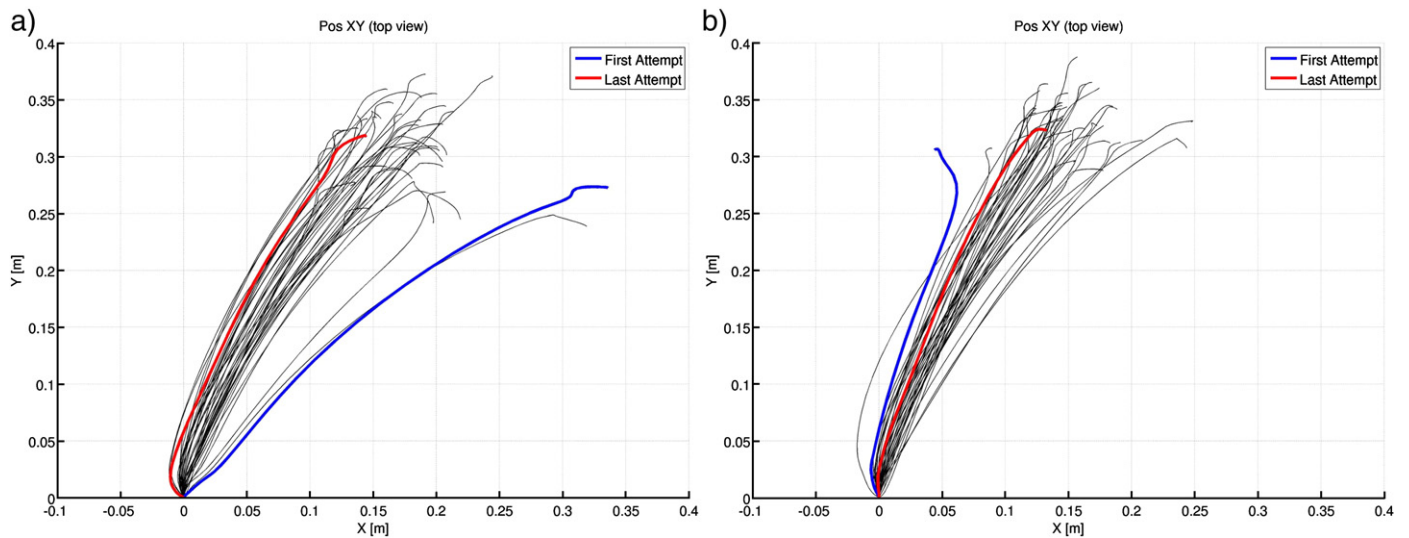
Fig. 2. Wrist trajectories in the *xy* plane for one complete catching session (a) and catching_bis session (b) of a representative subject.

Moreover, we looked for correlation (performed by Pearson's correlation) between ERD or ERS in different bands with performance indexes, respectively in CATCHING_PRE and CATCHING_POST conditions. Since subjects reached different levels of motor performance improvement, we also checked whether the amount of ERD or ERS in CATCHING_PRE condition correlated with an improvement of performance in CATCHING_POST condition. To this purpose, for each kinematic/dynamic index eventual changes between CATCHING_PRE and CATCHING_POST by the *t*-statistics between the values in the 2 conditions, i.e. $t = (\text{mean}_{\text{catching PRE}} - \text{mean}_{\text{catching POST}}) / \text{se} (\text{mean}_{\text{catching PRE}} - \text{mean}_{\text{catching POST}})$, being 'se' the standard error, were evaluated. The pooled variance was adjusted for the variance heterogeneity in case of a significant Levene's test. This measure gives indication about the statistical significance of difference between the two conditions and was correlated with band reactivity.

Results

Kinematic and dynamic data

The catching movement analyzed in our paper is a task involving a predictive strategy of intercepting the moving object, mostly based on feedforward control of interception. In fact, the time to view the moving handle was very short and the possibility of making effective feedback-based corrections was extremely limited. Therefore, interception is determined by motor programs prepared before movement onset (Schmidt and Lee, 2005). On the other hand, it is likely that in the REACHING condition the utilization of a prospective strategy with a feedback control of movement prevails. This entails that sensory input continuously contributes to generate motor output (Dessing et al., 2002).

Figs. 1c–f reports force and acceleration profiles of a representative subject measured during one trial of interception and catching, and *x* and *y* components of wrist velocity and position calculated from the planar acceleration. It is interesting to note that wrist velocity has a bell-shaped time evolution in accordance with the minimum jerk theory (Morasso, 1981; Flash and Hogan, 1985) and is characterised by a unique peak in accordance with the results on fast movements (<0.5 s) of manual interception of moving objects (Lee et al., 1997).

