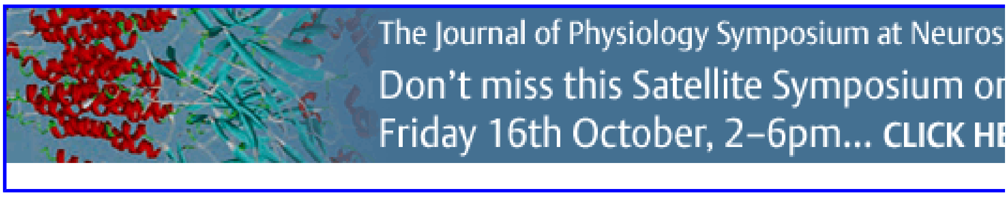


The Journal of Neuroscience

QUICK SEARCH:
Author: Keywo
Go
Year: Vol:

HOME | SEARCH | ARCHIVE | SUBSCRIBE | CONTACT | HELP

The Journal of Neuroscience, March 14, 2007, 27(11):2858-2865; doi:10.1523/JNEUROSCI.4623-06.2007

◄ Previous Article | Next Article ►

Behavioral/Systems/Cognitive

Synchronization of Neural Activity across Cortical Areas Correlates with Conscious Perception

Lucia Melloni,[1] * Carlos Molina,[1,2] Marcela Pena,[1,3] David Torres,[1] Wolf Singer,[4,5] and Eugenio Rodriguez[1,4,5] *

[1]Laboratorio de Neurociencias, Escuela de Psicología, Pontificia Universidad Católica de Chile, Vicuña Mackenna 4860, San Joaquin, 8940000 Santiago, Chile, [2]Radboud University Nijmegen, 6525 EK Nijmegen, The Netherlands, [3]International School for Advanced Studies, Cognitive Neuroscience Sector, 34014 Trieste, Italy, [4]Department of Neurophysiology, Max Planck Institute for Brain Research, 60528 Frankfurt am Main, Germany, and [5]Frankfurt Institute for Advanced Studies, Johann Wolfgang Goethe University, 60438 Frankfurt am Main, Germany

Abstract

Subliminal stimuli can be deeply processed and activate similar brain areas as consciously perc stimuli. This raises the question which signatures of neural activity critically differentiate consc processing. Transient synchronization of neural activity has been proposed as a neural correlate Here we test this proposal by comparing the electrophysiological responses related to the proce invisible words in a delayed matching to sample task. Both perceived and nonperceived words of local (gamma) oscillations in the EEG, but only perceived words induced a transient long-di widely separated regions of the brain. After this transient period of temporal coordination, the e unconscious processes continue to diverge. Only words reported as perceived induced (1) enha maintenance interval, (2) an increase of the P300 component of the event-related potential, and gamma oscillations before the anticipated presentation of the test word. We propose that the cri perception is the early transient global increase of phase synchrony of oscillatory activity in the

Key words: **visual awareness; electroencephalography; event-related potentials; gamma-b oscillatory neural synchrony**

Introduction

Stimuli that are masked and presented so briefly that they cannot be reported can still be highly activate motor responses (Marcel, 1983; Dehaene et al., 1998, 2001, 2004; Naccache et a patients suffering from blindsight (Goebel et al., 2001), hemineglect (Vuilleumier et al., 2002 Cipolotti, 2006), or prosopagnosia (Renault et al., 1989) supports the notion that unconsciou activate high-level cortical areas. This implies that complex cognition can proceed in the absen raising the question how the neuronal substrates of conscious and nonconscious processes diffe perception associates with enhanced sensory responses (Grill-Spector et al., 2000; Bar et al., 2 processing hierarchy (Beck et al., 2001; Dehaene et al., 2001; Kleinschmidt et al., 2002; M other studies suggest that this may not be a sufficient condition, because invisible stimuli activa and Zeki, 2002, 2006).

Alternatively, it has been proposed that conscious perception depends on the transient synchron (Engel et al., 1999; Engel and Singer, 2001; Thompson and Varela, 2001; Singer, 2002). would be local coordination of neural activity and propagation along sensory processing pathw global coordination of widely distributed neural activity by long-distance synchronization (Deh band phase synchrony is enhanced for consciously perceived stimuli (Meador et al., 2002; Gr 2005) and correlates with conscious perception in binocular rivalry (Fries et al., 1997, 2002 However, these studies have investigated synchronization in spatially restricted neural assembl global coordination. The purpose of this study was to disentangle the role of local processing a perception and to determine the nature and the time course of electrophysiological events that c

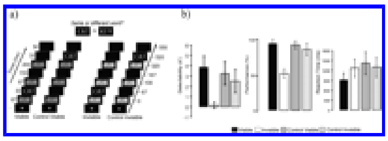
We recorded electroencephalographic (EEG) signals in subjects engaged in a delayed matching was manipulated such that the word was either consciously perceived or remained invisible but processing (Varela et al., 2001), we measured over a wide frequency range (1) time-resolved synchronization across recording sites. We found that visible and invisible conditions differed local neural processing. In addition, only consciously perceived stimuli gave rise to a cascade c associated with perception stabilization, maintenance in working memory, and generation of ex synchronization is the critical event that triggers these subsequent processes by enhancing the s permit access to consciousness.

Materials and Methods

Experiment 1

Subjects. Fifteen normal healthy subjects gave written informed consent to participate in the stud
age, 20.6 years). All were native Spanish speakers, right handed, had normal or corrected-to-no
naive to the purpose of the experiment.

