

# Pre- and Poststimulus Alpha Rhythms Are Related to Conscious Visual Perception: A High-Resolution EEG Study

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**Conscious and unconscious visuospatial processes have been related to parietooccipital cortical activation as revealed by late visual-evoked potentials. Here the working hypothesis was that a specific pattern of pre- and poststimulus theta (about 4–6 Hz) and alpha (about 6–12 Hz) rhythms is differently represented during conscious compared with unconscious visuospatial processes. Electroencephalographic (EEG) data (128 channels) were recorded in normal adults during a visuospatial task. A cue stimulus appeared at the right or left (equal probability) monitor side for a “threshold time” inducing about 50% of correct recognitions. It was followed (2 s) by visual go stimuli at spatially congruent or incongruent position with reference to the cue location. Left (right) mouse button was clicked if the go stimulus appeared at the left (right) monitor side. Then, subjects said “seen” if they had detected the cue stimulus or “not seen” if missed (self-report). Sources of theta and alpha rhythms during seen and not seen EEG epochs were estimated by low-resolution electromagnetic brain topography software. Results showed that the prestimulus “low-band” (about 6–10 Hz) alpha rhythms in frontal, parietal, and occipital areas were stronger in power in the seen than in the not seen trials. After the visual stimulation, the power of the “high-band” (about 10–12 Hz) alpha rhythms in parietal and occipital areas decreased more in the seen than in the not seen trials. The present results suggest that visuospatial consciousness covary—presumably with a facilitatory effect—with the power of both pre- and poststimulus alpha rhythms.**

**Keywords:** awareness, event-related desynchronization/synchronization (ERD/ERS), high-resolution EEG, human cortex, LORETA, subliminal stimuli, theta and alpha rhythms

## Introduction

Previous electroencephalographic (EEG) studies have shown that theta (about 4–7 Hz) and alpha (about 8–12 Hz) brain rhythms constitute an important neural substrate for human cognition (Klimesch 1997, 1999; Vogt and others 1998; Klimesch and others 1998, 2001, 2003, 2004; Sauseng and others 2002). In the prestimulus period, a good cognitive performance is predicted by high alpha power and low theta power. In the poststimulus period, a good cognitive performance is associated with an inversion of such a pattern, namely, low alpha power and high theta power (Neubauer and Freudenthaler 1995; Klimesch 1999).

The general relationships linking theta and alpha EEG rhythms with cognitive performance are well illustrated by evidence relative to encoding and retrieval processes. Encoding

new information implies extracting stimulus features and creating new connections into semantic or episodic long-term memory. Successful encoding processes would depend on the increase of the frontal theta power, reflecting the functional mode of loops including basal forebrain, hippocampus, and cerebral cortex (Klimesch 1999). Later, successful retrieval processes into semantic or episodic long-term memory would depend on the decrease of posterior alpha power, reflecting the functional mode of thalamocortical and corticocortical feedback loops (Klimesch 1999). A general rule is as follows: the stronger the prestimulus alpha power, the stronger its power reduction during the stimulus processing and the better the cognitive performance (Neubauer and Freudenthaler 1995; Klimesch 1999). Along this vein of reasoning, it was demonstrated that by “driving” the prestimulus alpha power via repetitive transcranial magnetic stimulation or neurofeedback training, one can improve cognitive performance (Klimesch and others 2003; Hanslmayr and others 2005).

An intriguing open issue is whether pre- and poststimulus theta and alpha rhythms affect not only actual cognitive performance but also the preliminary stimulus-processing stages resulting in visual consciousness. In precedence, neural correlates of conscious and unconscious visual processes have been studied in patients with unilateral brain lesions, particularly at the right posterior parietal cortex (Vallar and others 1988; Driver and others 1997; Driver and Vuilleumier 2001). During bilateral stimulations, these patients typically miss contralesional stimuli at the left visual hemifield (visual extinction), probably due to a pathological bias in visuospatial attention including hyperattention toward the right hemifield (Posner and others 1984; Vallar and others 1988; Desimone and Duncan 1995; Driver and others 1997; Cocchini and others 1999) and abnormal processes in parietooccipital cortical areas (Lhermitte and others 1985; Vallar and others 1991; Spinelli and others 1994; Verleger and others 1996; Marzi and others 2000, 2001; Oliveri and others 2000; Driver and Vuilleumier 2001; Vuilleumier and others 2001).

Uncontrolled effects of the brain lesion in “extinction” patients have required a confirmation of the mentioned findings in normal subjects (Shevrin and Fritzer 1968; Kostandov and Arzumanov 1977; Naatanen and Gaillard 1983; Brandeis and Lehmann 1986; Shevrin 1992; Wong and others 1994). During the so-called “oddball” paradigm, normal subjects had to respond (i.e., moving or counting) after rare but not after frequent stimuli of a sequence. Rare stimuli evoked a well-shaped late-positive event-related potential (P300), which is supposed to reflect

cognitive closure of the recognition processing and memory updating (Smith and others 1970; Hillyard and others 1971; Hillyard and Picton 1987; Iragui and others 1993). Compared with the unconscious (subliminal) perception of the rare stimuli, the conscious one evoked parietal P300 with higher amplitude (Shevrin 1976; Kostandov and Arzumanov 1977; Brandeis and Lehmann 1986; Shefrin and others 1988; Brazdil and others 1998, 2001, 2002). However, it might be argued that the movement or counting demands only impinged upon P300 of the trials with conscious perception of the rare supraliminal stimuli. This issue was overcome by a recent high-resolution EEG study from our group (Babiloni and others 2006) in which no oddball paradigm was used to study visual consciousness. Subjects were required to have the same motor response in the trials characterized by both conscious and unconscious perceptions (i.e., physical features of the stimuli were equal in all trials). Results showed that visual-evoked potentials (VEPs) at parietooccipital areas had the same peak latencies in consciously and unconsciously perceived cases. Cortical sources of these evoked potentials were located in occipital Brodmann area (BA) 19 and parietal BA 7, and source strength was significantly stronger in consciously than unconsciously perceived cases at about +300 ms poststimulus. We concluded that these features of the parietooccipital activation might relate to visuospatial consciousness (Babiloni and others 2006). In the present EEG investigation, the same data set of our previous study (Babiloni and others 2006) was used for testing a totally different working hypothesis, namely, how pre- and poststimulus theta and alpha rhythms actually relate to visual consciousness.