Improvement of motor performance was documented as a faster (lower IT and TTC) movement, characterized by higher JI and shorter and overlapped trajectories. Across subjects, all performance indexes were highly correlated.

Table 1
F-statistic and *p*-values of the ANOVA design for each band.

|		Anterior cingulate	Frontal	Supplementary motor	Premotor	Primary sensory-motor	Superior parietal	Inferior parietal	Occipital
THETA	Reactivity	(1, 10) = 38.1 0.000	–	–	(1, 10) = 30.20 0.000	(1, 10) = 7.5 0.021	–	–	–
	Reactivity*Condition	–	–	(3, 30) = 2.9 0.052	–	–	–	–	–
ALPHA-2	Reactivity	–	(1, 10) = 9.7 0.011	–	–	–	(1, 10) = 7.0 0.025	–	–
	Reactivity*Condition	–	–	–	–	–	–	(3, 30) = 3.6 0.024	(3, 30) = 2.9 0.050
	Reactivity*Hemisphere*Condition	–	–	–	–	(1.8, 17.6) = 3.7 0.052	(3, 30) = 4.6 0.010	–	–
BETA-1	Reactivity	–	(1, 10) = 9.7 0.011	(1, 10) = 9.7 0.011	–	–	(1, 10) = 18.1 0.002	(1, 10) = 5.8 0.036	–
	Reactivity*Hemisphere*Condition	–	–	–	(3, 30) = 2.9 0.017	(3, 30) = 5.2 0.005	–	–	–
BETA-2	Reactivity	(1, 10) = 7.8 0.018	(1, 10) = 23.9 0.001	F(1, 10) = 23.4 0.001	–	–	(1, 10) = 14.8 0.003	–	–
	Reactivity*Hemisphere*Condition	–	–	–	(3, 30) = 3.615 0.041	(3, 30) = 3.678 0.023	–	–	–
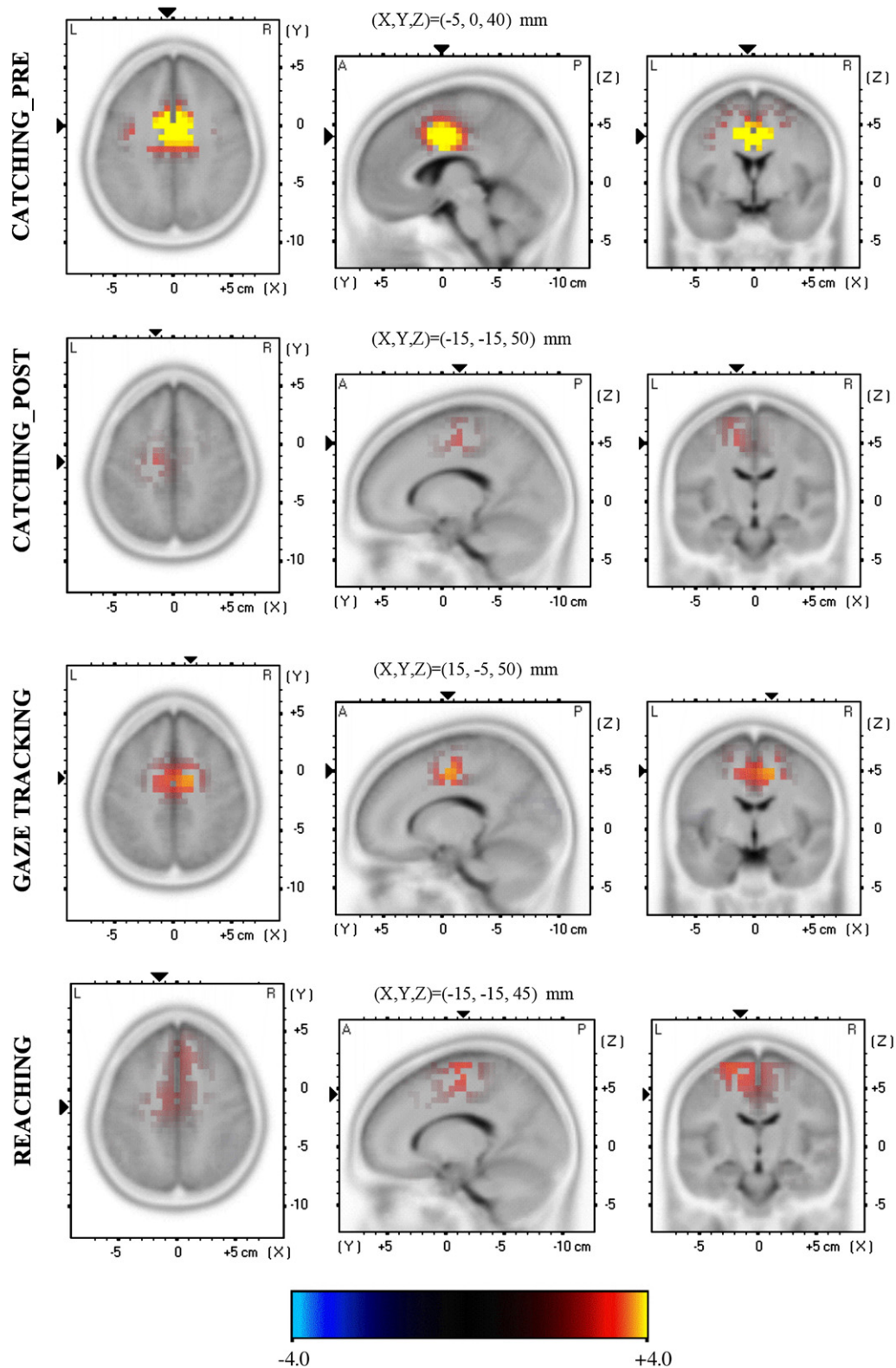
Fig. 3. sLORETA log-*F*-ratio Baseline vs Pre-movement, for each condition in theta band. The difference is significant for the two tailed *t*-test. Within each condition, from left to right, an axial, sagittal and coronal section through the voxels with maximal values are represented. Coordinates in Talairach space of the maximal-value voxel are also shown.