Stimuli and task. Participants were engaged in a two-alternative, forced-choice-delayed matching
trials), in which the sample stimuli could be either visible or invisible. The subjects' task was to
briefly presented 33 ms "sample word" was the same or different from a second "test word" pre
participants responded by pressing one of two different buttons mounted on a response pad, wi
participants, the same response was at the right button, whereas in eight participants, it was at t
followed by masking stimuli (67 ms each), which changed in luminance between trials renderi
conditions). To assess the responses to the masking stream itself, sample words were replaced
constant (control conditions). To render control trials perceptually similar to experimental trial
after the mask stream and before test word presentation (see Fig. 1*a*). This design enabled us to
subtracting the response elicited by the masking stimuli.



View larger version (18K):
[in this window]
[in a new window]

Figure 1. Design and behavioral results of experiment
a briefly presented word (sample word) with a subsequ
was controlled by changing the luminance of the mask
brain response to the mask stream. The left timeline sh
timeline shows the cumulative time. ***b***, Behavioral perf
detectability for all conditions, expressed as detectabili
rate. The right plot shows the reaction time for all cond

The stimulus set consisted of 40 disyllabic Spanish words. Syllables were consonant–vowel. A
(S. Sadowsky and R. Martínez, unpublished observation) and presented in Howard light font. T
color (luminance change) on a black background, rendering the sample word visible or invisibl
were set in a previous control experiment and were kept constant throughout the subjects. Mas
and diamonds drawn with identical line thickness as the font used for the sample words. All sti
enhanced graphic adapter mode (150 Hz refresh rate), located in the central area of the screen,
participant ran a training block of 20 trials. Experimental and control trials were pseudo-rando
with a variable rest pause. All conditions were equally presented within a block. The intertrial i
ms. The experiment was performed in a silent, dimly lit, and electrically shielded room. Specia
contamination of the EEG signal by the 50 Hz AC component, because the gamma band respo
artifact was reduced by recording inside a completely hermetic Faraday cage. All of the electri
the only exception of the monitor, which was electrically shielded.

Experiment 2

Twenty subjects took part in an unconscious semantic priming experiment (11 males; mean ag
used in the previous experiment. All subjects gave written informed consent, were native Spani
normal vision, and were naive of the purpose of the experiment. Participants performed a simpl

left or right index finger (response pattern was reversed for half of the subjects) to indicate whe
respectively. Unknown to them, another word, which could be either semantically congruent (e
dog) with the target word was presented for 33 ms before the target and surrounded by forward
duration of the prime and mask were the same as in the previous experiment (mask – prime –
word was presented for 300 ms, and the third mask remained on the screen until subjects respo
was 100 ms (33 ms prime + 67 ms forward mask).

Electrophysiological recording and analysis

EEG activity was recorded from a 64-electrode geodesic sensor net referenced to the vertex. T
and the initial bandpass recording filter was set at 0.01–100 Hz.

For the event-related potential (ERP) analysis, the continuous EEG signal was bandpass filtere
filter (Kaiser type), which has a linear phase response [passband gain, 99% (50–99.9%; –0.1 d
Hz (0.3–10 Hz)]. Then, the filtered signal was segmented in a series of 1100-ms-long epochs.
first mask. Trials that contained voltage fluctuations exceeding ±200 μV, transients exceeding
±70 μV were rejected. Artifact free trials were averaged in synchrony with first mask presentat
and baseline corrected over a 100 ms window. The EEGLAB Matlab toolbox was used for visu
Makeig, 2004).

For the analysis of time-frequency distributions and phase synchrony, a filter was designed tha
component but kept the biological 50 Hz signal. The amplitude and phase of the AC signal was
This eliminated selectively the periodic part of the 50 Hz component (line frequency). Then, a
(10–100 Hz) was applied, and the filtered signal was analyzed with a sliding-window fast Fouri
window overlap, 90%). For every time window and frequency bin, amplitude and phase were c
were zero-padded to complete 1024 points and fast Fourier transformed to get an interpolated f
Instantaneous amplitude was then computed by taking the real and imaginary Fourier coefficie
and taking the square root (sqrt) (i.e., for a given time window *t* and frequency bin *f*), as follow

$$\mathrm{Amp}(f,t)=\mathrm{sqrt}(C(f,t)_r{}^2+C(f,t)_i{}^2).$$

This amplitude corresponds to the length of the vector specified by the real and imaginary Fou
equivalent to the magnitude of the observed oscillation at a given time and frequency point.

During the same time window and frequency bin, phase was computed as the arc tangent (arctg
real one, as follows:

$$\mathbf{Phi}(f,t)=\mathrm{arctg}(C(f,t)_i/C(f,t)_r).$$

Phi is thus the angle of the vector specified by the real and imaginary Fourier coefficient. For a
position inside the oscillation cycle (peak, valley, rising, or falling slope).

These amplitude and phase values are evaluated in the 10–100 Hz frequency range and in the –
presentation. Phase information was then used to compute a time-varying phase-locking value
1999; Rodriguez et al., 1999). In brief, the method involves computing the phase difference
the stability of such phase difference through all trials. If φ_i and φ_j are unitary vectors represent
phase difference between such electrodes is a unitary vector obtained by multiplying the first v

$$\phi_{ij} = \phi_i \mathrm{conj}(\phi_j).$$

The PLV is thus the length of the vector resulting from the vector sum of difference vectors thr

$$PLV\mathbf{ij} = \mathrm{abs}(1/N \times \Sigma\phi_{ij}),$$

with the sum operating throughout all of the trials and where N is the number of trials. The PL synchronization (phase difference is perfectly constant throughout the trials) and value 0 repres Time-frequency charts of both phase synchrony and spectral power were normalized to a baseli involves subtracting the baseline average and dividing by the baseline SD on a frequency-by-fr average of the signal during the baseline period, and σ is the SD of the same baseline period. T

$$S_N = (S - \mu)/\sigma.$$

In another analysis aiming to analyze the theta activity associated with the retention interval (fr transform was computed over a 467 ms window, on the raw unfiltered EEG signal. Afterward, showed significantly ($p < 0.05$) higher amplitude (5–6 Hz) were added over trials and subjects

Statistical analysis

Because we were interested in long-range coordination of neural activity, we included all electr synchronization across a large frequency range. Behavioral and EEG data were analyzed with t for all tests.

