Visuo-spatial Consciousness and Parieto-occipital Areas: A High-resolution EEG Study

Conscious and unconscious visuo-spatial processes are mainly related to parieto-occipital cortical activation. In this study, the working hypothesis was that a specific pattern of parieto-occipital activation is induced by conscious, as opposed to unconscious, visuo-spatial processes. Electroencephalographic data (128 channels) were recorded in 12 normal adults during a visuo-spatial task. A cue stimulus appeared on the right or the left (equal probability) monitor side for a ‘threshold time’ inducing ~50% of correct recognitions. It was followed (after 2 s) by visual go stimuli at spatially congruent or incongruent positions with reference to the cue location. The left (right) mouse button was clicked if the go stimulus appeared on the left (right) monitor side. Subjects were required to say ‘seen’ if they had detected the cue stimulus or ‘not seen’ if they missed it (self-report). ‘Seen’ and ‘not seen’ electroencephalographic trials were averaged separately to form visual evoked potentials. Sources of these potentials were estimated by LORETA software. Reaction time to go stimuli was shorter during spatially congruent than incongruent ‘seen’ trials, possibly due to covert attention on cue for self-report. It was also shorter during spatially congruent than incongruent ‘not seen’ trials, as an objective sign of unconscious processes. Cue stimulus evoked parieto-occipital cortical potentials which has the same peak latencies in the ‘seen’ and ‘not seen’ cases. Sources of these potentials were located in occipital area 19 and parietal area 7. Source strength was significantly stronger in ‘seen’ than ‘not seen’ cases at ~+300 ms post-stimulus. These results may unveil features of visuo-spatial consciousness accompanying visuo-spatial consciousness.

Keywords: awareness, human cortex, LORETA, subliminal stimuli, visual evoked potentials (VEPs)

Introduction
A variety of visual stimuli is perceived and processed without any reportable consciousness (Merikle, 1982; Purcell et al., 1983; Holender, 1986; Reingold and Merikle, 1988; Kihlstrom et al., 1992). Neural correlates of conscious and unconscious visual processes have been fruitfully studied in patients with unilateral brain injuries, particularly at right posterior parietal cortex (Vallar et al., 1988; Driver et al., 1997; Driver and Vuilleumier, 2001). These patients can detect unilateral visual stimuli on either hemifields, thanks to intact visual fields and posterior occipital cortex. Instead, they typically miss contralateral stimuli at the left visual hemifield during bilateral stimulations. Such a ‘visual extinction’ is probably due to a pathological bias in spatial attention (Posner et al., 1984; Vallar et al., 1988; Desimone and Duncan, 1995; Driver et al., 1997; Cocchini et al., 1999).

In the above-mentioned patients, extinguished visual stimuli may be unconsciously processed. In fact, the reaction time to ‘go’ (target) stimuli on the ipsilateral visual hemifield is affected by concurrent undetected stimuli on the contralateral visual hemifield (Marzi et al., 1996; Vuilleumier and Rafal, 2000). Furthermore, ‘visual extinction’ is affected by the semantic relationship between concurrent ipsilateral (‘seen’) and contralateral (‘extinguished’ or ‘not seen’) stimuli (Baylis et al., 1993; Mattingley et al., 1997; Vuilleumier and Rafal, 2000).

Extinguished visual stimuli can be unconsciously processed by parieto-occipital areas, typically spared in the above-mentioned patients (Driver, 1996; Driver et al., 1997; Heilman et al., 1997; Driver and Mattingley, 1998; Robertson et al., 1997). Functional magnetic resonance imaging (fMRI) has been employed to test this hypothesis in a patient with left ‘visual extinction’ due to right parietal lesion (Rees et al., 2000; Vuilleumier et al., 2001). During bilateral stimulation, the patient consciously perceived only the stimuli delivered to the right hemifield. In the bilateral stimulation trials, right occipital striate and extra-striate visual areas including parietal cortex were activated despite the extinction of left visual stimuli. Furthermore, other converging evidence would suggest that these areas may represent the neural substrate for the unconscious residual processing of extinguished visual stimuli (Audet et al., 1991; Berti and Rizzolatti, 1992; Baylis et al., 1993; McGlinchey-Berroth et al., 1993; Cohen et al., 1995). However, an open issue remains: why are parieto-occipital responses to extinguished stimuli not able to produce visual consciousness?

