STUDYING SINGLE-TRIALS OF PHASE SYNCHRONOUS ACTIVITY IN THE BRAIN

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This paper introduces a new method, single-trial phase locking statistics (S-PLS) to estimate phase locking in single trials of brain signals between two electrodes. The possibility of studying single trials removes an important limitation in the study of long-range synchrony in brain signals. S-PLS is closely related to our previous method, phase locking statistics (PLS) that estimates phase locking over a set of trials. The S-PLS method is described in detail and applied to human surface recordings during the task of face-recognition. We compare these results with those provided by PLS and show that they are qualitatively very similar, although S-PLS provides better discrimination of synchronic episodes.

1. Introduction: Brain Integration and Synchrony

Cognitive acts require the transient integration of numerous functional areas widely distributed over the brain and in constant interaction with each other [Varela, 1995; Friston, 1997; Tonini & Edelman, 1998]. It has become a topic of much interest to explore the possibility that such large-scale integration could be mediated by neuronal groups that oscillate in the gamma range (30–80 Hz, also referred to as “40 Hz”) that enter into precise phase locking over a limited period of time. (Hereinafter we refer to these phenomena simply as “synchrony” or “phase synchrony”.) Hence the importance for a reliable and robust method for directly measuring such phase synchrony in this frequency band for experimentally recorded biological signals, which are not spikes, but local field potentials (LFP) of various degrees of spatial resolution. In this paper we present two effective methods to estimate the instantaneous phase relationship between two neuroelectric or biomagnetic signals, and apply it to surface recordings in humans. We also introduce the required statistical means to test the validity of the measured synchrony against the background fluctuations in a given experimental situation.

The role of synchronization of neuronal discharges, although not a new idea, has been greatly highlighted by results from microelectrodes in animals (see e.g. [Singer & Gray, 1995]). In fact, two scales of phase synchrony can be distinguished: most animal studies based on microelectrode recordings have dealt with short-range synchronies (e.g. [Gray et al., 1989; Neuenschwander et al., 1996]), or between adjacent areas corresponding to a single sensory modality (e.g. [König et al., 1995]). These local synchronies have been interpreted most commonly as subserving “perceptual
binding". More recently, single-unit evidence for long-range synchronizations between widely separated brain regions has also been found [Roelfsema et al., 1997]. This is in agreement with the more general notion that phase synchrony should subserve, not just binding of sensory attributes, but the overall integration of all dimensions of a cognitive act including associative memory, emotional tone and motor planning [Damasio, 1990; Varela, 1995].

These single-unit recording studies in animals have been complemented by studies at coarser levels of resolution in humans and animals. In fact, gamma band responses can be recorded during visual discrimination protocols on the human scalp [Tallon-Baudry et al., 1997] and in subdural electrocorticograms [Le van Quyen et al., 1997; Lachaux et al., 2000]. One can distinguish an early (100 ms) stimulus-locked response to the stimulus or evoked response, and a later (200 ms) induced response, not locked to the stimulus. Both these responses necessarily imply a degree of local phase locking, since otherwise no signal would reach the surface of cortex or scalp with enough amplitude: they would annihilate due to the summation of phases being distributed broadly. Also, there is some recent evidence to suggest that not only emission, but also long-range synchronization comparable to those found in single-unit studies in animals can also be detected between surface recordings [Rodriguez et al., 1999]. In fact, one of the conclusions of the present study is that, like for gamma emission, gamma synchronization appears as an induced, not stimulus-locked phenomenon, and that cannot be studied using averages over trials, whence the importance of method to study signal-trials or events in the brain as presented here.

The quantification of phase synchrony between macroelectrodes (EEG/MEG or intracortical recordings) requires methods which are entirely different from the cross-correlograms between spike discharges suffice for microelectrode studies. In this context, it is very important to distinguish very clearly between synchrony (as defined above), and the classical measures of spectral covariance or coherence that have been extensively used in neuroscience (see e.g. [Bressler et al., 1993; Menon et al., 1996; Bullock & McClune, 1989]). As usually practiced, coherence has two important limitations for our purposes here:

1. First, the classical tools for measuring coherence [Carter, 1987] based on Fourier analysis are highly dependent on the stationarity of the measured signal, which is far from being the case in the brain. The estimation of coherence used here based on a smoothed wavelet transform, goes some ways in improving this limitation towards estimating a stable, instantaneous coherence (as well as synchrony) between two concurrent brain signals.