## Subjects and Methods

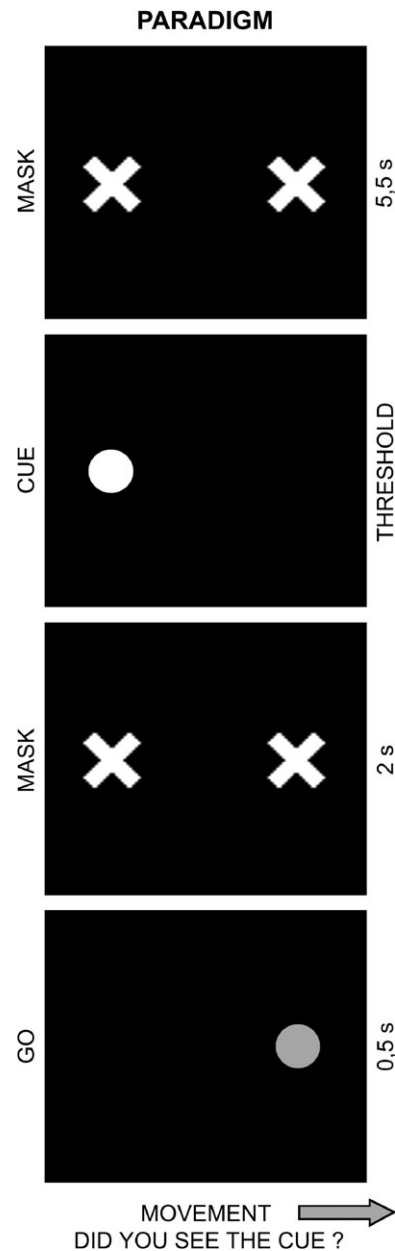
### Subjects

Experiments were performed on 12 healthy adult volunteers (mean age of 29.3 years  $\pm$  0.8 standard error [SE]) with normal or corrected-to-normal vision. They were right handed as revealed by the Edinburgh Inventory (81.2%  $\pm$  4.6 SE) and provided a written informed consent after the approval by the Ethics Committee.

### Experimental Task

Subjects were seated in a comfortable reclining armchair, placed in a dimly lit, sound-damped, and electrically shielded room. They kept their forearms resting on armchairs, with the right index finger resting between 2 buttons of a mouse connected to a computer monitor. The monitor of the computer was placed in front of them at a distance of about 100 cm. Preliminarily, we ascertained the individual threshold time (ms) of the cue stimulus (white circle of about 30' of visual angle in diameter) displayed 6° right or left aside a background central white cross and preceded and followed by a masking visual stimulus formed by 2 "X's" (about 45' visual angle), located at 6° right and left aside the central white cross. The subjects had to say "seen" any time they perceived the position of the cue stimulus. In detail, the procedure was as follows. The duration of the cue stimulus was randomized trial-by-trial within a 20- to 160-ms range for 80 trials (10 for each duration value). The procedure was repeated seven times. The threshold time to be used during the EEG recordings was defined as the duration of the cue stimulus determining about 50% of correct stimulus detections within a series of 10 trials in the majority of the 7 repetitions of the procedure. Just before the EEG recording, this threshold time was systematically varied up and down (10 ms) for some preliminary trials, to verify the stability of that time based on the subject's self-report. Across subjects, the mean threshold time of the cue stimulus was 101 ms ( $\pm$ 8.8 SE), with a post hoc verification showing that the recognition of the cue stimuli during the EEG recordings was 48% ( $\pm$ 2 SE) on across-subjects average.

The stimulation sequence was as follows (Fig. 1): 1) background stimulus as bilateral X's lasting 5.5 s before the cue stimulus, 2) cue stimulus as a "small circle" appearing at the right or left (50%) monitor



**Figure 1.** Sequence of events during a standard trial: 1) background stimulus as bilateral X's lasting 5.5 s before the cue stimulus, 2) cue stimulus as a small circle appearing at the right or left (50%) monitor side for the threshold time (same position of the previous X's), 3) masking stimulus as bilateral X's lasting about 2 s (i.e., 2 s minus the threshold time), 4) go target stimulus lasting about 0.5 s. The go stimulus was a small green circle with a diameter of about 0.5°, which appeared 6° right or left (50% of probability) side of the central white cross; 5) background stimulus as bilateral X's lasting 5.5 s before the cue stimulus, etc. The subjects had to click the left mouse button if the go stimulus appeared at the left monitor side and the opposite if the go stimulus was on the right side. Immediately after the motor response, the subjects had to say seen if they had detected the cue (seen trial) or not seen if they had missed it (not seen trial).

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the subjects had to say “seen” if they had detected the cue (“seen trial”) or “not seen” if they had missed it (“not seen trial”). Noteworthy, subjects denied the use of mental verbal codes for the cue or go stimuli after the experiment. A microphone connected to the computer recorded verbal reports. Of note, the same presentation time and physical features (shape, position, luminance, etc.) characterized both seen trials and not seen trials.

In some cases, the “standard” trials were replaced by “baseline” trials that were characterized by the following stimulus sequence: 1) masking: stimulus X’s lasting 5.5 s and 2) black screen: lasting the threshold time instead of the cue stimulus. The rest of the sequence was as that of the standard trials. Of note, the baseline trials were introduced to verify whether the self-report of the subjects (seen or not seen) during the present EEG recordings was reliable. It was expected that subjects stated not seen for all baseline trials. This was practically the case, as previously reported (Babiloni and others 2006). Less than 3% of the cases erroneously asserted to have seen the cue stimulus during the baseline condition (without cue stimulus).

#### **EEG Recordings**

During the experimental task, EEG data were recorded (band-pass: 0.1–100 Hz, sampling rate: 256 Hz) from 128 electrodes placed according to an augmented 10–20 system. Linked earlobes served as an electrical reference, and electrode impedance was kept lower than 5 kOhm. Vertical and horizontal electrooculographic activity was also recorded with the same features of the EEG data, to monitor eye movements and blinking. In parallel, involuntary and voluntary (following the go stimulus) hand motor responses were assessed by collecting electromyographic activity from extensor digitorum muscle of both arms. This allowed the monitoring of the voluntary right motor responses and of possible involuntary left mirror movements. Acquisition time for all data was set from –1 s to +5.5 s after the onset of the cue stimulation.

In all subjects, the EEG data were recorded in the aforementioned experimental task. On average, there were 270 standard trials (66.6%) and 135 baseline trials (33.3%) pseudorandomly intermingled.

#### **Behavioral Data Analysis**

Behavioral data analysis was mainly aimed at verifying the occurrence of unconscious visual processes in the “standard not seen” trials. The standard trials were classified as follows: 1) “congruent seen” trials in which the cue stimulus was detected and the go stimulus appeared at the cued location, 2) “incongruent seen” trials in which the cue stimulus was detected and the go stimulus appeared at the uncued location, 3) “congruent not seen” trials in which the cue stimulus was not detected and the go stimulus appeared at the cued location, and 4) “incongruent not seen” trials in which the cue stimulus was not detected and the go stimulus appeared at the uncued location. The “congruent” and “incongruent” trials were paired (50%).