In order to address this issue, parieto-occipital responses were evaluated in patients showing ‘visual extinction’ of left visual stimuli only in some bilateral stimulation trials, namely the ‘not seen’ trials (Marzi et al., 2000; Driver et al., 2001; Vuilleumier et al., 2001). In the remaining cases (‘seen’ trials), they consciously perceived both left and right visual stimuli. This allowed the comparison of fMRI activation in ‘seen’ versus ‘not seen’ trials. As a result, right occipital striate, right cuneus, bilateral fusiform gyrus and left parietal areas were more active in ‘seen’ than ‘not seen’ trials (Driver and Vuilleumier et al., 2001). Furthermore, coupling of occipital and frontal areas was stronger in magnitude in ‘seen’ than ‘not seen’ trials (Buchel and Friston, 1997). These results emphasized the strength of parieto-occipital activation for conscious visual processes.

To complement the high spatial resolution of fMRI, visual event-related potentials (ERPs) have been recorded to evaluate fine timing of cortical responses in ‘extinction’ patients (Lhermitte et al., 1985; Vallar et al., 1991; Spinelli et al., 1994; Verleger et al., 1996; Marzi et al., 2000; Driver and Vuilleumier et al., 2001). Of particular interest was a ‘visual extinction’ patient with a lesion of the right parietal cortex.
The subjects had to say 'seen' any time they perceived the position of 'Xs' (was preceded and followed by a masking visual stimulus formed by two circle (diameter threshold time (ms) of the cue stimulus. The cue stimulus was a white of the background central white cross (diameter 0.5 cm). The cue stimulus varied randomly trial-by-trial within the following values: 20, 40, 60, 80, 100, 120, 140, 160 ms 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 ~50% of correct stimulus detections within a series of 10 trials, in the majority of the seven 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 subject’s self-report. There was always a confirmation before the EEG recording of the threshold time of cue presentation as indicated by the above preliminary procedure. Subject-by-subject, the mean (± SE) threshold time of the cue stimulus was 101 ± 8.8 ms. It is worth noting that the global correctness of the procedure for the determination of that threshold time was supported by the post hoc verification and that the recognition of the cue stimuli during the EEG recordings was 48% (±2 SE) on across-subjects average.

Overall, these results emphasized spatio-temporal features of cerebral responses related to conscious and unconscious visual processes. However, uncontrolled effects of brain lesions motivated investigations in normal subjects (Shevrin and Fritzler, 1968; Kostandov and Arzumanov, 1977; Naatanen and Gaillard, 1983; Brandeis and Lehmann, 1986; Shevrin, 1992; Wong et al., 1994). In the most employed paradigm, subjects had to respond (i.e. movement or counting) after rare, but not frequent stimuli of a sequence, namely the 'P300 paradigm'. As is well known, rare stimuli evoke a well-shaped late positive ERP (P300), which is supposed to reflect cognitive closure of the recognition processing and memory updating (Smith et al., 1970; Hillyard et al., 1971; Hillyard and Picton, 1987; Iragui et al., 1993). It has been shown that parietal P300 was higher in amplitude after 'seen' (conscious perception) than 'not seen' (subliminal perception) rare stimuli (Shevrin, 1976; Kostandov and Arzumanov, 1977; Brandeis and Lehmann, 1986; Shefrin et al., 1988; Brazdil et al., 1998, 2001, 2002). However, it might be argued that sensorimotor interaction impinged only upon P300 of 'seen' trials (i.e. rare supraliminal stimuli), which required movement or counting. To overcome this issue, the present high-resolution ERP study did not use a P300 paradigm. Instead, an experimental paradigm was employed requiring the same post-stimulus motor demand in both 'seen' (conscious perception) and 'not seen' (unconscious perception) trials. The working hypothesis was a specific spatio-temporal pattern of parieto-occipital activation in 'seen' when compared to 'not seen' trials.