The statistical analyses of the time-frequency distributions and phase synchrony were all perfo electrophysiological responses of all sensors during the entire segment (–500 to 1000 ms after frequency and phase-synchrony chart per experimental condition per subject. Then, those chart permutation test in search of time-frequency windows showing significant effects (Burgess and frequency windows were analyzed with a two-tailed, within-subject ANOVA. The α level was

In the permutation test, the time-frequency charts belonging to different conditions are mixed t statistical significance of the results. The permutation test assumes that the "real" differences b permutation test has advantages over the Bonferroni correction for multiple comparisons, becau independent, an assumption that is too strong and weakens the power of the statistical test. In c all of the measures.

For the topographical analysis of phase synchrony, we controlled for the statistical effects of m threshold ($p < 0.00005$). This threshold was set as a function of the distribution of synchrony v probability smaller than 0.00005. This threshold was computed by counting the number of case This fraction should give a value smaller than 0.00005. By choosing this significance level, one the fact that there were 64 electrodes with 2016 possible combinations (64 x 63/2 = 2016).

Results

Behavioral measures of visibility

Behavioral results showed that, in the experimental condition in which sample words could be 904.5; $p < 0.001$), the mean d' being 3.85, which implies a highly significant difference from c experimental condition that rendered sample words invisible, performance dropped to chance l $F_{(1,14)} = 2.097$; $p = 0.170$), and the mean *d'* value did not differ from zero ($d' = 0.16$; $F_{(1,14)} =$ 0.129) (Fig. 1*b*). In control conditions, the success rates were 92.50 and 86.17%, and the respec were 3.27 and 2.50, indicating that participants were able to detect the control words.

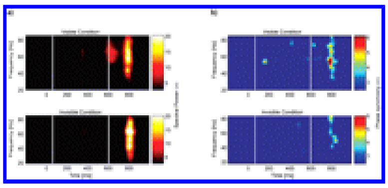
Reaction times were significantly shorter in the visible compared with the invisible condition (ms, respectively; $F_{(1,14)} = 76.139$; $p = 0.000018$), despite the fact that speed of response was n between the two control conditions did not differ (1269 and 1296 ms; $F_{(1,14)} = 0.361$; $p = 0.55$

To determine to which extent the invisible words in the experimental condition were still proce processing of the invisible words in an unconscious priming task (Marcel, 1983), using the sa word–mask-target word), and determined priming effects with a reaction time task. This contro effects of the invisible word. That is, subjects responded significantly faster in the congruent c to the same semantic category) compared with the incongruent condition (prime and target wor categories) (effect size was 15 ms difference between congruent and incongruent trials; $n = 20$ Therefore, masked words, although invisible, were still processed.

Activity patterns related to perceptual awareness

The analyses described below have all been performed after eliminating effects caused by diffe traces obtained after presentation of the high and low luminance mask alone (control condition corresponding experimental condition for an analysis window extending from 500 ms before t mask. The subtracted conditions are referred here as "visible" and "invisible," respectively.

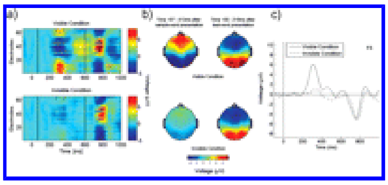
The first significant difference between visible and invisible words was observed from 80 to 13 During this period, the mean phase synchrony at 50–57 Hz over all electrode pairs was signific invisible condition ($F_{(1,14)} = 5.041$; $p = 0.044$) (Fig. 2*b*). During the same interval, neither the oscillations (50–57 Hz; $F_{(1,14)} = 0.616$; $p = 0.448$) nor the mean ERPs calculated over all as we between conditions (ERP effect over all electrodes: $F_{(1,14)} = 0.005$, $p = 0.774$, 0.0245 µV diffe electrodes: $F_{(1,14)} = 1.036$, $p = 0.329$, 0.3350 µV difference) (Figs. 2*a*, 3).



View larger version (26K):
[in this window]
[in a new window]

Figure 2. Spectral power and phase synchrony to visible a (visible – control_visible) and invisible condition (invisibl frequency plot shows the grand average of all electrodes. average for all of the electrode pairs. The color scale indic ms baseline. Zero corresponds to first mask onset. Vertical presentation. ***a***, Time – frequency plot. Two increments of is only present in the visible condition, and the second is p synchrony. There are three statistically significant bursts o peaks occur only in the visible condition. No significant di

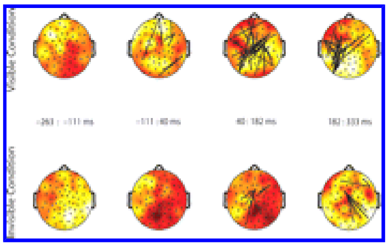
Figure 3. ERPs elicited by visible and invisible words. ***a***,



View larger version (27K):
[in this window]
[in a new window]

invisible words at different electrodes. The *x*-axis shows ti color scale is expressed in microvolts. Zero represents the sample-word and test-word presentation. Small lines at the windows corresponding to the voltage scalp maps in ***b***. ***b***, ` indicated for visible and invisible conditions. The first diff presentation, as a P300a-like component. Then, a P1-like c word presentation, for both conditions. ***c***, Time course of t F3.