The analysis of different motion indexes in the two catching conditions (CATCHING_PRE, CATCHING_POST) showed a marked inter-subject variability in improvement of motor performance. The ANOVA on IT and TTC showed a *Subject*Condition* interaction [$F(9,712) = 10.518, p<0.0005$; $F(9,712) = 12.486, p<0.0005$], revealing

that for some subjects a faster and more efficient interception was achieved, while others did not show a significant reduction of these indexes. Analogous results were observed for the jerk through JI (interaction *Subject*Condition*; $F(9,712) = 10.873, p<0.0005$). No significant results were obtained for the other motion indexes as regards
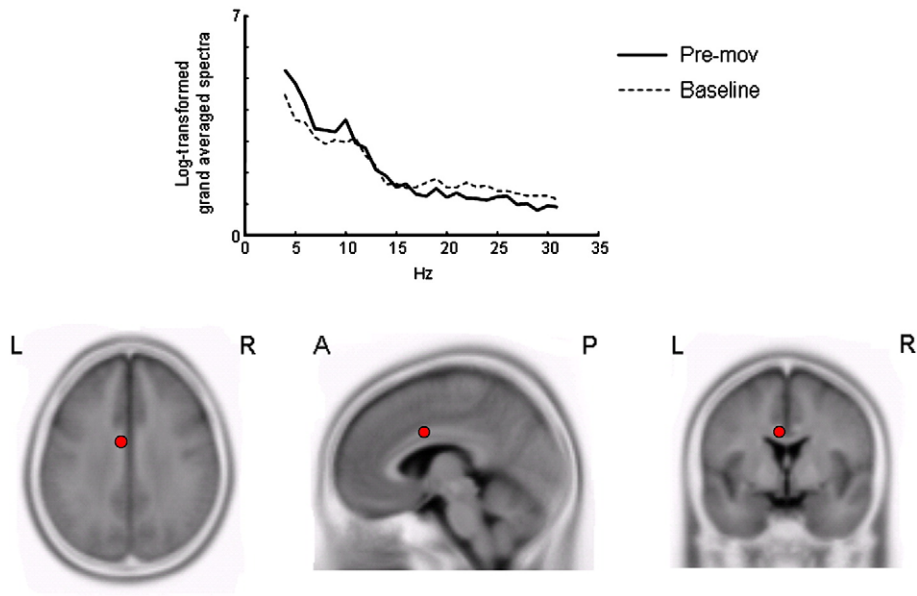
Fig. 4. Example of sLORETA signal: grand-average of sLORETA power spectral density at anterior cingulate cortex ROI in the 2–30 Hz frequency range. The position of the ROI baricentre is marked by a circle.