Materials and Methods

Subjects

Experiments were performed on 12 healthy adult volunteers (age 29.3 ± 0.8 years, mean ± SE). They were right-handed, as revealed by the Edinburgh Inventory (81.2 ± 4.6%), and had no previous psychiatric or neurological history. Their sight was normal or corrected-to-normal. All experiments were undertaken with the understanding and written consent of each participant, according to Code of Ethics of the World Medical Association (1997) and the standards established by the Author’s Institutional Review Board. The study was approved by local ethical committee.

Experimental Task

The 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 the armchairs, with the right index finger resting between two buttons of a mouse, which was connected to a computer monitor. The monitor of the computer was placed in front of them at a distance of ~100 cm.

For each subject, a preliminary procedure ascertained the individual threshold time (ms) of the cue stimulus. The cue stimulus was a white circle (diameter ~0.5° of visual angle) appearing at 6° to the right or left of the background central white cross (diameter 0.5°). The cue stimulus was preceded and followed by a masking visual stimulus formed by two 'Xs' (~0.8°), located at 6° to the right and left of 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 varied randomly trial-by-trial within the following values: 20, 40, 60, 80, 100, 120, 140, 160 ms for 80 trials (10 for each duration value). The threshold time to be used during the EEG recordings was defined as the duration of the cue stimulus determining ~50% of correct stimulus detections within a series of 10 trials, in the majority of the seven 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 subject’s self-report. There was always a confirmation before the EEG recording of the threshold time of cue presentation as indicated by the above preliminary procedure. Subject-by-subject, the mean (± SE) threshold time of the cue stimulus was 101 ± 8.8 ms. It is worth noting that the global correctness of the procedure for the determination of that threshold time was supported by the post hoc verification and that the recognition of the cue stimuli during the EEG recordings was 48% (±2 SE) on across-subjects average.

Figure 1. Sequence of events during a ‘standard’ trial: (i) the masking stimulus ‘Xs’ lasting 5.5 s; (ii) the cue stimulus ‘small circle’ appearing on the right or left (50%) monitor side for the threshold time; (iii) the masking stimulus ‘Xs’ lasting ~2 s (i.e. 2 s minus the threshold time); (iv) go stimulus lasting ~0.5 s. The go stimulus was a green circle with a diameter of ~0.5°, which appeared on the right or the left monitor side. Subjects had to click the left mouse button if the go stimulus appeared on the left monitor side, whereas they had to click the right mouse button if the go stimulus appeared on the right monitor side (self-report). The computer receiving mouse inputs registered the corresponding reaction time and the side of the mouse button clicked. After hand motor response, subjects had to say ‘seen’ if they had detected the cue stimulus (‘seen’ trial) or ‘not seen’ if they had missed the cue stimulus (‘not seen’ trial).
minus the threshold time); (iv) a go (target) stimulus lasting ~0.5 s. The go stimulus was a small green circle with a diameter of ~0.5°, which appeared to the right or left (50% of probability) of the central white cross. The subjects had to press the left mouse button if the go stimulus appeared on the left monitor side, whereas they had to press the right mouse button if the go stimulus appeared on the right monitor side. The computer receiving the mouse inputs registered the corresponding reaction time and the side of the button pressed. Immediately after the hand motor response, the subjects had to say 'seen' if they had detected the cue stimulus ('seen trial') or 'not seen' if they had missed the cue stimulus ('not seen trial'). It is noteworthy that subjects denied the use of mental verbal codes for the cue or go stimuli after the experiment. Verbal self-report was registered by a microphone connected to the computer, and was also noted manually by an experimenter. The experimenter controlled that subjects watched the computer monitor during the task. Note that the same presentation time and physical features (shape, position, luminance, etc.) characterized the cue stimuli consciously perceived ('seen trials') and those not consciously perceived ('not seen trials'). Therefore, these features cannot explain the reason why some cue stimuli were 'seen' and others were consciously 'not seen'.