To obtain more detailed information about activation patterns related to the visible and invisibl spectral power and phase synchrony were computed for the interval from 260 ms before to 330 (frequency, 50–57 Hz; 150 ms sliding window). Although the patterns of gamma activity were two conditions, the patterns of phase synchrony were markedly different (Fig. 4). In the invisib exhibited significant phase synchronization. In the visible condition, in contrast, numerous elec hemispheres, showed significant phase-locking between occipital, parietal, and frontal sites in t word presentation. In the window between 180 and 330 ms, the pattern of phase synchrony bec restricted to occipito-parietal electrodes, which agrees with the fact that the task involves langu



View larger version (35K):
[in this window]
[in a new window]

Figure 4. Scalp topography of induced gamma power and condition. Top row, Visible condition. Bottom row, Invisil indicates induced gamma power averaged in a 50–57 Hz fi average of a 150 ms time window. Time 0 indicates the on of electrodes displaying significant synchronization ($p <$ (statistically differ between visible and invisible conditions the visible condition during the 40–180 ms time window ii electrodes, with intrahemispheric and interhemispheric coi 330 ms, the pattern of phase synchrony lateralizes over the parietal electrodes.

The finding that phase-locking in the visible condition increases without a concomitant increas comparison was restricted to individual electrodes, suggests that the main difference between v period, is the coherence of activity among cortical regions rather than the amount of local neura

Electrophysiological signatures of further processing of visible stimuli

A second significant difference between perceptual conditions was apparent in the ERP from 1: In this interval, the mean amplitude of a fronto-central positivity, peaking at 240 ms after samp higher in the visible than in the invisible condition ($F_{(1,14)} = 37.766$; $p = 0.00002$; 2.3394μV di P3-like component starts to diverge at a point in time when the differences in phase synchrony been related to the updating of contents kept in working memory (Donchin, 1981⊞). In additior Hz) increased significantly over frontal electrodes in the visible condition during the interval in memory (time interval, 67–520 ms) (see supplemental Fig. 1, available at www.jneurosci.org a: oscillations have been assigned a role in the maintenance of short-term memories (Jensen and T Although it would have been interesting to see whether the theta enhancement started only afte

necessity to use long windows for the assessment of the low-frequency oscillations precluded d
enhanced theta.

A third and more delayed difference between the visible and invisible conditions was observed
presentation. Here, both phase synchrony and gamma power were significantly higher during t
The increase in synchrony, averaged over all electrodes, occurred in the high gamma range (67
ms after test-word presentation (visible vs invisible: $F_{(1,14)} = 11.803$; $p = 0.005$). Interestingly,
was also enhanced and in exactly the same frequency range (visible vs invisible: $F_{(1,14)} = 8.00$
latency, these effects might reflect anticipatory processes that occur only when the subjects hav
and Lamarre, 2005). This anticipation was possible because the interval between sample- and
significantly shorter reaction times observed in the visible condition support this interpretation.

Finally, there were two significant effects related to test-word presentation that did not differen
conditions. First, there was a significant increase in phase synchrony in the frequency band fro
ms after test-word presentation (visible vs baseline: $F_{(1,14)} = 22.869$, $p < 0.001$; invisible vs ba
visible vs invisible conditions: $F_{(1,14)} = 0.199$, $p = 0.663$)

Second, there was a significant increase in power of gamma oscillations in a broad frequency r
155–230 ms after test-word presentation (visible vs baseline: $F_{(1,14)} = 63.524$, $p < 0.001$; invisi
0.001; visible vs invisible condition: $F_{(1,14)} = 2.030$, $p = 0.180$).

In the ERP, test-word presentation evoked P1–N1 components, the latency, amplitude, and spa
the visible and invisible conditions ($F_{(1,14)} = 2.896$; $p = 0.115$; 1.205 µV difference).

Because word visibility was manipulated by changing mask luminance, it could be argued that
invisible conditions are attributable to luminance variations. To control for this possibility, we
which visible trials were subtracted from invisible trials (visible plus light effect) and contraste
visible and control invisible trials (referred to as light effect). This contrast should remove any
persisting effects should only reflect processes related to conscious perception of the sample w
described above. There were two episodes of enhanced phase synchrony. One was associated w
80 ms after sample-word presentation; frequency range, 50–57 Hz; $F_{(1,14)} = 5.806$; $p = 0.033$)
(starting10 ms after test-word presentation, frequency range 75–80 Hz ($F_{(1,14)}) = 8.811$, $p = 0.0$
oscillations was enhanced in association with the presentation of the test word (starting 20 ms
range, 60–75 Hz; $F_{(1,14)} = 6.875$; $p = 0.022$) (see supplemental Fig. 2, available at www.jneuro

Enhanced synchronization can be mimicked by volume conduction if it occurs with zero phase
be considered that a single generator oscillating in the respective frequency increases its power
the signals measured on the scalp. Conversely, reduction in the activity of other oscillators can
source, producing again stronger synchronization on the scalp. We consider it unlikely that this
for the following reasons. First, if the observed synchronization were attributable to activation
generators, it should show up as a difference in the induced gamma activity or in the ERPs bet
not the case in our experiment. During the interval of enhanced phase-locking, neither the ERP
differed between conditions, suggesting that the activity of the contributing generators was un

Second, synchronization caused by volume conduction must occur with zero phase difference b angles at which synchronization occurred were not centered on zero and exhibited considerable at www.jneurosci.org as supplemental material). This means that the most prominent synchroni from volume conduction. Furthermore, the scatter in phase lag implies that the observed synchr to trial, which is incompatible with instantaneous volume conduction. Third, phase synchroniza distance-dependent gradient on the scalp (i.e., phase synchrony should decay with interelectrod for a distance-dependent gradient in PLVs. In fact, the scalp topography shows that synchroniz electrodes.