2. A second and very different limitation is that classical coherence is a measure of spectral covariance, and thus does not separate the effects of amplitude and phase in the interrelations between signals. Since we are interested in exploring the hypothesis that phase locking is the relevant biological mechanism of brain integration, coherence provides only an indirect measure. A direct test of the synchrony hypothesis requires tools where the phase component can be obtained separately from the amplitude component for a given frequency or frequency range. Only then can one proceed to test the synchrony hypothesis for brain integration, while still keeping instantaneous coherence as a first approximation, and this is the main novelty of our recent studies [Lachaux et al., 1999; Rodriguez et al., 1999]. In brief, coherence and synchrony provide convergent, but not identical results.

2. Measuring Synchronies in the Brain

Detecting phase locking between two distant brain recordings such as EEG, MEG, and intracortical recordings is not simple. This is due to several factors specially when working, beyond the single cell level, to neuronal populations from macroscopic electrodes. Neuronal populations in the brain manifests a high degree of diffusion, of spontaneous oscillations (giving spurious synchronies), and, in non-invasive signals the true synchronies are buried in a considerable background noise. This requires new, adapted methods to extract the true synchronies during a cognitive task.

2.1. Phase locking statistics: PLS

We have recently developed two complementory methods called Phase Locking Statistics (PLS) [Lachaux et al., 1999] and Single-trial Phase Locking Statistics (S-PLS). Both methods share the same basic procedure: exploiting a complex wavelet to
quantify the stability of the phase difference between two signals in a predefined frequency range. However S-PLS allows to measure the significance of synchronies in single trials, and does not depend on block repetitions of events.

The analysis is always done around a chosen frequency value (for instance 40 Hz); the choice is necessarily based on a previous detailed time-frequency analysis of the signals which we do not cover here [Lachaux et al., 2000]. Thus a frequency range is defined around this chosen value (e.g. 35–45 Hz), and the subsequent analysis is done on the frequency components of the signals in this frequency range. The procedure is usually iterated in other frequency ranges to cover the whole meaningful part of the spectrum (typically 1–80 Hz).

The first step common to both methods is to measure the instantaneous phase difference between signals around the frequency of interest. The phase of the signals is extracted from the coefficients of their wavelet transform at the target frequency. Specifically, let an electrode record a neural signal \( x(u) \). Then these wavelet coefficients as a function of time \( \tau \) and frequency \( f \) are defined as:

\[
W_x(\tau, f) = \int_{-\infty}^{+\infty} x(u) \cdot \Psi_{r,f}^*(u) du
\]  

(1)

Where \( \Psi_{r,f}^*(u) \) is the complex conjugate of the Morlet wavelet (or Gabor function) defined by frequency \( f \) and time \( \tau \) by:

\[
\Psi_{\tau,f}(u) = \sqrt{f} \cdot \exp(i \pi f(u - \tau)) \cdot \exp \left( -\frac{(u - \tau)^2}{2\sigma^2} \right)
\]  

(2)

where \( \Psi_{\tau,f}(u) \) is the product of a sinusoidal wave at frequency \( f \), with a Gaussian function centered at time \( \tau \), with a standard deviation \( \sigma \) proportional to the inverse of \( f \). It depends solely on \( \sigma \), which sets the number of cycles of the wavelet: \( n_{co} = 6f \sigma \). This value \( n_{co} \) determines the frequency resolution of the analysis by setting the width of the frequency interval for which the phase is measured. This width is roughly equal to \( 4f/n_{co} \) so that the frequency range under study corresponds approximately to

\[
\left[ f_{\text{target}} - \frac{4f}{n_{co}}, f_{\text{target}} + \frac{4f}{n_{co}} \right]
\]

For instance at 40 Hz this corresponds to [20, 60] Hz, with \( n_{co} = 8 \). In most of our studies, we chose \( n_{co} \) between 3 and 8.