In some cases, the 'standard' trials were replaced by 'baseline' trials, which were characterized by the following stimulus sequence: (i) the masking stimulus 'Xs' lasting 5.5 s; (ii) a black screen lasting the threshold time, instead of the cue stimulus. The rest of the sequence was the same as that of the 'standard' trials. The 'baseline' trials were delivered to evaluate the subjective self-reports' reliability on the detection of cue stimuli. Such reliability was indexed by the percentage of false recognitions of the cue stimuli during the 'baseline' trials, i.e. when the subjects said 'seen' even if the baseline trials had no cue stimulus.

Electroencephalographic Recordings

During the experimental task, electroencephalographic (EEG) data were recorded (bandpass 0.1–100 Hz; sampling rate 256 Hz) from 128 electrodes placed according to an augmented 10-20 system. Linked ear lobes served as an electrical reference and electrode impedance was kept <5 kΩ. 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%) pseudo-randomly interleaved.

In addition, a control condition was added in seven subjects. In this condition, there were only 'standard' trials (i.e. no 'baseline' trial), so that 'not seen' and 'seen' trials occurred with a percentage of ~50% each. As a consequence, ERPs due to the trials in which the subjects recognized the cue stimuli ('seen' trials) were as frequent as the trials in which the subjects did not recognize the cue stimuli ('not seen' trials). This allowed pairing the variable 'frequency' of the 'seen' compared to the 'not seen' trials, theoretically able to enhance positive ERPs around +300 ms post-stimulus — the so called 'P300 effect'. In total, the control condition consisted of 160 'standard' trials given without the occurrence of 'baseline' trials.

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: (i) 'congruent seen' trials, in which the cue stimulus was detected and the go stimulus appeared on the cued location; (ii) 'incongruent seen' trials, in which the cue stimulus was detected and the go stimulus appeared on the uncued location; (iii) 'congruent not seen' trials, in which the cue stimulus was not detected and the go stimulus appeared on the cued location; and (iv) 'incongruent not seen' trials, in which the cue stimulus was not detected and the go stimulus appeared on the uncued location. There were equal numbers of 'congruent' and the 'incongruent' trials (50%). The 'baseline' trials (i.e. those having no cue stimulus) were grouped into a unique, separate class.

The reaction time for each trial class was defined as the period between the onset of the go stimulus and the mouse button click. The trials showing a reaction time longer than 1.2 s were considered as affected by 'partial distraction', and thus were not considered any further.

Statistical Analysis of the Behavioral Data

A run test was performed to evaluate if both the 'seen' and 'not seen' trials were randomly intermingled, according to the hypothesis that 'not seen' trials were not purely determined by fatigue or boredom at the end of the session. This test is based on the number of 'runs' defined as the changes from 'seen' to 'not seen' in the trial sequence. The null hypothesis (H₀) was the randomness in the sequence of 'seen' and 'not seen' trials, which reflected the fluctuation of attention/awareness towards the cue stimuli. If Nₛ is the number of the subliminal trials, Nₜ the number of the supraliminal ones, and U the number of 'runs' in the whole sequence, then the distribution of U for large samples approaches normality with a mean of

\[ \mu_U = \frac{2N_SN_T}{N} + 1 \]

and a standard deviation of

\[ \sigma_U = \sqrt{\frac{2N_SN_T(N_S - N_T)}{N^2(N - 1)}} \]

where N = Nₛ + Nₜ. The probability values can be computed by

\[ Z = \frac{|U - \mu_U| - 0.5}{\sigma_U} \]

The 0.5 in the numerator of Z is a correction for continuity. By Z, we can obtain the probability value for the H₀ hypothesis (P > 0.05).