the *Subject*Condition* interaction. Finally, the plot of motion trajectories evidenced motor learning in all subjects; in fact, wrist trajectories in the *xy* plane for the two sessions of dynamic trials (i.e. CATCHING_PRE and CATCHING_POST) showed two main phenomena: (i) the set of 40 trajectories tend to move towards minor *x* values; and (ii) trajectories of the CATCHING_POST session tend to overlap each other (Fig. 2).
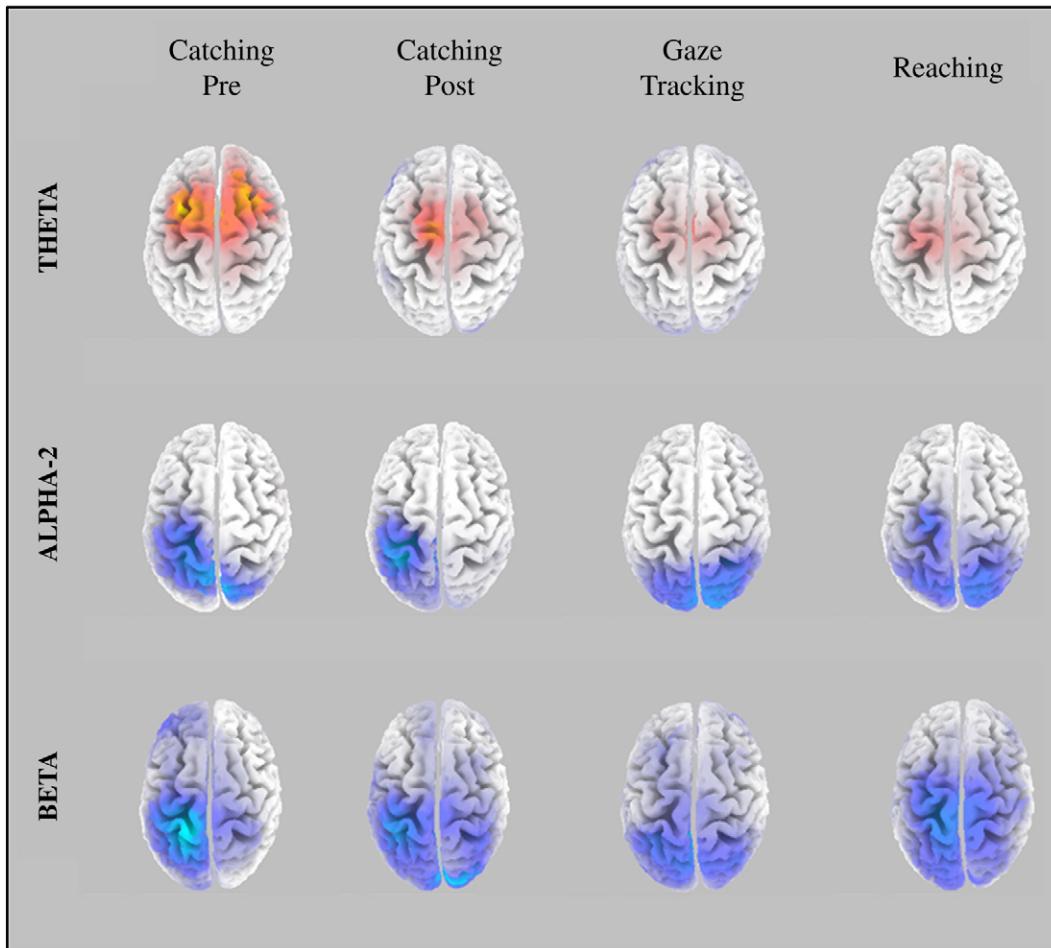

Fig. 5. For each condition, in theta, alpha-2 ad beta (beta1 and beta-2) bands, sLORETA log-F-ratio Baseline *vs* Pre-movement are shown. The difference is significant for the two tailed *t*-test.

ERD/ERS changes

The analysis of band activity in the time frame (1 s) preparing CATCHING or REACHING movement or GAZE TRACKING with respect to a baseline was performed applying a reduced ANOVA model separately in each ROI, as for each band a significant *ROI*Condition*Reactivity* interaction was found.

Theta band

A significant ERS in ACC was found in all conditions (*Reactivity* factor, Table 1, Figs. 3, 4). The ERS in CATCHING_POST condition was significantly lower than in CATCHING_PRE condition ($p = 0.002$).