Now, as a second step, the phase difference between the signals at frequency \( f \) and time \( \tau \) can be derived from the angles of their wavelet-coefficients.

\[
\exp(j(\phi_y(f, \tau) - \phi_x(f, \tau))) = \frac{W_x(\tau, f)W_y^*(\tau, f)}{|W_x(\tau, f)W_y(\tau, f)|}
\]  

(3)

Both PLS and S-PLS evaluate the variability of this phase difference across successive measurements. Both PLS and S-PLS evaluate the statistical variability of this phase difference. However PLS is designed to detect stability of phase across the trials, while S-PLS detects stability within each trial. We first developed PLS to estimate phase locking in experimental situations, common in neurocognitive studies, where a subject is presented with a sequence of similar stimuli. For instance, in the experimental study described here (see below), one presents 100 complex figures separated by a variable inter-stimulus interval of \( 1 \pm s \), and the subject has to decide for each of them, whether they contain a face or not. PLS measures for every time point following stimulation at fixed latencies (for instance 100 ms after the presentation of each stimulus). The stability of the phase differences across the trials is quantified by a phase locking value (PLV):

\[
\text{PLV}(f, t) = \left| \frac{1}{N_{\text{trial}}} \sum_{\text{trial}=1}^{N_{\text{trial}}} \exp(j(\phi_y, \text{trial}(f, \tau) - \phi_x, \text{trial}(f, \tau))) \right|
\]  

(4)

where \( N_{\text{trial}} \) is the total number of trials. PLV is a normalized index, with perfect phase synchrony corresponding to the value of 1.

As a third and final step, the degree of statistical significance of each phase locking values is determined by comparing it to values obtained between shifted-trials. These surrogate values are computed from the same signals \( x \) and \( y \), using (4), but after permuting the order of all trials for \( y \), in such a way that the phase differences are no longer computed between signals recorded during the same trial, but during different trials

\[
\text{PLV}_{\text{surrogate}}(f, t) = \frac{1}{K} \sum_{j=1}^{K} \left| \frac{1}{N_{\text{trial}}} \sum_{\text{trial}=1}^{N_{\text{trial}}} \exp(j(\phi_y, \text{perm}_{j}(\text{trial})(f, \tau) - \phi_x, \text{trial}(f, \tau))) \right|
\]  

(5)
We typically create 200 surrogate functions PLV(\(f, t\)) from \(K = 200\) different permutations and measure for each of them their maximum. These 200 values are used to estimate the significance of PLV between original signals \(x\) and \(y\). The proportion of surrogate values greater than the original PLV (between \(x\) and \(y\)) for a time \(t\), is called Phase Locking Statistics (PLS). In most cases, we used a criterion of 5\% (PLS < 5\%) to characterize significant synchrony.

2.2. Single-trial phase locking statistics: S-PLS

Here we introduce a variant of PLS, S-PLS, in order to estimate phase locking in single-trials, at a slight cost of temporal resolution. In this second method, the variability of phase difference is not measured across trials, but across successive time-steps, around a target latency. Specifically, a smoothed or single-trial Phase Locking Value (S-PLV) is defined for each individual trial as

\[
S-\text{PLV}(f, t) = \left| \frac{1}{\delta} \left[ \exp(j(\phi_y(f, \tau) - \phi_x(f, \tau))) d\tau \right] \right|
\]

As for PLV, S-PLV ranges from 0 to 1 with 1 indicating the strongest phase locking. The significance of each S-PLV is estimated via a comparison with a distribution of S-PLV obtained between independent white-noise signals (200 pairs) with the same duration as the generation of the original signals. For each of them, the maximum S-PLV is measured to build a distribution of 200 values. The proportion of surrogate values higher than the original S-PLV (between \(x\) and \(y\)) for a time \(t\) is correspondingly called Single-trial Phase Locking Statistics (S-PLS).