In order to corroborate the run test's results, we used an ANOVA. The working hypothesis was that the percentage of the 'seen' trials was not higher at the beginning than at the end of the experimental session. The one-way ANOVA design included the percentage of the 'seen' trials (dependent variable) during three periods of the experimental session, i.e. 'beginning', 'medium' and 'final'. Each period lasted a third of that session. Duncan's test was used for post hoc comparisons (P < 0.05).

ANOVA for repeated measures served to evaluate the following hypothesis. In line with well-known previous evidence (McCormick, 1997; Ivanoff and Klein, 2003; C. Babloni, F. Vecchio, M. Mirillo, G.L. Romani and P.M. Rossini, submitted), 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, due to the 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 visuo-spatial processes. The confirmation of these hypotheses was a crucial prerequisite for the subsequent comparison of the ERPs related to 'seen' trials (related to conscious perception) versus 'not seen' trials (supposed to be related to unconscious perception). The ANOVA design included the factor Condition ('baseline', 'congruent seen', 'incongruent seen', 'congruent not seen', 'incongruent not seen'). Mauchley's test, to evaluate the sphericity assumption and correct for the degrees of freedom, was made by the Greenhouse-Geisser procedure. Duncan's 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 classified only in the three following classes: 'baseline', 'seen' and 'not seen'. Indeed, the conscious and unconscious processes accompanying the cue stimulation preceded the go stimulus, so that they could not be affected by
the spatial congruence between cue and go stimuli. This made the classification meaningless for the EEG data analysis, but useful for the behavioral one (i.e. 'congruent seen', 'incongruent seen', etc.).

Individual artifact-free EEG data were then interpolated by a spline function (Babiloni et al., 1995), in order to obtain potentials at 105 electrode sites of an augmented 10-20 system. These electrodes were disposed over a three-dimensional template head model digitized at the Brain Imaging Center of the Montreal Neurological Institute (http://www.bic.mni.mcgill.ca/). The head model was co-registered to Talairach atlas (Talairach and Tournoux, 1988). This made the electrode position across subjects consistent for the subsequent data analyses. The potentials at these 105 electrodes were then averaged within the proper trial class (‘baseline’, ‘seen’ and ‘not seen’) to form the ERPs. It is noteworthy that the same number of ‘baseline’, ‘seen’ and ‘not seen’ trials were selected in each subject, so that ERPs for the three classes could be correctly compared in amplitude. The mean number of trials per group was 83 ± 5 (±SE). It is worth noting that the presence of ERPs in the ‘baseline’ trials should not be a surprise, since a blank screen was delivered for a threshold time in these trials, in spite of the cue stimulus. These ERPs were indeed evoked by the visual scene’s changing from the ‘baseline’ to the ‘not seen’ and ‘seen’ ERPs. The ANOVA design included the factors Condition (‘baseline’, ‘congruent seen’, ‘incongruent seen’, ‘congruent not seen’, ‘incongruent not seen’). Planned post hoc comparisons provided the following results. According to the control hypothesis and previous evidence (McCormick, 1997; Ivanoff and Klein, 2003; C. Babiloni et al., submitted), the mean reaction time was shorter (P < 0.026) during the ‘congruent seen’ trials (687 ± 15 ms) than during the ‘incongruent seen’ ones (719 ± 44 ms) — this is possibly an effect of covert attention on cued location. Similarly, the reaction time was shorter (P < 0.034) during the ‘congruent not seen’ trials (732 ± 42 ms) than during the ‘incongruent not seen’ ones (764 ± 45 ms), confirming the occurrence of unconscious processes during ‘not seen’ trials.