Discussion

The first electrographic difference between conscious and nonconscious stimulus processing w locking of induced gamma oscillations across widely distributed cortical regions. This suggests synchronization could be the event that triggers ignition of the global workspace of consciousn Dehaene and Naccache (2001) and Dehaene et al. (2006).

Local and long-range neural synchrony and their putative role in conscious and unconsci
Our results show similar activation patterns at individual electrodes in the visible and invisible generators are activated in both cases. In contrast, phase synchronization across electrodes clea enhanced long-range coordination of oscillatory activity only in the visible condition. Several a should be related to coordinated dynamical states of the cortical network, rather than to the acti 2002; Engel et al., 1999; Engel and Singer, 2001; Thompson and Varela, 2001; Singer, 2 support for this notion. In addition, our results and the results from a previous study investigati somatosensory stimuli (Palva et al., 2005) are in line with a recent proposal (Dehaene et al., 2 information with local coordination of neural activity in resonant loops of medium range and re of distant neural activity by long-range synchronization. Interestingly, the global long-distance very transient and the earliest event differentiating conscious from nonconscious processing. A P3a and theta oscillations, continue to differentiate between consciously and nonconsciously pe synchronization plays a role in triggering the cognitive processes associated with conscious aw to be clarified through which mechanism long-distance synchronization exerts an impact on sul

The transient character of the long-distance synchronization is not entirely compatible with mo Changeux, 2005; Dehaene et al., 2006) and reentrant activity (Lamme, 2006) because thes perceived stimuli. Our results show increased neural synchrony for the visible condition, which short time window (~50 ms), suggesting that neural synchronization could last longer but is no

The discrepancy between sustained and transient activity found in different studies could also b paradigms. Most of the experiments that have reported sustained activity used either the attenti al., 2005) or inattentional blindness (Dehaene and Changeux, 2005). It is still controversial v conscious perception or memory processes. It has been argued that subjects could have conscio presentation, yet simply forget it when they are asked to report it (Wolfe, 1999). In fact, exper blindness show that unattended objects could be fleetingly represented and reported but that the is presented or if the eyes move to a new location (Landmann et al., 2003). Thus, the sustaine paradigms could reflect the transfer or maintenance of a stable representation in working memo perception itself.

Early wave of activation that distinguishes conscious from unconscious processing

In contrast to previous experiments, the results of which suggest a late wave of activation as co
al., 2004; Sergent et al., 2005), our results indicate that access to consciousness is triggered
(synchronization) of widely distributed neuronal assemblies starting as early as 80 ms after stin
(2005) and Fries et al. (2001) for a similar finding]. This difference might be explained by tv
stimuli used in our experiment might have imposed pressure on the perceptual processes, leadi
devoted to each stimulus. Second, in contrast to previous experiments, in our study the neural p
segregated in time from those related to decision making and execution of motor responses. Th
described previously might thus reflect a mixture of cognitive processes (e.g., perception and d
the brief and early episode of phase-locking. The responses observed after test-word presentati
presentation of the test word also triggered a sequence of cognitive processes, but these could b
perception, decision making, and acting). In this case, the induced synchronization occurred wi
was in the range described in previous experiments. The present finding that the first electrogra
has a short latency is in agreement with the evidence that areas at the highest level of the proce
active as early as 100 ms after stimulation (Nowak and Bullier, 1997) and that high cognitive
categorization, can be accomplished within 120 ms (Thorpe et al., 1996; Kirchner and Thorpe
with a series of studies showing that conscious and unconscious perception can be rapidly disti
(Dehaene et al., 2001; Pins and Ffytche, 2003; Palva et al. 2005). Additionally, in the same
synchronization episode (80–120 ms), Walsh and Cowey (1998) found that applying a TMS
circumstriate areas can impair visual perception of a briefly presented stimulus, suggesting that
conscious perception. In accordance with the present data, these results suggest that the brain c
and that the divergence of conscious and unconscious processing occurs within 100 ms after sti
early wave of activation might be an essential correlate of conscious perception (Pins and Ffytc

Late correlates of conscious processing

Previous studies investigating electrographic correlates of conscious and unconscious processi
ERPs (Sergent et al., 2005) or dynamic measures such as spectral power or phase synchrony (
2004; Doesburg et al., 2005; Palva et al., 2005). The combination of the different methods
temporal characterization of the putative EEG events differentiating between conscious and un
suggest that only consciously perceived stimuli give rise to a cascade of processes that have dis
summary, these consisted of (1) an early and global phase-locking of gamma oscillations, (2) a
of the ERP and of sustained theta oscillations over frontal areas that are likely to reflect transfe
stimuli in working memory, and (3) an enhancement of power and phase-locking of gamma os
presentation that may be a correlate of the anticipation of the matching between short-term me
results on ERPs agree with the data of Sergent et al. (2005), which suggests that ERPs evoke
start to diverge around 270 ms. Interestingly, these ERP differences occur only after the end of
synchrony. Thus, it seems as if the fast and transient large-scale synchronization enhances the
sufficiently to permit access to consciousness and thereby triggers a sequence of processes suc
maintenance in working memory, and generation of expectancies that are associated with cons
clarified whether the early large-scale synchronization is already the neuronal correlate of phen
emerges only from the entirety of the processes following this coordinated state.