S-PLS depends on two parameters then: \(n_{co}\) and the size of the window of temporal integration, which can be expressed in a number of cycles at a chosen frequency \(f\): \(n_{cy} = f \cdot \delta\). In this sense, \(n_{cy}\) determines the temporal resolution of the analysis where the synchrony estimation remains stable. Small values of \(n_{cy}\) provide better temporal resolution, and ultimately, S-PLS can match the resolution of PLS with an integration window reduced to 1 point, but at the cost of statistical resolution because compared to long-lasting episodes, short-lasting episodes of phase locking are more likely to arise by chance alone. We usually chose \(n_{cy}\) between 6 and 10.

![Figure 1](image_url)

Fig. 1. Synchrony between a representative pair of a single-trials between two surface electrodes, recorded during a perceptual experiment (see below). Significance level for S-PLS is indicated. Below: the corresponding wavelet used in the analysis. Notice the amazing degree of overlap between the two traces during a brief time.
An example of the transient synchrony between a pair of surface electrodes in humans during a single trial of a perceptual experiment (see Results below) is shown in Fig. 1 as a clear illustration of what S-PLS can provide.

2.3. Coherence and synchrony

S-PLS can be slightly modified to measure the coherence between two brain signals as a function of time, i.e. the correlation between the spectral components of the signal at a target frequency. Single-trial wavelet-based coherence, or S-WCS, is different from S-PLS because it not only measures the covariance of the phase between two signals, but also of the correlation between their respective amplitude waveforms. As we shall see below, however, it is an important complementary measurement for the types of neural events that concerns us. We insist that the distinction between coherence and synchrony proper is rarely done; in most reports in neuroscience, spectral coherence is taken to be equivalent to a measure of synchrony. In fact, coherence corresponds only to a first approximation of the synchrony between two signals at a given frequency. For instance, a concurrent but independent increase in amplitude (no phase locking) will also lead to an increase in S-WCS but not in S-PLS.

The wavelet-coherence $WCo(t, f)$ is defined at time $t$ and frequency $f$ by:

$$WCo(t, f) = \frac{|SW_{xy}(t, f)|}{|SW_{xx}(t, f) \cdot SW_{yy}(t, f)|^{1/2}}$$

where $SW_{xy}(t, f)$ is the wavelet cross spectrum between these signals, computed from their wavelet transform coefficients

$$SW_{xy}(t, f) = \int_{t-\delta/2}^{t+\delta/2} W_x(\tau, f) \cdot W^*_y(\tau, f) \, d\tau$$

The statistical significance of wavelet-coherence is estimated using a procedure identical to the one previously described for S-PLS.

3. Results from Surface Recordings during Visual Perception

3.1. Long-range synchronies track visual perception

These methods have allowed us to show, for the first time in humans, that the perception of meaningful complex forms is accompanied by synchronous activities recorded over distinct brain regions [Rodriguez et al., 1999]. In this study, EEG was recorded by 30 electrodes at the scalp surface. Ten subjects were shown upright and as upside-down Mooney figures (high-contrast outlines of famous faces), and a decision was to be made as rapidly as possible whether a face could be perceived or not, at first glance, by a two-choice button press. Mooney figures are made of two-tone asymmetrically lighted photographs of faces. They are easily perceived ($79 \pm 2\%$) as faces when presented upright, despite the necessary perceptual binding and contour reconstruction. By contrast, upside-down Mooneys are usually perceived ($76 \pm 2\%$) as meaningless black and white forms.

The pattern of phase synchrony via PLS in the gamma band showed marked quantitative and qualitative differences between the "perception" and "no perception" conditions. Indeed, very few synchronous patterns were observed under the no perception condition, whereas the synchronous pattern under the perception condition yielded a structured spatial and temporal dynamics. In Fig. 2, we show a chart of the level of synchrony over time and frequencies when pooling together all electrodes and subjects, in a grand ensemble for both perceptual conditions. As clearly visible, between 200–260 ms, a first period of significant synchronization was observed. It involved left parieto-occipital and fronto-temporal regions and may be related to the perception process itself. It was followed by a massive period of phase-scattering peaking around 500 ms. In fact, it can be said that this phase-scattering is the most massive effect we found (Fig. 2). Finally, at the time of the motor response, a new and different synchronous episode appeared.