**Spatio-temporal Evolution of the ERPs**

Figure 2 plots grand average (n = 12) waveforms of the scalp ‘baseline’, ‘not seen’ and ‘seen’ ERPs recorded at representative midline electrodes (AFz, Fz, FCz, Cz, CPz, Pz, POz, and Oz). It is noteworthy that the peak latencies were the same in ‘baseline’, ‘not seen’ and ‘seen’ ERPs. On average, these latencies were +178 ms (±10 SE), +314 ms (±16 SE), and +398 ms (±16 SE) for posterior ERPs such as N1, P2 and P3 respectively. In contrast, ‘baseline’, ‘not seen’ and ‘seen’ ERPs differed as P3 amplitude (Table 1). An ANOVA analysis showed that this difference was statistically significant [F(2,22) = 18.17; P < 0.00001]. Post hoc testing indicated that the P3 amplitude was significantly higher in the ‘seen’ than in both ‘not seen’ (P < 0.00008) and ‘baseline’ (P < 0.0001) ERPs. No amplitude difference was observed between ‘not seen’ and ‘baseline’ ERPs.

To control whether different P3 amplitude between ‘not seen’ and ‘seen’ ERPs merely depended on attention, we compared (Fig. 3) the grand average (n = 12) waveforms of ‘not seen’ and ‘seen’ ERPs formed by selected trials in which reaction times were similar (P > 0.05). Indeed, attention can be defined as subject’s readiness to respond. Again, P3 amplitude predominated in the ‘seen’ rather than the ‘not seen’ ERPs.

Another important control was whether different P3 amplitude between ‘not seen’ and ‘seen’ ERPs depended on lower
frequency of 'seen' trials than on trials in which cue stimulus was missed ('baseline' and 'not seen' trials). In other words, we wondered if P3 amplitude was modulated by a sort of 'P300' effect. For this reason, we compared the grand average (n = 7) ERP waveforms relative to control blocks in which no 'baseline' trial was delivered. In these blocks, there were only 'seen' and 'not seen' trials (50% each). P3 amplitude still prevailed in 'seen' rather than 'not seen' ERPs. Keeping in mind these results, P3 was employed as an input for LORETA source analysis.

**P3 Sources Computed by LORETA**

Figure 5 maps the grand average (n = 12) of LORETA solutions (i.e. $z$-current density at cortical voxels) modeling the distributed ERP sources of 'baseline', 'not seen' and 'seen' P3. Main P3 sources were estimated in occipital (Brodmann areas [BA] 19) and parietal (BA 7) regions. At BA 7, Talairach coordinates of maximal LORETA values were 39, -74, 50 for 'seen' P3; 32, -74, 50 for 'not seen' P3; and 25, -74, 50 for 'baseline' P3. At BA 19, they were 39, -74, 43 for 'seen' P3; 32, -74, 43 for 'not seen' P3; and 39, -74, 43 for 'seen' P3; 32, -74, 43 for 'not seen' P3; and

**Table 1**

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<th>Not-seen Amplitude</th>
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**Figure 2.** Grand average (n = 12) waveforms of event-related potentials (ERPs) recorded at representative midline electrodes (AFz, Fz, FCz, Cz, CPz, Pz, POz and Oz sites of 10-20 system). These potentials were obtained averaging separately 'baseline', 'not seen' and 'seen' trials. See Materials and Methods for the definition of these trial classes.

**Figure 3.** Grand average (n = 12) waveforms of ERPs formed by selected trials in which reaction time was comparable in 'not seen' and 'seen' trials ($P > 0.05$). These waveforms were illustrated to control whether differences in amplitude of ERPs between 'not seen' and 'seen' trials were dependent on attention defined as 'subject’ readiness to respond' (i.e. reaction time).
of interest \(F(1,11) = 17.95; P < 0.002\) indicated a stronger amplitude of the P3 LORETA solutions in the parietal BA 7 than occipital BA 19.