In SMA (BA8) a significant interaction *Reactivity*Condition* (Table 1) was found. Post-hoc comparison showed that theta ERS in CATCHING_PRE condition was slightly different from GAZE TRACKING ($p = 0.061$, Fig. 5) and REACHING ($p = 0.059$). A bilateral ERS in premotor (mean baseline vs pre-movement: 1.128 ± 0.112 vs 1.274 ± 0.111) and primary sensorimotor areas (0.791 ± 0.145 vs 0.851 ± 0.151), independent of condition, was also found, as revealed by the significant *Reactivity* factor (Table 1).

Alpha band

The significant interaction *Reactivity*Condition* (Table 1) in alpha-1 band revealed an ERD in parieto-occipital areas only in GAZE TRACKING condition.

In alpha-2 band a triple interaction *Reactivity*Condition*Hemisphere* was found in primary sensorimotor and superior parietal areas (Table 1). In primary sensorimotor area, a significant ERD was found

only in left hemisphere in both catching conditions (Fig. 6). No activation was present in the right hemisphere (consistently $p > 0.350$ in all conditions). The comparison between the two conditions (CATCHING vs REACHING) showed in alpha 2 band a higher power decrease (ERD) at the level of contralateral sensorimotor region in the CATCHING condition with respect to REACHING one (Fig. 6).

In superior parietal areas, a bilateral ERD was observed in all condition except for CATCHING_POST, where no activation was present in the right hemisphere ($p > 0.200$, Fig. 5). In particular, comparing alpha-2 ERD CATCHING_PRE vs CATCHING_POST conditions in the two hemispheres (within subject factors: *Condition*, CATCHING_PRE and CATCHING_POST, *hemisphere*, left and right) a *Condition*Hemisphere* interaction was found ($F(1,10) = 5.233$; $p = 0.045$). In fact, while ERD was similar in the 2 hemispheres in CATCHING_PRE (paired *t*-test, $p > 0.900$; -0.24 ± 0.25 left; -0.24 ± 0.24 right hemisphere), it was different in CATCHING_POST ($p = 0.026$; -0.23 ± 0.27 left, -0.10 ± 0.39 right hemisphere). Nevertheless, focusing the analysis in the right hemisphere, the difference between the CATCHING_PRE and CATCHING_POST conditions did not reach significance ($p > 0.100$).

Beta band

A bilateral ERD was found in all condition in frontal (1.449 ± 0.224 vs 1.360 ± 0.238), supplementary motor (0.427 ± 0.168 vs 0.348 ± 0.158), superior (0.183 ± 0.183 vs -0.030 ± 0.172) and inferior (0.248 ± 0.224 vs 0.150 ± 0.221) parietal areas, as documented by the significant *Reactivity* factor (Table 1, Fig. 5). Similar activation was found in beta-2 band (frontal: 1.369 ± 0.210 vs 1.202 ± 0.210; SMA:
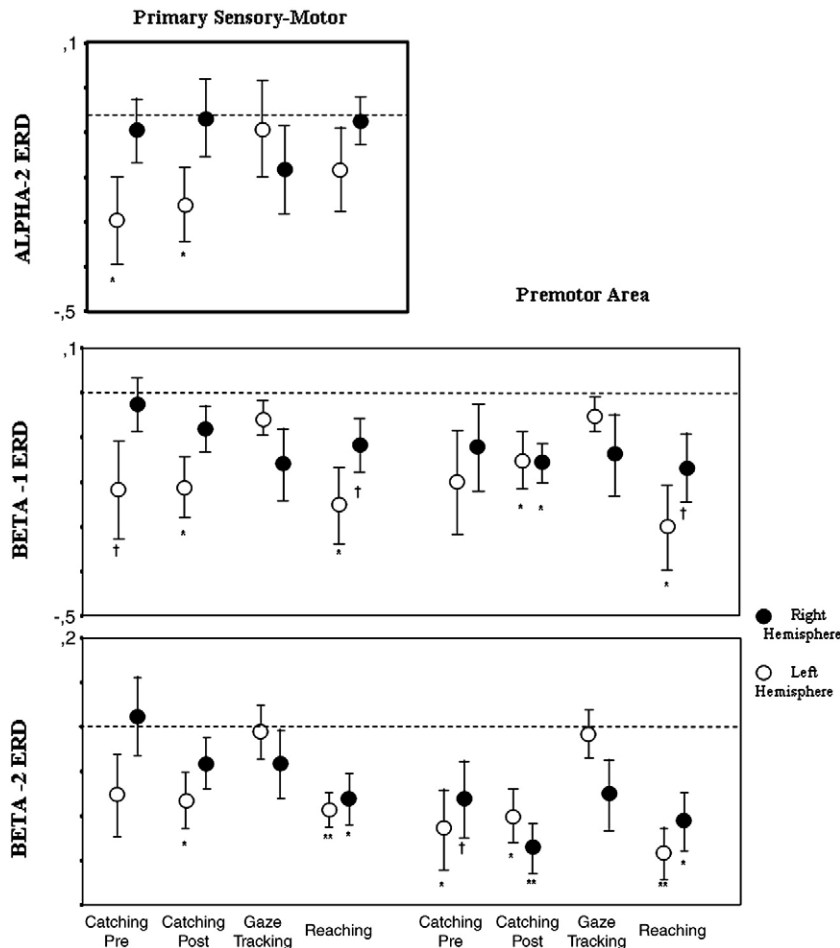