#### **Statistical Analysis of the Behavioral Data**

Details of the statistical analysis of the behavioral data were reported in a previous study (Babiloni and others 2006); here we summarized them for the readers’ convenience. Analyses of variance (ANOVAs) for repeated measures served to evaluate the following hypothesis. In line with well-known previous evidence (McCormick 1997; Ivanoff and Klein 2003), it was predicted that the reaction time to go stimuli (dependent variable) should be shorter in the congruent seen trials than in the incongruent seen ones, as an effect of the covert attention on cued location for the self-report. Similarly, the working hypothesis stated that the reaction time to go stimuli should be shorter in the congruent not seen than in the incongruent not seen trials, as a sign of unconscious visuospatial processes. The ANOVA design included the factor condition (baseline, congruent seen, incongruent seen, congruent not seen, incongruent not seen). Furthermore, a control ANOVA design included the factors condition (seen and not seen) and congruence (congruent and incongruent). Mauchley’s test, evaluating the sphericity assumption and correction of the degrees of freedom, was made by Greenhouse-Geisser procedure. Duncan test was used for post hoc comparisons ( $P < 0.05$ ).

#### **Preliminary EEG Data Analysis**

EEG single trials contaminated by blinking, eye movements, and involuntary motor acts during the cue stimulation were rejected off-

line. For the EEG data analysis, the artifact-free trials were re-referenced to common average and classified in the 2 classes seen and not seen.

To eliminate phase-locked VEPs from background EEG data, VEPs for each channel were obtained by averaging the EEG over all the trials. Then, a correction factor was calculated for each single trial by cross-correlation between average VEP and the same EEG single trial. Finally, the average VEP for each channel, corrected by the specific trial factor, was subtracted from the corresponding EEG trial (Klimesch and others 1999; Pfurtscheller and Lopez da Silva 1999).

Individual artifact-free EEG data were then interpolated by a spline function (Babiloni and others 1995), and signals from 105 electrode sites of an augmented 10–20 system were obtained, rendering consistent the electrode position across subjects.

#### **Determination of the Peak of Individual Alpha Frequency**

Power spectrum analysis in a 1-s epoch before the visual CUE stimulus was based on a standard technique, as for the determination of the individual alpha frequency (IAF) peak (Klimesch 1996, 1999; Klimesch and others 1998) defined as the maximal power density frequency in the 6–12 Hz range. The following IAFs were identified: theta as IAF – 6 Hz to IAF – 4 Hz, alpha 1 as IAF – 4 Hz to IAF – 2 Hz, alpha 2 as IAF – 2 Hz to IAF, and alpha 3 as IAF to IAF + 2 Hz.

For each condition (not seen and seen), the artifact-free EEG single trials were divided in 2 half groups. One group contained seen EEG single trials, whereas the other included not seen EEG single trials. The power density at the aforementioned prestimulus period was calculated at theta, alpha 1, alpha 2, and alpha 3 for each condition.

We had to reject EEG data from 1 of the subjects. The EEG data of that subject did not show any alpha peak in the power spectrum, a crucial anchor point for the individual analysis of the EEG data. Therefore, the results of the present study were based on 11 individual EEG data sets.

#### **Cortical EEG Source Analysis by Low-Resolution Electromagnetic Brain Topography**

Low-resolution electromagnetic brain topography (LORETA) was used for the EEG source analysis (Pascual-Marqui and Michel 1994; Pascual-Marqui and others 1999, 2002) because several independent research groups have repeatedly demonstrated that LORETA solutions are able to reliably model cortical responses to sensorimotor events (Wang and others 1999, 2003; Frei and others 2001; Jausovec N and Jausovec K 2001; Carretie and others 2004; Gamma and others 2004; Herrmann and others 2004).

LORETA computed 3-dimensional linear solutions (LORETA solutions) for the EEG inverse problem within a three-shell spherical head model including scalp, skull, and brain compartments. The brain compartment was restricted to the cortical gray matter/hippocampus and was coregistered to the Talairach probability brain atlas, digitized at the Brain Imaging Center of the Montreal Neurological Institute (Talairach and Tournoux 1988). This compartment included 2,394 voxels (7-mm resolution), each containing an equivalent current dipole. LORETA solutions consisted of voxel spectral density of estimated z-current density values able to predict spectral data at scalp electrodes. In nonformal terms, LORETA estimation is based on a table of correspondences among the values of EEG spectral power density at each scalp electrode and the values of spectral power density at each cortical voxel (i.e., the so-called lead field matrix of linear inverse source estimation). From the infinite possible correspondences, LORETA selects a unique solution of spectral power density at cortical voxels. It is the solution in which that spectral power density is maximally smoothed across the source space and fits EEG spectral power density at scalp electrodes (i.e., as a regularization of the linear inverse source estimation). Formal details of the use of LORETA to compute sources of EEG frequency rhythms can be found in previous papers (Pascual-Marqui and Michel 1994; Pascual-Marqui and others 1999, 2002; Frei and others 2001).

#### **Event-Related Desynchronization/Synchronization**

Magnitude of the brain rhythmicity at the LORETA solutions was indexed by the computing event-related desynchronization (ERD)/event-related synchronization (ERS) of theta, alpha 1, alpha 2, and alpha 3 bands on the spectral pattern. The ERD/ERS was defined as the

percent decrement/increment of instant power density at the post-stimulus period compared with a prestimulus according to the following equation

$$\left(\frac{\text{post-pre}}{\text{pre}} \times 100\right).$$

The pre- and poststimulus EEG periods lasted 1 s. This allowed the computation of LORETA source power with 1-Hz frequency resolution, suitable for the individual ERS/ERS analysis of theta and alpha subbands.

### ERD/ERS at Regions of Interest

Because the LORETA procedure intrinsically provides “low-resolution” EEG source solutions, we decided to evaluate these solutions at the rough level of 1 representative BA for each of the 3 lobar regions of interest (frontal, parietal, and occipital). The LORETA solution at this level was defined as the mean of the LORETA solutions across all the voxels of that BA. The extension of the frontal (including BAs 4, 6, 8, 9, 10, 11, 44, 45, 46, 47), parietal (including BAs 5, 7, 30, 39, 40, 43), and occipital (including 17, 18, 19) regions of interest was defined in terms of standard lobar anatomy. Of note, this approach globally overcomes the methodological limitation that neighbor BAs might be affected by the same LORETA EEG source.