**Discussion**

*Behavioral Results Disclose Unconscious Visuo-spatial Processes*

The low rate of false recognition (~3% of 'baseline' trials) confirmed the reliability of the subjects’ self-reports and validated the present approach for the study of conscious and unconscious visuo-spatial processes (Schacter, 1999). This agrees with several lines of evidence showing reliability of self-report and reaction time for similar purposes (Schacter, 1999).

In the present study, reaction time was shorter when the go stimuli appeared on the cued location in both ‘seen’ and ‘not seen’ trials. This confirmed the occurrence of unconscious visuo-spatial processes during ‘not seen’ trials, in line with previous evidence (McCormick, 1997; Ivanoff and Klein, 2003; C. Babiloni et al., submitted). In contrast, the present results are apparently at odds with previous findings on ‘inhibition of return’ mechanism (Posner and Cohen, 1984; Posner et al., 1985). According to ‘inhibition of return’, the reaction time to the (extrafoveal) go stimuli should be lengthened by non-informative cue stimuli at the same location or hemifield (Tassinari and Berlucchi, 1993; Berlucchi et al., 2000). This paradox is just apparent. In contrast to the paradigms inducing ‘inhibition of return’, the present paradigm forced subjects to attract attentional 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 cued location. This explanation agrees with the previous results showing that subliminal visuo-spatial 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 et al., 1980, 1994; Posner, 1987; Merikle and Daneman, 1999; Berlucchi et al., 2000).

**ERPs Disclose Spatio-temporal Cortical Pattern of Conscious Visuo-spatial Processes**

Here cue stimulation evoked three major ERP components such as posterior N1, P2 and P3, which had the same peak latencies in ‘baseline’, ‘not seen’ and ‘seen’ potentials. These results hint that conscious and unconscious visuo-spatial processes are related to quite similar temporal evolution of parieto-occipital activity. In contrast, P3 amplitude was higher in ‘seen’ than ‘not seen’ and ‘baseline’ ERPs (Table 1). Mere effects of attention did not provoke this result, since it was still found when attention (indexed by reaction time) was paired in ‘seen’ and ‘not seen’ ERPs. Furthermore, P3 modulation was not due to relative frequency of the ‘seen’ and ‘not seen’ trials (the so-called P300 effect). In fact, it was still recognized in control blocks in which ‘seen trials’ were as frequent as ‘not seen’ trials (50%) and there were no ‘baseline’ trials.

LORETA analysis of P3 sources showed a strong activity of the extrastriate occipital (BA 19) and posterior parietal (BA 7) areas in both ‘seen’ and ‘not seen’ ERPs, indicating that conscious and unconscious visuo-spatial processes basically impinge upon the
same cortical 'dorsal' stream. However, there was an important statistical difference. Parieto-occipital P3 sources were greater in magnitude in 'seen' than 'not seen' LORETA solutions. This supports the hypothesis of specific spatial (occipital BA 19 and parietal BA 7) and temporal (~+300 ms post-stimulus) features of cortical responses to visuo-spatial consciousness.

The present results showed that amplitude of parieto-occipital activation is important for visual consciousness not only in patients with 'visual extinction' (Driver 1996; Driver et al., 1997; Heilman et al., 1997; Robertson et al., 1997; Driver and Mattingley, 1998) but also in normal subjects. In patients with 'visual extinction', ERPs were modulated by visual consciousness ('seen trials') at early latencies spanning 100–200 ms post-stimulus (Lhermitte et al., 1985; Vallar et al., 1991; Spinelli et al., 1994; Verleger et al., 1996; Marzi et al., 2000; Driver and Vuilleumier et al., 2001). In the present normal subjects, visual consciousness modulated parieto-occipital sources of late ERPs, namely at ~+300 ms post-stimulus (P3). That latency difference is compatible with side effects of brain lesions on the flow of conscious visuo-spatial processes and motivates further comparative investigations on these processes in normal subjects and patients.