Long-range synchronization, conscious perception, and the depth of processing

It can be argued that the electrophysiological signatures associated with conscious perception a
processing rather than reflecting mechanisms specifically associated with awareness. We consi
The finding that visible and invisible words induced gamma oscillations of similar power and

were thoroughly processed. In addition, in the control experiment with the subliminal priming t unperceived word using the same protocol as in the main experiment. Prime words, although n that the unconsciously perceived words are processed. Therefore, we consider it likely that the early long-distance synchronization of neural assemblies, rather than the mere depth of process word processing.

Footnotes

Received Oct. 25, 2006; revised Jan. 16, 2007; accepted Feb. 5, 2007.

*L.M. and E.R. contributed equally to this work.

L.M. was supported by the Comisión Nacional de Investigación Científica y Tecnológica (Chil (Germany). E.R. was supported by Max Planck Gesellchaft, Volkswagen Stiftung, and the Frar

Correspondence should be addressed to Dr. Lucia Melloni, Brain Imaging Center and Cognitiv Universität, Schleusenweg 2-16, 60528 Frankfurt am Main, Germany. Email: melloni@mpih-f

References

Bar M, Tootell R, Schacter D, Greve B, Fischl B, Mendola J, Rosen B, Dale A (2001) Cortical explicit visual object recognition. Neuron 29:529–535.[CrossRef][Web of Science][Medline]

Beck D, Rees G, Frith C, Lavie N (2001) Neural correlates of change detection and change bli 4:645–650.[CrossRef][Web of Science][Medline]

Burgess A, Gruzelier J (1999) Methodological advances in the analysis of event-related desync Handbook of electroencephalography and clinical neurophysiology, revised series (Pfurtschell Amsterdam: Elsevier Science.

Cappelletti M, Cipolotti L (2006) Unconscious processing of Arabic numerals in unilateral neg [Web of Science][Medline]

Carmel D, Lavie N, Rees G (2005) Conscious awareness of flicker in human involves frontal a Science]

Courtemanche R, Lamarre Y (2005) Local field potential oscillations in primate cerebellar cort active and passive expectancy. J Neurophysiol 93:2039–2052.[Abstract/Free Full Text]

Dehaene S, Changeux J (2005) Ongoing spontaneous activity controls access to consciousness: Biol 3:911–927.

Dehaene S, Naccache L (2001) Towards a cognitive neuroscience of consciousness: basic evid 38.[CrossRef][Web of Science][Medline]

Dehaene S, Naccache L, Le Clec HG, Koechlin E, Mueller M, Dehaene-Lambertz G, van de M semantic priming. Nature 395:597–600.[CrossRef][Medline]

Dehaene S, Naccache L, Cohen L, Le Bihan D, Mangin JF, Poline JB, Riviere D (2001) Cerebı
unconscious repetition priming. Nat Neurosci 4:752–758.[CrossRef][Web of Science][Medline

Dehaene S, Jobert A, Naccache L, Ciuciu P, Poline JB, Le Bihan D, Cohen L (2004) Letter bin
masked words: behavioral and neuroimaging evidence. Psychol Sci 15:307–313.[CrossRef][W

Dehaene S, Changeux JP, Naccache L, Sackur J, Sergent C (2006) Conscious, preconscious, ar
taxonomy. Trends Cogn Sci 10:204–211.[CrossRef][Web of Science][Medline]

Delorme A, Makeig S (2004) EEGLAB: an open source toolbox for analysis of single-trial EE
component analysis. J Neurosci Methods 134:9–21.[CrossRef][Web of Science][Medline]

Doesburg S, Kitajo K, Ward L (2005) Increased gamma-band synchrony precedes switching o
binocular rivalry. NeuroReport 16:1139–1142.[CrossRef][Web of Science][Medline]

Donchin E (1981) Surprise!... Surprise? Psychophysiology 18:493–513.[Web of Science][Med

Engel A, Singer W (2001) Temporal binding and the neural correlates of sensory awareness. T
[Web of Science][Medline]

Engel A, Fries P, Konig P, Brecht M, Singer W (1999) Temporal binding, binocular rivalry, an
8:128–151.[CrossRef][Web of Science][Medline]

Fries P, Roelfsema P, Engel A, Konig P, Singer W (1997) Synchronization of oscillatory respo
perception in interocular rivalry. Proc Natl Acad Sci USA 94:12699–12704.[Abstract/Free Full

Fries P, Reynolds JH, Rorie AE, Desimone R (2001) Modulation of oscillatory neuronal synch
Science 291:1560–1563.[Abstract/Free Full Text]

Fries P, Schroeder J, Roelfsema P, Singer W, Engel A (2002) Oscillatory neuronal synchroniza
correlate of stimulus selection. J Neurosci 22:3739–3754.[Abstract/Free Full Text]

Goebel R, Muckli L, Zanella FE, Singer W, Stoerig P (2001) Sustained extrastriate cortical acti
revealed by fMRI studies of hemianopic patients. Vision Res 41:1459–1474.[CrossRef][Web o

Grill-Spector K, Kushnir T, Hendler T, Malach R (2000) The dynamics of object-selective acti
performance in humans. Nat Neurosci 1:91–100.[Web of Science]

Gross J, Schmitz I, Schnitzler K, Kessler K, Shapiro B, Hommel A, Schnitzler A (2004) Modu
reflects temporal limitations of visual attention in humans. Proc Natl Acad Sci USA 101:13050