### Statistical Analysis

Regional solutions were analyzed by ANOVA for repeated measures. Mauchly’s test evaluated the sphericity assumption, and correction of the degrees of freedom was made by Greenhouse-Geisser procedure. Duncan test was used for post hoc comparisons ( $P < 0.05$ ). Separate ANOVAs tested LORETA solutions relative to each band of interest such as theta, alpha 1, alpha 2, and alpha 3. The dependent variable of the ANOVAs was the LORETA solution at the level of BA (source power density or ERD/ERS). The ANOVAs included the factors “condition” (seen trials and not seen trials), “hemisphere” (left and right), and “lobe of interest” (BAs showing the maximum frontal, parietal, and occipital rhythms).

The first scope of the study was to investigate the (poststimulus) ERD/ERS as a neural correlate of consciousness. To do so, the ERD/ERS for the seen versus not seen trials was compared with ANOVA for each band of interest. The frontal, parietal, and occipital regions of interest were represented by the BAs showing the voxel with maximum value of ERD/ERS within each region of interest (i.e., BA 19 for occipital regions, BA 7 for parietal regions, etc.). Namely, the voxel with the largest value of ERD/ERS for seen trials was selected to define the BA of interest, and then the magnitudes for both seen and not seen were taken from that selected BA to be entered into the ANOVA design. To remove the possible linear effects of prestimulus EEG source power on the poststimulus ERD/ERS, the prestimulus EEG source power for the mentioned BAs (i.e., where the maximum ERD/ERS was seen) was used as a covariate.

The second scope of the study was to investigate the prestimulus EEG source power as a variable predicting consciousness of upcoming cue stimulus. To do so, the EEG source power for the seen versus not seen trials was compared with ANOVA for each band of interest. The frontal, parietal, and occipital regions of interest were represented by the BAs showing the voxel with maximum value of prestimulus EEG source power within each region of interest. Namely, the voxel with the highest value of prestimulus source power for seen trials was selected to define the BA of interest, and then the magnitudes for both seen and not seen were taken from that selected BA to be entered into the ANOVA design. It should be remarked that these BAs were not necessarily the same BAs in which the maximum poststimulus ERD/ERS occurred.

## Results

### Behavioral Results

Behavioral results were reported in detail in a previous study (Babiloni and others 2006). According to the control hypothesis, mean reaction time was shorter ( $P < 0.026$ ) during the congruent seen trials (687 ms  $\pm$  15 SE) than during the

incongruent seen trials (719 ms  $\pm$  44 SE), as a possible effect of covert attention on cued location. Analogously, the reaction time was shorter ( $P < 0.034$ ) during the congruent not seen trials (732 ms  $\pm$  42 SE) than during the incongruent not seen trials (764 ms  $\pm$  45 SE), confirming the occurrence of unconscious processes during the not seen trials. Furthermore, the reaction time was faster in the seen than not seen trials ( $P < 0.0003$ ) as well as in the spatially congruent than incongruent trials ( $P < 0.0006$ ).

### Individual Alpha Frequency

Table 1 reports the IAF for each subject (i.e., in all 11 subjects the IAF was the same for both seen trials and not seen trials). As a result, the mean peak of the IAF was 10 Hz ( $\pm 0.2$  SE).

### Prestimulus Theta and Alpha Rhythms as Revealed by the LORETA Sources

For illustrative purposes, Figure 2 plots the grand average ( $N = 11$ ) of prestimulus power density spectra of the scalp EEG in the seen and not seen trials at representative midline electrodes (Fz, Cz, Pz, and Oz). Around extended theta-alpha frequency band (about 4–12 Hz), the values of power density were greater in the not seen than seen trials at the vertex. On the contrary, there were values of power density greater in the seen than not seen trials close to the occiput.

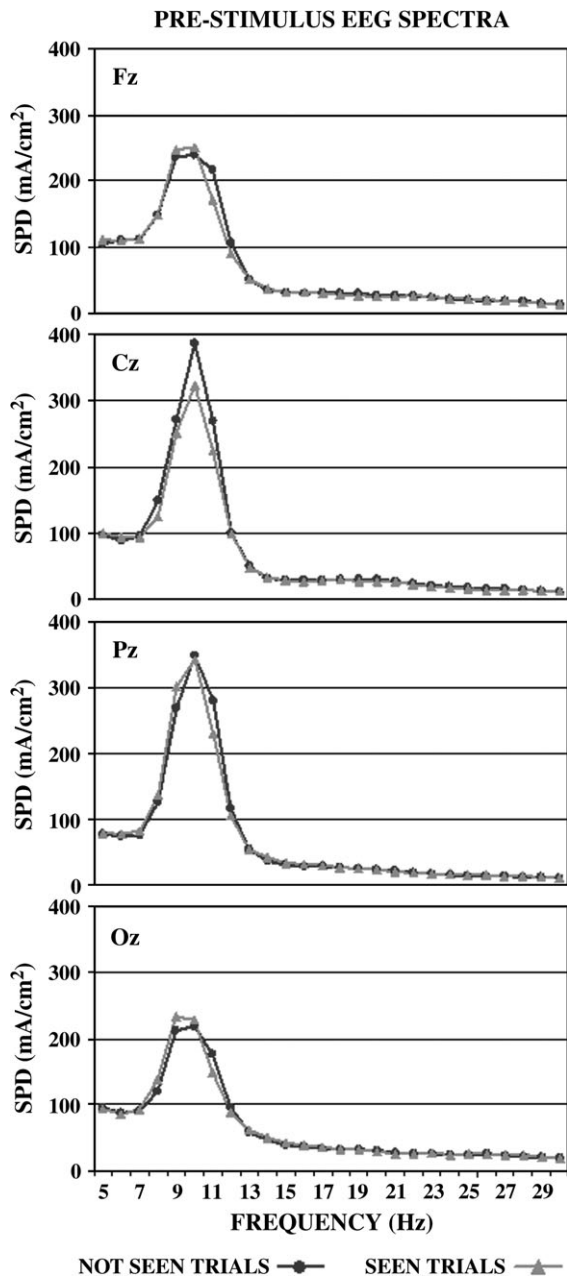
Figure 3 shows the grand average ( $N = 11$ ) of LORETA solutions modeling the distributed EEG sources of prestimulus theta and alpha power density in the seen and not seen trials. In general, maximum values of these EEG sources were seen in frontal BA 6m, parietal BA 7, and occipital BA 19 regions for all bands of interest. Figure 4 plots means across subjects ( $\pm$ SE) of the prestimulus LORETA sources in the seen versus not seen trials referred to the factors condition (seen trials and not seen trials), hemisphere (left and right), and lobe of interest (frontal BA 6m, parietal BA 7, and occipital BA 19). For the alpha 1 and alpha 2, sources appeared stronger in the seen than not seen trials, especially at parietooccipital cortical areas.