The first synchrony phase was observed between parietal and occipito-temporal leads bilaterally. Parietal regions are known to be involved in perceptual coherence [Dolan et al., 1997; Friedman et al., 1995] and episodic memory [Shallice, 1994]. Interactions between these regions and temporal regions, in particular the ventral fusiform gyrus, have been related to the perceptual learning of degraded Mooney-like faces [Dolan et al., 1997]. Thus our results support that phase interactions between parietal and temporal regions underlie perceptual binding processes necessary to the perception of upright Mooneys as faces as well as processes related to episodic memory formation.
Fig. 2. Activity and phase synchrony through all frequencies in the Mooney face recognition experiment [Rodriguez et al., 1999]. Upper panels represent the “perception” condition, while lower panels depict “nonperception” condition. Left panels are time-frequency charts of spectral power emission and right panels show phase synchrony. All the charts are grand average results through all electrodes and subjects. Vertical axis is frequency in Hertz, horizontal axis is time in milliseconds, with zero indicating stimulus onset. The color scale represents either power (for left panels) or phase synchrony (for right panels) in a normalized scale (Z-score). On the left panels we can see that emission shows a similar time frequency pattern between condition (upper versus lower panels) except for the power level at 300 ms. On the right panels we observe a massive phase-scattering effect induced by stimulation for both conditions, and an early synchronization effect present for the perception condition only (upper panel). Also on both conditions a final synchronic period is present coinciding with the motor response.

Note that such a stage of active phase-scattering has never been reported before, but it appeared as a massive effect in our results. In agreement with previous proposals [Varela, 1995], it suggests that an active uncoupling procedure may be necessary for the transition between different synchronous neural assemblies. Indeed, it was followed by a period of synchronization between central and right temporal regions. This final period coincided with the subject’s button press and may thus be related to the motor response elaboration under both conditions. This is the only period of time where some similarity between the phase synchrony patterns under the two conditions was noted.

By contrast, gamma emission power studied in the same frequency band was found to be distributed rather homogeneously over the scalp, with no qualitative difference between the “perception” and “no perception” conditions. The gamma emission was observed to be higher for the “perception” than the “no perception” condition around 230 ms poststimulus onset only. Such a peak of gamma activity has already been reported and is generally described as a correlate of the perceptual process per se.

In conclusion, only the phase synchrony pattern analysis yields qualitative differences between the “perception” and “no perception” conditions. Moreover, such an analysis is necessary to test for the hypothesis of the role of gamma activities in cognitive integration. Indeed, only the kind of measures used here can reveal interactions between different activated brain regions. Our results provide evidence for the existence of long-distance phase synchrony during a cognitive task, and support its role in large-scale cognitive integration processes and complex cognitive acts.

3.2. PLS and S-PLS give comparable results

The above results are the first of the published works on large-scale synchrony in the brain
It is therefore of utmost interest to confirm these results by means of another method. In this section, we compare the same data as analyzed by the S-PLS method. Although both methods share a common starting point, the important differences between the two calculations have been highlighted above. Thus, both approaches can be pitched against each other for confirmation.

In Fig. 3, we present the grand average values of phase synchrony (through all trials and electrode pairs) for one representative subject as computed by PLS and S-PLS methods. The similarity between both indicators is clear during the entire time span. However, S-PLS detects better the important synchronic period situated around 300 ms after stimulation onset. Both are equally good to detect the synchronization period around 800 ms corresponding to the motor response. Finally, the phase-scattering period around 500 ms is more pronounced in the PLS curve but also present in S-PLS. These results strongly suggest, then, that both methods yield comparable estimators of the synchrony process, and confirms that, in spite of a relatively low signal/noise ratio, noninvasive recordings can capture the dynamics of synchrony.