Fig. 6. Logarithmic ratio 'Pre-movement' vs 'Baseline' (ERD) for alpha-2, beta-1 and beta-2 bands in left (empty circles) and right (full circles) primary sensory-motor and premotor areas. Symbols indicate a significant difference between 'Baseline' and 'Pre-movement' condition (significant ERD) evaluated by *t*-test: †<0.100; *<0.050; ** <0.005.
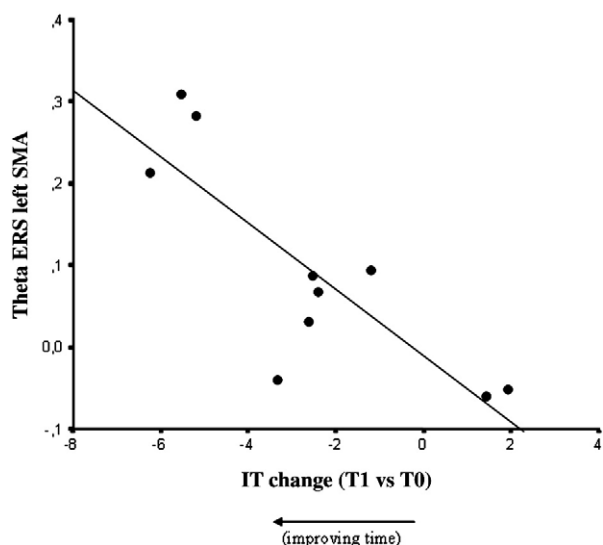
Fig. 7. Scatter-plot of IT improvement between CATCHING_POST and CATCHING_PRE condition (evaluated by *t*-value, T0 = _PRE and T1 = _POST) and theta ERS in left premotor area during CATCHING_PRE condition.

0.255 ± 0.219 vs 0.072 ± 0.193; superior parietal: -0.563 ± 0.216 vs -0.699 ± 0.190).

In premotor and primary sensorimotor areas a triple interaction *Reactivity*Hemisphere*Condition* was found both in beta-1 and in beta-2 band. In both bands, a significant ERD was present in the contralateral primary sensorimotor area for both CATCHING conditions, more evident in the second one, was absent in GAZE TRACKING condition and was bilateral in REACHING (Figs. 5, 6).

In premotor areas, a high inter-subject variability in ERD was observed in CATCHING_PRE condition without a significant activation in beta 1 band (Fig. 6), while a bilateral activation in CATCHING_POST was revealed in both beta 1 and beta 2 bands. In REACHING condition we observed a bilateral ERD with clear left prevalence, and finally in GAZE TRACKING no significant changes were present (Fig. 6).

It is worth of note that a significant ERD was found in all condition in ACC (0.904 ± 0.220 vs 0.688 vs 0.145; *Reactivity factor*, Table 1, Fig. 4).

Correlations between ERD/ERS changes and motor performance

No relationship between ERS/ERD changes (activation in pre-movement period) and performance indexes was found.

A higher theta ERS in left SMA in CATCHING_PRE condition correlated with an improvement of IT in CATCHING_POST with respect to CATCHING_PRE condition ($r = 0.824$, $p = 0.003$; Fig. 7).

Discussion

The present study deals with locoregional changes in human brain EEG rhythms in the time frame for preparing a 2D catching task, also involving a predictive strategy of interception. This last scenario was compared with a reaching condition, supported by a prospective strategy overall based on a feedback control. Moreover, evidence of motor learning was found in the second session of catching movements, and for the first time a correlation between cortical EEG rhythms changes and improvement of motor performance was evidenced.