Prestimulus sources illustrated in Figure 4 were used as an input for the ANOVA of the theta, alpha 1, alpha 2, and alpha 3 in the seen versus not seen trials which—for each band—included the same factors as before. A main effect condition was seen for the ANOVAs relative to alpha 1 ( $F_{1,10} = 5.91$ ,  $P < 0.03$ ) and alpha 2 ( $F_{1,10} = 6.31$ ,  $P < 0.03$ ). These results indicated that, at

**Table 1**  
IAF values for all subjects

Subject number	IAF (Hz)
1	11
2	9
3	9
4	10
5	11
6	10
7	10
8	10
9	9
10	10
11	11
Mean	10
SE	$\pm 0.2$

Note: These values were equal for both seen trials and not seen trials. IAF was defined as the frequency showing the higher power density at the 6–12 Hz range of the power density spectrum.



**Figure 2.** Grand mean across subjects ( $N = 11$ ) of EEG power density spectra for the seen and not seen trials. The spectra refer to representative electrodes of the scalp midline (Fz, Cz, Pz, and Oz sites of 10–20 system). The seen trials were those in which subjects consciously perceived the visual cue stimuli, whereas the not seen trials were those in which subjects were unable to refer any visual perception.

the alpha 1 and alpha 2 bands, prestimulus EEG sources in frontal BA 6m, parietal BA 7, and occipital BA 19 were stronger in the seen than not seen trials.

### Cortical Theta and Alpha ERD/ERS

Figure 5 shows the grand average ( $N = 11$ ) of LORETA solutions modeling distributed EEG sources of the theta and alpha ERD/ERS in the seen and not seen trials. In general, maximum values of the ERD/ERS were observed in frontal, parietal, and occipital regions. Maximal theta ERS were seen in frontal BA 10, parietal BA 43, and occipital BA 18. The alpha 1 presented negligible

ERD values. For the alpha 2 and alpha 3, substantial ERD values were only seen in parietal BA 39 and occipital BA 19. Figure 6 plots the means ( $\pm$ SE) of the ERD/ERS computed from source solutions at theta, alpha 1, alpha 2, and alpha 3. The mean values refer to the factors condition (seen trials and not seen trials), hemisphere (left and right), and lobe of interest (frontal, parietal, and/or occipital). For the alpha 2 and alpha 3, stronger sources were in the seen than not seen trials.

The mean ERD/ERS values for the cortical regions indicated in Figure 6 were used as an input for the ANOVA. Namely, they included theta ERS at the BAs 10, 43, and 18; alpha 2 ERD at the BAs 39 and 19; and alpha 3 ERD at the BAs 39 and 19. The alpha 1 subband was not evaluated because no ERD was detected at that subband. The ANOVA design for each band (considered separately) included the factors condition, hemisphere, and lobe of interest as previously. Prestimulus band power theta, alpha 2, and alpha 3 served as covariates in the corresponding 3 ANOVA designs. The unique statistically significant result was observed for the alpha 3 ERD, namely, a main effect condition ( $F_{1,10} = 5.45$ ,  $P < 0.04$ ). This result indicated that the alpha 3 ERD was stronger in the seen than not seen trials in both parietal and occipital areas.

### Control Analyses

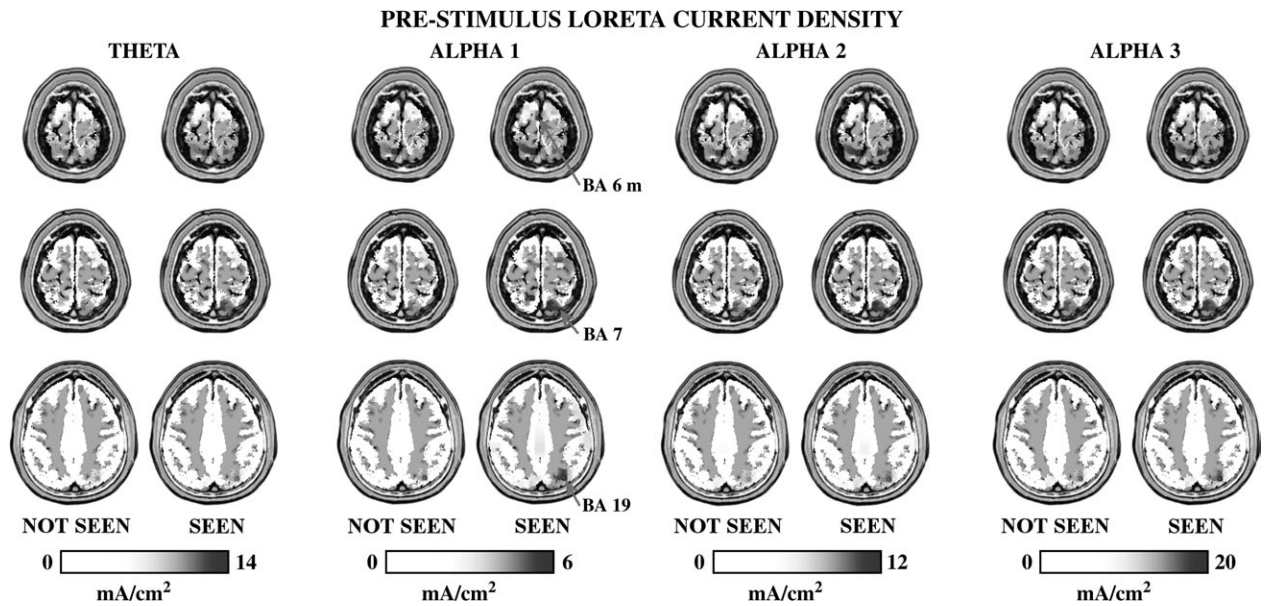
To control the effects of the cue stimulus lateralization, the ERD/ERS for left and right cue stimuli were analyzed separately. For each band of interest (theta, alpha 1, alpha 2, and alpha 3), the ANOVA of the corresponding LORETA solutions included the factors condition (seen trials and not seen trials), hemisphere (left and right), lobe of interest (BAs showing the maximum frontal, parietal, and occipital rhythms), and stimulus side (left and right). These control analysis showed no statistically significant ( $P > 0.05$ ) interaction between the factors condition and stimulus side.

Finally, we performed a control LORETA analysis using a 500-ms window analysis to have 2 Hz of frequency resolution. The pre- and poststimulus EEG periods were immediately before and after the cue stimulus. This frequency resolution still allowed to roughly disentangle the 3 alpha subbands. We obtained very similar results when compared with those showed by the LORETA analysis using 1-s time window, namely, a statistical main effect of the factor condition for alpha 3 ( $F_{1,10} = 5.20$ ,  $P < 0.0457$ ). The new results indicated that alpha 3 ERD was higher in the seen than not seen EEG single trials.