Jensen O, Tesche C (2002) Frontal theta activity in humans increases with memory load in a w
15:1395–1399.[CrossRef][Web of Science][Medline]

Kirchner H, Thorpe S (2006) Ultra-rapid object detection with saccadic eye movements: visual
46:1762–1776.[CrossRef][Web of Science][Medline]

Kleinschmidt A, Buchel C, Hutton C, Friston C, Frackowiak R (2002) The neural structure exp
letter recognition. Neuron 34:659–666.[CrossRef][Web of Science][Medline]

Lachaux J, Rodriguez E, Martinerie J, Varela F (1999) Measuring phase-synchrony in brain sig

[CrossRef][Web of Science][Medline]

Lamme V (2006) Towards a true neural stance on consciousness. Trends Cogn Sci 10:494–501

Landmann R, Spekreijse H, Lamme V (2003) Large capacity storage of integrated objects befo
164.[CrossRef][Web of Science][Medline]

Marcel A (1983) Conscious and unconscious perception: experiments on visual masking and w
237.[CrossRef][Web of Science][Medline]

Marois R, Yi D, Chun M (2004) The neural fate of consciously perceived and missed events in
472.[CrossRef][Web of Science][Medline]

Meador K, Ray P, Echauz J, Loring D, Vachtsevanos G (2002) Gamma coherence and conscio
[Abstract/Free Full Text]

Moutoussis K, Zeki S (2002) The relationship between cortical activation and perception inves
Acad Sci USA 99:9527–9532.[Abstract/Free Full Text]

Moutoussis K, Zeki S (2006) Seeing invisible motion: a human fMRI study. Curr Biol 16:574–
[Medline]

Naccache L, Gaillard R, Adam C, Hasboun D, Clemenceau S, Baulac M, Dehaene S, Cohen L
emotions evoked by subliminal words. Proc Natl Acad Sci USA 102:7713–7717.[Abstract/Fre

Nakatani C, Ito J, Nikolaev A, Gong P, van Leeuwen C (2005) Phase synchronization analysis
Neurosci 17:1969–1979.[CrossRef][Web of Science][Medline]

Nowak LG, Bullier J (1997) The timing of information transfer in the visual system. In: "Extra
Rockland K, Peters A, eds) Vol 12: pp. 205–241. New York: Plenum.

Palva S, Linkenkaer-Hansen K, Naatanen R, Palva M (2005) Early neural correlates of conscio
25:5248–5258.[Abstract/Free Full Text]

Pins D, Ffytche D (2003) The neural correlates of conscious vision. Cereb Cortex 13:461–474.

Renault B, Signoret JL, Debruille B, Breton F, Bolgert F (1989) Brain potentials reveal covert
Neuropsychologia 27:905–912.[CrossRef][Web of Science][Medline]

Rodriguez E, Lachaux JP, Martinerie J, Renault B, Varela FJ (1999) Perception's shadow: long
brain activity. Nature 397:430–433.[CrossRef][Medline]

Schack B, Klimesch W, Sauseng P (2005) Phase synchronization between theta and upper alph
Int J Psychophysiol 57:105–114.[CrossRef][Web of Science][Medline]

Sergent C, Baillet S, Dehaene S (2005) Timing of the brain events underlying access to conscio
Neurosci 8:1391–1400.[CrossRef][Web of Science][Medline]

Singer W (2002) Consciousness from neurobiological perspective. In: Neural correlates of con
137. Cambridge, MA: MIT.

Srinivasan R, Russell D, Edelman G, Tononi G (1999) Increased synchronization of neuromag
perception. J Neurosci 19:5435–5448.[Abstract/Free Full Text]

Thompson E, Varela F (2001) Radical embodiment: neural dynamics and consciousness. Trenc

Thorpe S, Fize D, Marlot C (1996) Speed of processing in the human visual system. Nature 38

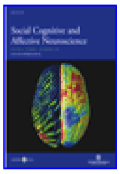
Varela F, Lachaux J, Rodriguez E, Martinerie J (2001) The brain web: phase synchronization a
Neurosci 2:229–239.[CrossRef][Web of Science][Medline]

Vuilleumier P, Armony J, Clarke K, Husain M, Driver J, Dolan R (2002) Neural response to er
awareness: event-related fMRI in a parietal patient with visual extinction and spatial neglect. N
[CrossRef][Web of Science][Medline]

Walsh V, Cowey A (1998) Magnetic stimulation studies of visual cognition. Trends Cogn Sci

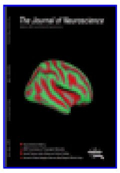
Wolfe JM (1999) Inattentional amnesia. In: Fleeting memories: cognition of brief visual stimul
Cambridge, MA: MIT.