Catching a moving object is a complex task, requiring a careful planning of action and control of motor coordination. A predictive strategy supported by a feedforward control of movement is probably used by the subjects to perform the interception as fast and precisely as possible. The analysis of dynamic and kinematic data confirmed this

hypothesis; anyway, the potential role of the sensory input (feedback control) in the initial phase of learning could not be ruled out. Thus, the examination of cortical changes in the time period preceding the movement onset seems to be particularly suitable to give evidence of the areas involved in the control of the interception. Moreover, the analysis of motion indexes provided evidence of motor improvement, through a significant reduction of interception time (IT and TTC) and an increase of acceleration rate (as assessed by higher JI values) in the second session of catching (CATCHING_ POST) with respect to the first one (CATCHING_PRE).

The analysis of oscillatory brain activity in theta band preceding the movement onset showed new and interesting data. Previous studies tried to analyze the role of theta rhythms in humans performing episodic and working memory task (Gevins et al., 1997; Klimesch, 1999). Gomarus et al., (2006) reported that frontal midline theta reactivity is linked only with attentional processes. Moreover, previous studies have suggested that a bulk of theta activity is observed when a continuous attention is required to perform a task (Yamaguchi, 1981), and is also related to working memory load (Gevins et al., 1997; Jensen and Tesche, 2002). Specifically, the work of Sauseng et al., (2007) clearly demonstrated that local theta in ACC reflects the activation of an attentional system that allocate cognitive resources and it is related to the amount of mental effort. Our results showed that in the time preparing movement a significant power increase (ERS) of theta band was observed in the ACC (BA24) and in the bilateral fronto-mesial (SMA, premotor) and sensorimotor regions, supporting the hypothesis that theta oscillations could play an important role in the attention and sensorimotor integration processes (Tesche and Karhu, 2000). Even if we are well aware that sLORETA analysis (processing signals coming from a 32-channels EEG system) has a limited spatial resolution power, not guaranteeing the precise 3-D localization of the abovementioned theta ERS, our data are consistent with previous reports (Sauseng et al., 2007), linking the frontal midline theta activity to cingular cortex, as demonstrated by different techniques (i.e. MEG; Asada et al., 1999; Ishii et al., 1999). Interestingly, in our study the theta ERS localized in the ACC displayed a clear decrease linked to motor learning. This could reflect a reduction in attention-demanding sensory processing in CATCHING_POST compared to CATCHING_PRE condition, becoming the interception movements simpler and more automatic. In this way, our data are consistent with the results of a recent study that followed-up with functional magnetic resonance the neural shifts from a naïve to a skilled stage (learning) and, finally, to an overlearned stage (automatization), showing a progressive decrease of neuronal activation in ACC in both initial learning and automatization phases (Puttemans et al., 2005).

Moreover, theta power increase (ERS) at the level of SMA (BA8) was higher in CATCHING compared to REACHING and GAZE TRACKING conditions, showing a prevalent involvement of this area in the tasks utilizing a feedforward control of movement and a careful planning of action. The role of SMA in motor control is still debated, especially with regard to whether it has a hierarchically higher function than primary motor area — M1 ('supramotor' area) or a 'supplementary motor' function in relation to M1 (Tanji, 1994). There are several experimental and clinical studies supporting both 'supramotor' (Tanji and Kurata, 1982; Rao et al., 1993; Oliveri et al., 2003) and supplementary motor functions (Shibasaki et al., 1993) of the SMA. A recent work (Ohara et al., 2000) suggests that background cortical activity in SMA proper has a specific temporal pattern with respect to self-paced movement, and that the SMA proper is involved in motor preparation earlier than primary sensorimotor regions in a bilaterally organized manner. In our work we did not analyze the chronology of activation of SMA and sensorimotor areas; however, correlation with performance improvement indexes showed a clear link with left SMA. In detail, a higher theta ERS in the left SMA during the first session of catching correlated with a performance improvement as evidenced by reduction of interception time in the second session with respect to

the first one. Even with the caution due to the aforementioned limits of the sLORETA analysis spatial resolution, we believe that this last is a new and important finding providing for the first time a correlation between changes of cortical rhythms in the time preparing an interception movement and motor learning measures. These results are also consistent with evidence coming from previous functional imaging studies (Jenkins et al., 1994; Hikosaka et al., 1995, 1996; Van Mier et al., 1999), investigating actions with sequential character and indicating that the SMA proper stores sequential movements which require a precise timing (Hazeltine et al., 1997; Van Mier et al., 1999). Moreover, it is worth noting that activation in the SMA proper exists in the left hemisphere not only when using the contralateral right hand, but also in tasks carried out by the left hand or with both hands (Hazeltine et al., 1997; Grafton et al., 2002; Babiloni et al., 2003). Thus, our findings on the analysis of cortical EEG oscillations in theta band in the time preparing catching movement according to functional imaging studies seem to corroborate the evidence that left SMA plays a dominant role in the performance of sequential actions and motor learning. Anyway, further exams and experimental designs are mandatory to confirm this observation.