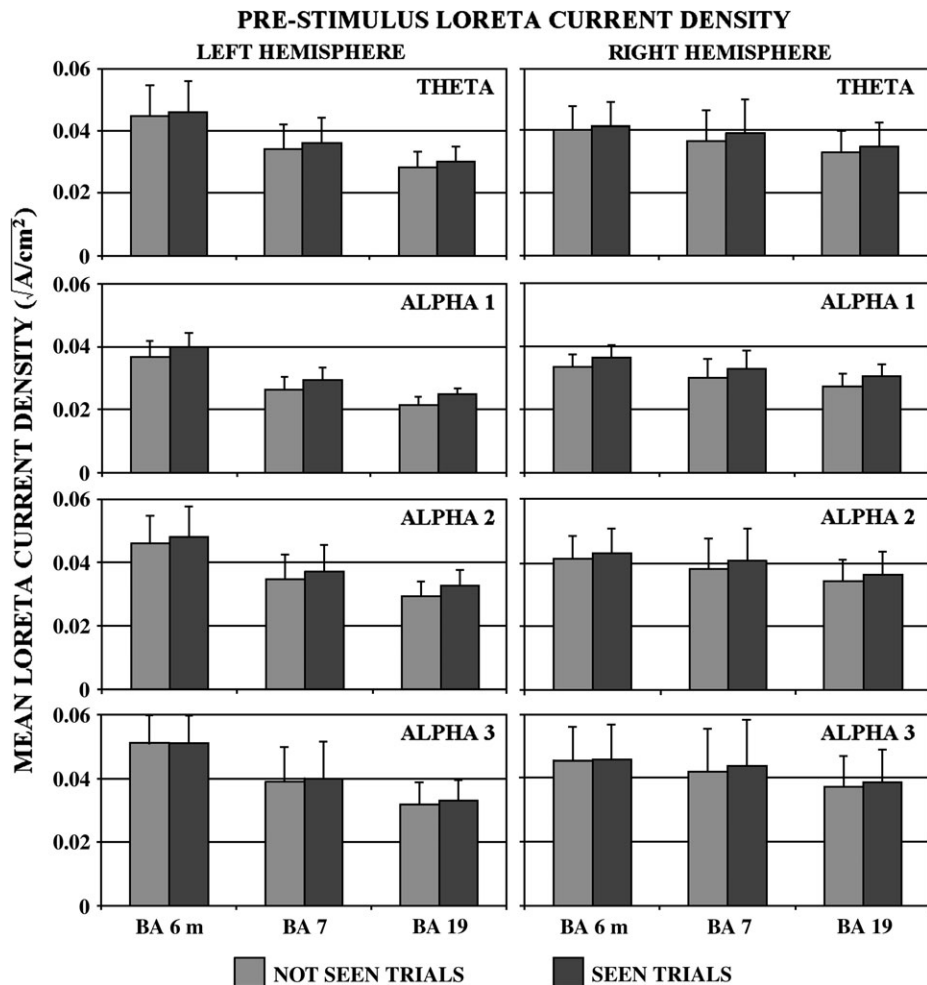
### Discussion

#### Behavioral Results

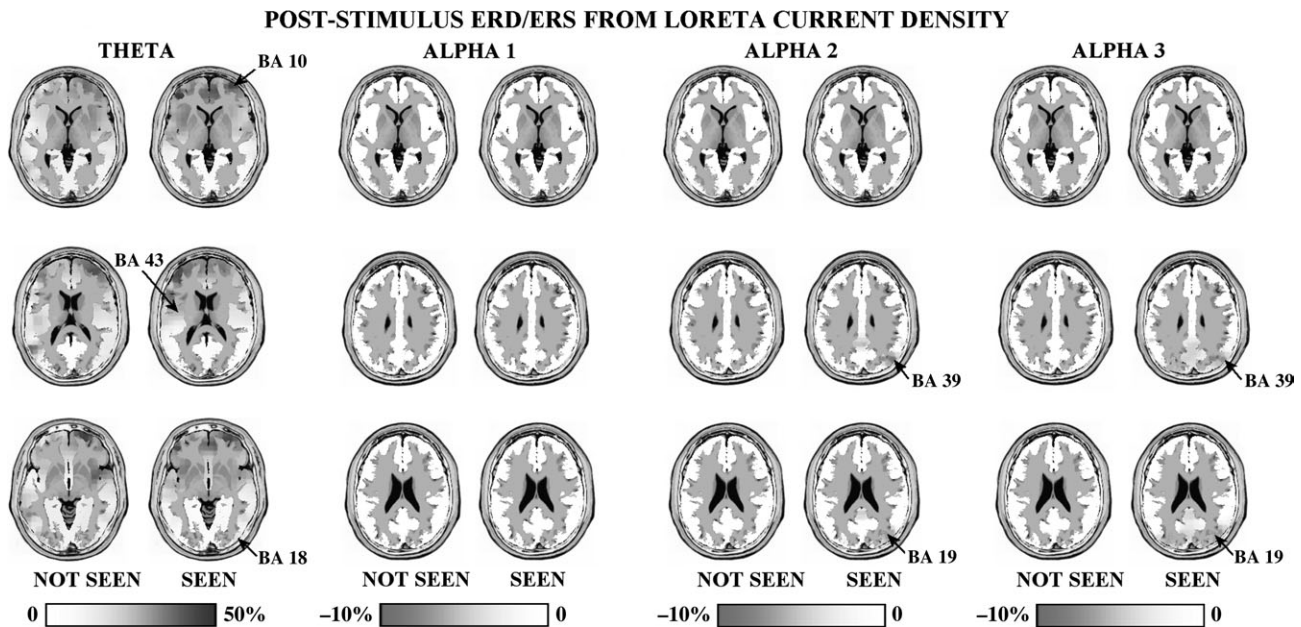
According to the control hypothesis and previous evidence (McCormick 1997; Ivanoff and Klein 2003; Babiloni and others 2006), mean reaction time was shorter during the congruent seen trials than during the incongruent seen trials, as a possible effect of covert attention on cued location. Analogously, the reaction time was shorter during the congruent not seen trials than during the incongruent not seen trials, confirming the occurrence of unconscious processes during not seen trials in line with previous evidence (McCormick 1997; Ivanoff and Klein 2003). In contrast, the present results are apparently at odds with previous findings on “inhibition of return” mechanism (Posner and Cohen 1984; Posner and others 1985). According to inhibition of return, the reaction time to



**Figure 3.** Grand mean across subjects ( $N = 11$ ) of the LORETA solutions modeling the distributed sources of prestimulus EEG spectral power density in the seen and not seen trials. These solutions refer to theta (about 4–6 Hz), alpha 1 (about 6–8 Hz), alpha 2 (about 8–10 Hz), and alpha 3 (about 10–12 Hz) bands and were maximum in power at the regions of interest, namely, frontal BA 6m, parietal BA 7, and occipital BA 19.