This article has been cited by other articles:



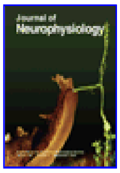
Social Cognitive and Affective Neuroscience ▸HOME

C. Kuhbandner, S. Hanslmayr, M. A. Maier, R. Pekrun, B. Spitzer, B. Pastotter, and K.-H. Bauml
Effects of mood on the speed of conscious perception: behavioural and electrophysiological evidence
Soc Cogn Affect Neurosci, September 1, 2009; 4(3): 286 - 293.
[Abstract] [Full Text] [PDF]



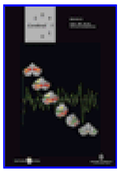
The Journal of Neuroscience ▸HOME

J. Chapuis, S. Garcia, B. Messaoudi, M. Thevenet, G. Ferreira, R. Gervais, and N. Ravel
The Way an Odor Is Experienced during Aversive Conditioning Determines the Extent of the Network Recruited during Retrieval: A Multisite Electrophysiological Study in Rats
J. Neurosci., August 19, 2009; 29(33): 10287 - 10298.
[Abstract] [Full Text] [PDF]



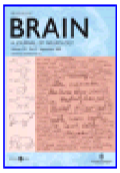
Journal of Neurophysiology ▸HOME

J. B. Swettenham, S. D. Muthukumaraswamy, and K. D. Singh
Spectral Properties of Induced and Evoked Gamma Oscillations in Human Early Visual Cortex to Moving and Stationary Stimuli
J Neurophysiol, August 1, 2009; 102(2): 1241 - 1253.
[Abstract] [Full Text] [PDF]



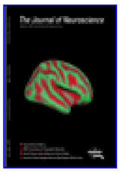
Cerebral CORTEX ▸HOME

Q. Luo, D. Mitchell, X. Cheng, K. Mondillo, D. Mccaffrey, T. Holroyd, F. Carver, R. Coppola, and J. Blair
Visual Awareness, Emotion, and Gamma Band Synchronization
Cereb Cortex, August 1, 2009; 19(8): 1896 - 1904.
[Abstract] [Full Text] [PDF]



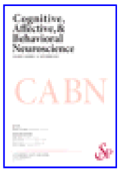
BRAIN HOME

M. Arthuis, L. Valton, J. Regis, P. Chauvel, F. Wendling, L. Naccache, C. Bernard, and F. Bartolomei
Impaired consciousness during temporal lobe seizures is related to increased long-distance cortical-subcortical synchronization
Brain, August 1, 2009; 132(8): 2091 - 2101.
[Abstract] [Full Text] [PDF]



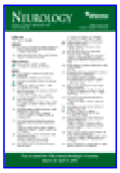
The Journal of Neuroscience HOME

A. Compte, R. Reig, V. F. Descalzo, M. A. Harvey, G. D. Puccini, and M. V. Sanchez-Vives
Spontaneous High-Frequency (10-80 Hz) Oscillations during Up States in the Cerebral Cortex In Vitro
J. Neurosci., December 17, 2008; 28(51): 13828 - 13844.
[Abstract] [Full Text] [PDF]



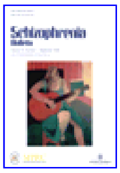
Cognitive, Affective, & Behavioral Neuroscience HOME

S. Scherbaum, M. Dshemuchadse, and A. Kalis
Making decisions with a continuous mind
Cogn Affect Behav Neurosci, December 1, 2008; 8(4): 454 - 474.
[Abstract] [PDF]



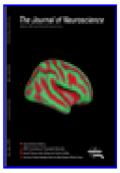
Neurology HOME

E. E. Benarroch
The midline and intralaminar thalamic nuclei: Anatomic and functional specificity and implications in neurologic disease
Neurology, September 16, 2008; 71(12): 944 - 949.
[Abstract] [Full Text] [PDF]



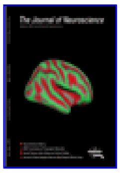
Schizophrenia Bulletin HOME

P. J. Uhlhaas, C. Haenschel, D. Nikolic, and W. Singer
The Role of Oscillations and Synchrony in Cortical Networks and Their Putative Relevance for the Pathophysiology of Schizophrenia
Schizophr Bull, September 1, 2008; 34(5): 927 - 943.
[Abstract] [Full Text] [PDF]



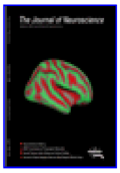
The Journal of Neuroscience HOME

J.-P. Thivierge and P. Cisek
Nonperiodic Synchronization in Heterogeneous Networks of Spiking Neurons
J. Neurosci., August 6, 2008; 28(32): 7968 - 7978.
[Abstract] [Full Text] [PDF]



The Journal of Neuroscience HOME

S. van Gaal and J. J. Fahrenfort
The Relationship between Visual Awareness, Attention, and Report
J. Neurosci., May 21, 2008; 28(21): 5401 - 5402.
[Full Text] [PDF]



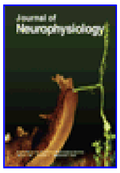
The Journal of Neuroscience ▸HOME

V. Wyart and C. Tallon-Baudry

Neural Dissociation between Visual Awareness and Spatial Attention

J. Neurosci., March 5, 2008; 28(10): 2667 - 2679.

[Abstract] [Full Text] [PDF]



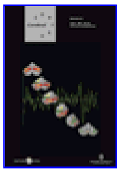
Journal of Neurophysiology ▸HOME

R. C. Muresan, O. F. Jurjut, V. V. Moca, W. Singer, and D. Nikolic

The Oscillation Score: An Efficient Method for Estimating Oscillation Strength in Neuronal Activity

J Neurophysiol, March 1, 2008; 99(3): 1333 - 1353.

[Abstract] [Full Text] [PDF]



Cerebral CORTEX ▸HOME

M. Steinschneider, Y. I. Fishman, and J. C. Arezzo

Spectrotemporal Analysis of Evoked and Induced Electroencephalographic Responses in Primary Auditory Cortex (A1) of the Awake Monkey

Cereb Cortex, March 1, 2008; 18(3): 610 - 625.

[Abstract] [Full Text] [PDF]

---

eLetters:

Read all eLetters

Stimulus-related synchronization,'visual binding' and signal-to-noise ratio in the

walter g. sannita

J. Neurosci. Online, 3 Apr 2007 [Full text]

Home | Search | Archive | Subscribe | Contact | Hel