Due to the smoothing involved in single trial analysis, S-PLS allows for a further estimation of phase synchrony as the threshold cumulative histogram of significant individual synchronic events. Significant synchronic bins are added up through trials so that the resulting curve does not represent a mean of synchrony, but rather the bias in the probability of occurrence of synchronic events. In Fig. 3(b) we compare S-PLS against its histogram computed for $p < 0.01$.

Both curves are almost identical during the post stimulus period, but during the pre-stimulation period, the histogram is able to eliminate a spurious variation present in the raw S-PLS values. This is important because it points directly at the important noise limitation for the measure of synchrony on surface recordings. Noise can appear from two sources: (1) it can be due to diffusion of brain activity to the reference electrode thus contaminating the entire data set, or (2) it can be due to transient muscular artifacts not removed during acquisition which are of such amplitude as to affect the averages. In fact, such background noise can be seen in the prestimulation period in this individual with a level of synchrony that is comparable to the poststimulus response. However, one can differentiate between noisy, background synchrony and true

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Fig. 3. Comparing phase synchrony measurements according to the methods discussed here: PLS, S-PLS, as well as a cumulative histogram for S-PLS. The curves show ensemble averages (through all trials and electrode pairs) of synchrony for one subject involved in the visual perception experiments described in the text. Horizontal axis is time in milliseconds, zero stands for stimulation time. Vertical axis is phase synchrony in a normalized scale (Z-score). (a) PLS versus S-PLS. The temporal behavior of both estimators (PLS and S-PLS) is quite similar, but note that S-PLS is better in detecting a synchronic period near 300 ms. (b) S-PLS versus a histogram computed with the significant synchronic events detected by S-PLS through the trials ($p < 0.01$). Each synchronic event is given a value “one” if significant and “zero” if not. Thus the histogram represents not an average value of synchrony, but a bias in the probability that a synchronic event occurs. Comparing both estimators, one can see that the histogram eliminates the strong but spurious fluctuation present during the prestimulation period. The poststimulation period remains almost identical between both estimators.
Fig. 4. Variability of synchrony and coherence across trials for a single pair electrodes (FC2 and PO10). (a) Upper plots show, in black bars, the results of episodes of significant ($p < 0.001$) (left panel) synchrony and (right panel) coherence between the selected pair of electrodes for 120 trials in one block (perception of Mooney faces), and for one subject. Synchrony was detected by S-PLS and coherence by wavelet-coherence; all values were computed around a target frequency of 40 Hz, with $n_{co} = 4$ and $n_{cy} = 8$. (b) Mean values (percent of significant events) of S-PLS and wavelet-coherence across all 120 trials. (c) Distribution of the durations of significant synchrony and coherence episodes across all the trials.
synchrony by the fact that only the latter is correlative to the stimulation, while the prestimulation disappears in the cumulative histogram, as expected.

We can also take a closer view of these results by not averaging the pairs of electrodes, but considering their regional distribution. This allows us to see which individual electrode pairs exhibit synchrony effects [Rodriguez et al., 1999]. Although the results are not shown here, we confirm our previous findings that only a few selected electrodes are contributing to the general effect of synchronization or desynchronization. Furthermore, here again the histogram of S-PLS seems to eliminate the prestimulus variation present in both PLS and S-PLS while enhancing poststimulus differences in the already active electrode pairs.

In brief, on this exemplary data set, the histogram of S-PLS seems to be the most precise method for evaluating phase synchrony. On the other hand S-PLS is slower than PLS. The fact that for grand average data both PLS and S-PLS methods yield comparable results suggests the utilization of PLS for prospective multifrequency exploration and, once the good frequency bands have been identified, the use of S-PLS for finer analysis.

### 3.3. Dissecting a series of trials into individual synchronies

We are now in the position of taking our analysis of synchronies for Mooney responses one step further into their detailed constitution. We have compared in this analysis the complementary nature of the synchrony and coherence analysis, using S-PLS and S-WCS (that is phase locking or wavelet-coherence statistics). In Fig. 4 we computed these values for one subject, for each individual trial in the perception condition. We chose the same parameters for both methods: the target frequency was 40 Hz and \( n_c \) was set to 4, in order to study frequencies ranging form 20 to 60 Hz; \( n_{cy} \) was set to 8 to guarantee a fair trade-off between temporal resolution and statistical power. Figure 4, in contrast, presents all trials keeping only the significant episodes with a black bar.