**Figure 4.** Grand mean across subjects ( $\pm$ SE,  $N = 11$ ) of the LORETA solutions of prestimulus EEG spectral power density for each condition (seen trials and not seen trials), hemisphere (left and right), lobe of interest (frontal BA 6m, parietal BA 7, and occipital BA 19), and band (theta, alpha 1, alpha 2, and alpha 3).



**Figure 5.** Grand mean across subjects ( $N = 11$ ) of the LORETA solutions modeling the distributed sources of theta and alpha ERD/ERS for the seen and not seen trials. These solutions were maximum in frontal BA 10, parietal BA 43, and occipital BA 18 for the theta ERS and in parietal BA 39 and occipital BA 19 for the alpha 2 and alpha 3. The alpha 1 ERD values were negligible.

(extrafoveal) go stimuli should be lengthened by noninformative cue stimuli at the same location or hemifield (Tassinari and Berlucchi 1993; Berlucchi and others 2000). This paradox is just apparent. In contrast to the paradigms inducing inhibition of return, the present paradigm forced subjects to focus attention and memory resources on the cue stimulus for the final self-report (i.e., to say seen or not seen). It is reasonable that covert attention on cue position speeded the reaction time at cue location. This explanation agrees with the previous results showing that “subliminal” visuospatial cue stimuli cancel inhibition of return effects when associated with self-report (McCormick 1997; Ivanoff and Klein 2003). In that sense, self-report would produce effects similar to those reported when the cue is spatially informative on the subsequent go stimuli (Posner and others 1980; Posner 1987, 1994; Merikle and Daneman 1999; Berlucchi and others 2000).

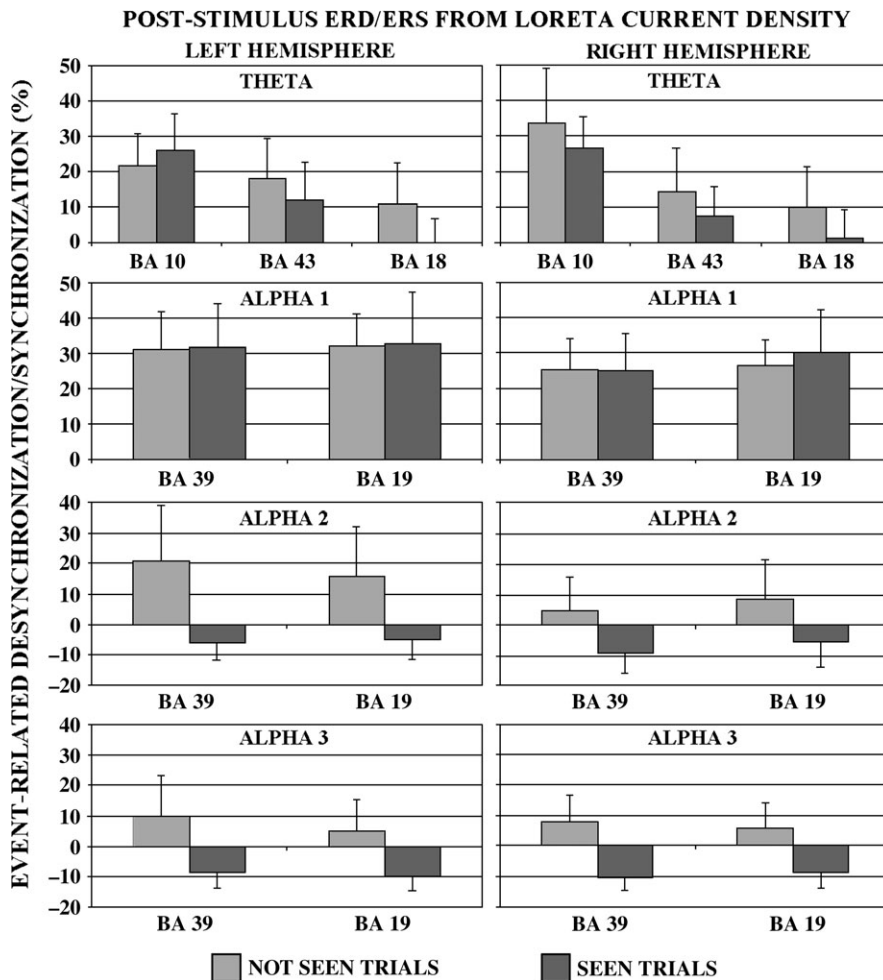
#### ***Prestimulus Cortical Alpha Rhythms Affect Visual Consciousness***

The main result of the present study is that visual consciousness highly covaries with prestimulus cortical alpha rhythms. Indeed, the prestimulus alpha rhythms (about 6–10 Hz) in frontal BA 6m, parietal BA 7, and occipital BA 19 were stronger in power in the seen than not seen trials. These results extend to visual consciousness previous EEG evidence that a good cognitive performance is predicted by the high power of the prestimulus alpha rhythms (Neubauer and Freudenthaler 1995; Klimesch 1997, 1999; Vogt and others 1998; Klimesch and others 1998, 2003).

As for the functional meaning of “low-band” (about 6–10 Hz) alpha rhythms (Steriade and Llinas 1988; Brunia 1999; Pfurtscheller and Lopez da Silva 1999), it is worth reminding that they are generated by thalamocortical and (especially) corticocortical loops and are associated with the subject’s global attention (Jasper and Penfield 1949; Buser and others 1987; Steriade and Llinas 1988; Rossini and others 1991;

Klimesch 1996, 1999; Klimesch and others 1997, 1998). According to previous evidence, we speculate that the prestimulus alpha rhythms present high power in the case of low subcortical cholinergic and serotonergic inputs arousing the cortex (Dringenberg 2000; Ricceri and others 2004). A psychophysiological concomitant effect would be a low cortical excitability and a mental relaxation as characterized by scarcely focused thinking and low attention to external stimuli. A large prestimulus alpha synchronization would be representative of a widely activated corticocortical network, which would allow a quick shift to local information processing and visual consciousness after the stimulus presentation (Nunez and others 2001). In contrast, the prestimulus alpha rhythms would show low power in the case of concurrent arousing inputs to the cortex. The resulting cortical excitability and mental activity might interfere with information processing and visual consciousness after the stimulation.