The present results complement those of previous studies using P300 paradigms. These studies have shown that, in normal subjects, the amplitude of frontal and parietal P300 was higher after 'seen' (conscious perception) than 'not seen' (subliminal perception) rare stimuli (Shevrin, 1976; Kostandov and Arzumanov, 1977; Brandeis and Lehmann, 1986; Shefrin et al., 1988; Brazdil et al., 1998, 2001, 2002). Without the typical sensori-motor demands of the P300 paradigm, the present results indicate that conscious visuo-spatial processes modulate late ERPs at the latency of P300, but they have a parieto-occipital rather than frontal representation. Reasonably this topographical difference depended on more demanding executive functions elicited by P300 paradigms than by the present experimental condition.

In the present study the visuo-spatial consciousness modulated late parieto-occipital activation in both hemispheres. This is compatible with the notion that both the hemispheres are involved in visual consciousness, probably with peculiar aspects. Previous studies have emphasized the role of the left hemisphere for consciousness, whereas others have favored the right hemisphere (Galin, 1974; Kostandov and Arzumanov, 1977; Brandeis and Lehmann, 1986; Shefrin et al., 1992; Gazzaniga, 1993; Henke et al., 1993). In this framework, the left hemisphere may subserve sequential organization of percepts and linguistic elaboration, whereas the right one may subserve global visuo-spatial search and somatic perceptive processes, as revealed by well-known neurological syndromes such as neglect, visual extinction, prosopagnosia, etc. (Berti and Rizzolatti, 1992; Wallace, 1994; Baudena et al., 1995; Farah and Feinberg, 1997; De Renzi, 2000). In this regard, the specific demand of the present experiments was mainly visuo-spatial. Indeed, subjects had to click the mouse button as a function of the position of the go stimulus. They were not asked to say the position of the cue during self-report and they denied the use of mental verbal codes after the experiment. Moreover, the cue stimulation evoked potentials whose sources had greater

![Figure 5. Grand average of LORETA solutions (i.e. z-current density at cortical voxels) modeling the distributed sources for P3 component of the ERPs. These solutions refer to the ERPs formed by 'baseline', 'not seen', and 'seen' trials (n = 12).](image-url)
In this study we did not observe any clear spatiotemporal difference in 'baseline' and 'not seen' P3s, although the unconscious processes were confirmed by the fact that 'unseen' spatially congruent trials were associated with quick reaction times. It can be speculated that, in our experimental conditions, the unconscious processes were not macroscopically related to the temporal synchronization of cortical pyramidal neurons that mainly generate scalp visual evoked potentials. This is true at least on the basis of the present non-invasive EEG approach. Future investigations merit addressing the issue of the neural correlates underlying these unconscious processes by evaluating event-related changes in brain rhythmicity (i.e. alpha, gamma) rather than gross visual evoked potentials (Doppelmayr et al., 1998; Klimesch et al., 1998.). In order to have much more spatial detail and sensitivity for operative high-frequency components of EEG, another promising approach might be the use of intracerebral stereo EEG in epilepsy patients during the pre-surgical monitoring of cerebral functions (Rektor et al., 2002, 2003; Kuba et al., 2003; Babiloni et al., 2004).

**Conclusions**

Can visuo-spatial consciousness induce a specific spatio-temporal pattern of parieto-occipital activation? In the present study, the reaction time was shorter when go stimuli appeared on the cued location in both 'seen' trials (conscious perception of the cue) and 'not seen' trials (cue missed). This confirmed the occurrence of unconscious visuo-spatial processes during 'not seen' trials. Cue stimulus evoked parieto-occipital activity (LORETA sources at BA 19 and 7) with the same temporal pattern in 'seen' and 'not seen' trials. In contrast, this activity was significantly stronger in 'seen' than 'not seen' trials at ~300 ms post-stimulus. This may be considered as a specific spatio-temporal pattern of parieto-occipital activation accompanying visuo-spatial consciousness in normal subjects.

**Notes**

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