ERD changes in alpha 2 and beta bands revealed interesting data which significantly discriminated CATCHING vs REACHING conditions. In fact, a clear contralateral ERD in alpha 2 and beta bands was observed only in the CATCHING conditions (more evident in the CATCHING_POST), while in the REACHING the significant left lateralization of ERD was lost, and in beta 2 band this became clearly bilateral. The catching task studied in our paper is a stimulus-induced movement preceded by a warning signal. The ERD only begins after the stimulus unless it is rhythmic and therefore predictable (Alegre et al., 2003), as in our task. Moreover, previous go/no-go paradigms, in which the subject decides to move or not to move depending on the characteristics of the stimulus, showed that both central alpha and beta energy decrease began after the 'go' decision, reaching minimum values during the movement (Alegre et al., 2004). As in aforementioned works, in our study central alpha and beta bands decreased significantly in the primary sensorimotor regions before movement, while no changes were seen in GAZE TRACKING session, where the subject did not perform any limb movement, therefore suggesting that both alpha and beta ERD are linked to motor preparation and not just to attentional processes. Moreover, the increase amount of ERD at level of the contralateral primary sensorimotor areas observed in CATCHING condition – namely in CATCHING_POST – probably reflects the higher activation of this regions in the planning and preparation of more complex and high demanding task. Present results are consistent with the learning-related increases of activation shown in the contralateral primary motor cortex during motor training (Seitz et al., 1990; Van Mier et al., 1999), probably reflecting the building of a specific motor representation (Karni et al., 1995, 1998; Nudo et al., 1996; Ungerleider et al., 2002).

The comparison of the ERD changes in alpha 2 band between CATCHING_PRE and CATCHING_POST conditions showed a shift of neuronal activation from the bilateral superior parietal areas to the homologous area of the left hemisphere. Due to its connectivity and functional properties, the superior parietal area has been described as an association area involved in sensory integration, spatial attention, coordinate transformation and the formation of early plans for movement execution based on visual data (Colby and Goldberg, 1999; Battaglia-Mayer et al., 2001; Andersen and Buneo, 2002). Recent observations indicate that neurons in motor cortex and superior parietal area (BA 7) process different parameters of the stimulus depending on the kind of stimulus motion, and that this information is used in a predictive fashion in motor cortex to trigger the interception movement (Merchant et al., 2004). Therefore, the high degree of bilateral parietal activation during initial performance decreased across learning toward focal localization in the left side, underscores the involvement of this region in sensory processing

during visuo-spatial attention and proprioceptive discrimination (Meyer et al., 1991; Pardo et al., 1991; Jenkins et al., 1994). In fact, these processes were important during novel performance to discover the new spatiotemporal relationship between hand and moving object. As soon as the exact spatiotemporal pattern was established and memorized, less spatial attention was required and activation levels dropped considerably. This was also confirmed by the theta activity reduction in ACC. Finally, whereas the right hemisphere of the parietal cortex is predominantly involved during initial learning, the left parietal area is activated in the late phase of motor learning (Halsband and Lange, 2006). In particular, acquired skill is represented in the posterior parietal cortex of the left hemisphere and is related to a body-centred frame (Halsband and Lange, 2006).

The diffuse ERD in beta band at the level of the bilateral fronto-parietal network was similar in different conditions, supporting the well known role of these regions in action planning and sensorimotor integration processes. The bilateral ERD in the premotor cortex observed in CATCHING and REACHING conditions confirmed previous observations, showing a bilateral activation of this area during the early stages of skill learning (Deiber et al., 1997; Inoue et al., 1997). Moreover, information about body part and target location is known to be integrated in the premotor cortex (Hoshi and Tanji, 2000). No significant changes in beta rhythm discriminated the two CATCHING conditions (CATCHING_PRE vs CATCHING_POST) or catching vs reaching actions.

Conclusions

Movements requiring different strategies (predictive versus prospective) are supported by specific cortical changes. Motor learning and movement automatization was paired with an activity reduction of anterior cingulate cortex (ACC) – an area devoted to focused attention – and with a shift of neuronal activation from the bilateral superior parietal areas to the homologous area of the left hemisphere. Finally, our findings are consistent with the well known role of supplementary motor, premotor and prefrontal areas in motor planning and preparation. In particular, theta ERS in left SMA correlated with an improvement of motor performance.

Acknowledgments

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