The above speculation relies on several lines of previous evidence. First, the power of resting alpha rhythms correlates with global cognitive performance in subjects with mild cognitive impairment and Alzheimer’s disease (Dierks and others 1993, 2000; Holschneider and others 1998; Rodriguez, Copello, and others 1999; Rodriguez, Nobili, and others 1999; Huang and others 2000; Mesulam 2004; Moretti and others 2004; Babiloni, Cassetta, and others 2005). In these subjects, the posterior alpha rhythms are characterized by low power (Muzur and others 2002) and the cortical excitability is enhanced (Ferri and others 1996; Babiloni and others 2000; Alagona and others 2001; Pennisi and others 2002; Ferreri and others 2003; Babiloni, Binetti, and others 2005). Second, the resting alpha rhythms are lowered by experimental or clinical impairment of the cholinergic basal forebrain such as Alzheimer’s disease (Dierks and others 1993, 2000; Sarter and Bruno 1997, 1998; Holschneider and others 1998; Rodriguez, Copello, and others 1999; Rodriguez, Nobili, and others 1999; Huang and others 2000; Kobayashi and Isa 2002; Babiloni and others 2004;



**Figure 6.** Grand mean across subjects ( $\pm$ SE,  $N = 11$ ) of the LORETA solutions modeling the sources of the theta, alpha 2, and alpha 3 ERD/ERS in the seen versus not seen trials. The mean data refer to the factors condition (seen trials and not seen trials), hemisphere (left and right), and lobe of interest (frontal BA 10, parietal BA 43, and occipital BA 18 for the theta ERD; parietal BA 39 and occipital BA 19 for the alpha 2 and alpha 3).

Mesulam 2004; Moretti and others 2004), whereas the brainstem cholinergic innervations of the thalamus are relatively spared in Alzheimer's disease patients (Mash and others 1985; Geula and Mesulam 1989, 1996, 1999; Mesulam 2004; Mesulam and others 2004). Third, the decrement of the alpha rhythms in both mild cognitive impairment and Alzheimer's disease subjects is associated with deficits of visual attention, possibly related to visual consciousness (Wang and Zhou 2002; Arnaiz and Almkvist 2003) and memory functions (Wolf and others 2003). Fourth, serotonergic inputs of the brainstem raphe nuclei induce cortical arousal independently of the cholinergic inputs of the basal forebrain, so that both serotonergic and cholinergic inputs to the cortex are crucial to sustain cognitive performances (Dringenberg 2000).

#### ***Poststimulus Cortical Alpha Rhythms Affect Visual Conscious Processing***

Another intriguing result of the present study is that the efficacy of visual consciousness is also linked to poststimulus cortical alpha rhythm characteristics. Indeed, the poststimulus alpha rhythms (about 10–12 Hz) in parietal BA 39 and occipital BA 19 decreased in power more in the seen than not seen trials regardless—at least in part—of their prestimulus level. These results extend to visual consciousness previous EEG evidence

showing that the desynchronization of the “high-band” (about 10–12 Hz) alpha rhythms would reflect the oscillation of specific neural systems for the elaboration of sensorimotor or semantic information and for the memory recognition/recall (Neubauer and Freudenthaler 1995; Klimesch 1997, 1999; Klimesch and others 1998, 2003; Vogt and others 1998).

The relationship between poststimulus alpha rhythms and visual consciousness might rely on the thalamocortical and corticocortical networks, which display different spontaneous rhythms dependent on the state of vigilance. Corticofugal volleys are effective in synchronizing slow (<15 Hz) and fast (20–50 Hz) rhythms in thalamocortical networks (Steriade 1997). In the case of transient visual stimulation, resting parietooccipital alpha rhythms would be blocked by the inhibition of the oscillations generated by cortical and subcortical neurons. These rhythms would be replaced by fast (beta and gamma) cortical oscillations, mainly induced by the depolarizing effects of subcortical cholinergic and serotonergic inputs (Dringenberg 2000; Steriade 2003). The fast oscillations of the membrane potentials at cellular level might sustain visual consciousness (Engel and others 1999, 2001; Engel and Singer 2001; Crick and Koch 2003).

The present results on alpha rhythms complement previous evidence, showing that amplitude of the parietooccipital



activation is important for visual consciousness not only in patients with “visual extinction” (Lhermitte and others 1985; Vallar and others 1991; Spinelli and others 1994; Driver 1996; Verleger and others 1996; Driver and others 1997, 2001; Heilman and others 1997; Robertson and others 1997; Driver and Mattingley 1998; Marzi and others 2000; Vuilleumier and others 2001) but also in healthy subjects (Shevrin 1976; Kostandov and Arzumanov 1977; Brandeis and Lehmann 1986; Shefrin and others 1988; Brazdil and others 1998, 2001, 2002). The present results on the (non-phase locked) alpha rhythms complement those of the analysis of the VEPs from the same data set (Babiloni and others 2006). That analysis had emphasized the phase-locked concomitant of the EEG response related to the visual consciousness, namely, a late-positive potential over the parieto-occipital cortex (+300 ms poststimulus; P3).

### ***Cortical Theta Rhythms Did Not Affect Visual Consciousness in the Present Conditions***

Our findings showed that visual consciousness did not relate to pre- or poststimulus cortical theta rhythms, at least in the present experimental conditions. This was true in the face of previous evidence showing the predicting value of the theta rhythms for episodic memory performance and the sensitivity of the theta rhythms to mental workload and conscious remembering (Klimesch and others 1996, 2001). Indeed, it is well-known that lesions of human hippocampus and related temporal regions impair the conscious memory retrieval of new events. Keeping in mind these data, it can be speculated that the theta rhythms are crucial for the conscious experience related to the encoding and retrieval of information into the semantic or episodic memory but not for the visual consciousness of visual spatial stimuli to be accounted for few seconds.

### **Conclusions**

Is visuospatial consciousness related to prestimulus other than poststimulus EEG rhythms at theta and alpha frequencies? Results showed that the prestimulus low-band alpha rhythms in frontal, parietal, and occipital areas were stronger in power in the seen than not seen trials. After the visual stimulation, the power of the high-band alpha rhythms in parietal and occipital areas decreased more in the seen than not seen trials. The present results strongly support the view that there is an association between these 2 aspects. Following this idea, visuospatial consciousness is facilitated by the power of both pre- and poststimulus alpha rhythms. The alpha rhythms as a neural correlate of human consciousness might be strictly associated with variations of EEG rhythms at higher frequencies (i.e., beta and/or gamma). Following simple visual stimulations, the modulation of these rhythms is quite low with respect to background noise. Therefore, this issue should be addressed by techniques of stereo intracerebral EEG in epilepsy patients in the course of the presurgical evaluation.

Future researches should use new EEG source analysis procedures combined with time-frequency analysis, to disclose short-latency modulation of cortical EEG rhythms in correlation with consciousness processes.

### **Notes**

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