A comparison of the results of these two methods shows that wavelet-coherence detects more significant episodes than S-PLS, although raw values of coherence and phase locking, before the statistical analysis, were comparable (results not shown). The difference is due to the fact that significant phase locking is harder to distinguish from background fluctuations than significant coherence. In fact, spurious high coherence values arise between two independent signals only when by chance both phases or amplitudes are correlated, while spurious high phase locking values need just correlation between phases. Phase locking values between two independent signals are thus typically higher than coherence values, and rejecting the null-hypothesis that two signals are independent on the basis of phase locking is correspondingly more difficult. This representative example indicates clearly that a degree of significant synchrony is a rare event when detected over the scalp, and superposition over several subjects is, in general, necessary. In this particular case, we see no direct evidence for synchrony during perceptual recognition, but coherence does complement this analysis by given indirect evidence that the two recordings are indeed interdependent. This illustrates well the complementary nature of both indicators as handled through our methods.

This study of individual trials illustrates an important feature of synchrony and coherence, previously unnoticed: their time-course varies greatly from trial to trial [Fig. 4(a)]. Episodes of significant synchrony and coherence are present both before and after the stimulation, and they appear at latencies that vary considerably between trials. Further analysis will be needed, in order to track the variable delays relative to stimulation, and, correspondingly, to characterize the prestimulation period as being more or less prone to a synchronous arising. This means that short spontaneous phase coupling episodes emerge all the time, with a life-span range rarely exceeding 200 ms [Fig. 4(c)].

In brief, the presentation of the visual stimulation is not followed by systematic, fixed synchrony patterns, but rather it creates a bias in the distribution of the phase locking episodes that can be detected here when averaging across the trials. It is reassuring that the mean wavelet-coherence, averaged across trials, follows a time-course similar to the phase synchrony [Rodriguez et al., 1999]. It reaches a peak around 250 ms, followed by a sharp decrease around 500 ms and a second rise around 700 ms, about the reaction time. This constitutes yet a third validation of our initial results.

### 4. Conclusions

We conclude that these observations are convincing evidence that significant long-range synchronies
are established during this cognitive task involving parietal and frontal regions. These synchronies cannot be explained by volume-conduction; it seems more likely they represent a partial correlate of the functional integration mechanism during the perceptual process. The present results, along with previous reports (e.g. [Bressler et al., 1993; Desmedt & Tomberg, 1994; Friston et al., 1997; Roelfsema et al., 1997; Rodriguez et al., 1999]) strongly support the view that gamma synchrony acts as distributed unifying mechanism in human cognitive activity.

It should be mentioned here that in parallel to our approach to synchrony measurement, Tass et al. [1998] introduced an alternative method for estimating phase locking between bivariate data based on the Hilbert transform. This method has several advantages such as being well defined for variable frequency bands and in including synchronies of several multiple ratios. A benchmark comparison between these two approaches would be highly desirable.

The possibility of studying single trials removes an important limitation of the study of synchrony between brain signals. In fact, synchrony is a highly variable process both in amplitude and in delays. In consequence, focusing on the detection of phase locking between pair recordings across trials: i.e. the likelihood that phase difference between the oscillations of two neural populations remains the same from trial to trial for a given delay in time is only a first approximation. This procedure excludes those synchronies that are not established with a fixed delay from trial to trial. In order to extract such information one needs, as S-PLS does, to work on the basis of single trials, not averages. As mentioned in the Introduction, an analogy from the study of gamma band emission can be helpful here. PLS can be compared to the procedures that detect the evoked gamma emission, but fail to detect the induced responses. In fact, induced responses are not stimulus locked and thus requires a trial by trial analysis to construct a probability distribution [Tallon-Baudry et al., 1997; Lachaux et al., 2000]. Similarly, the present results show that long-range synchrony is an induced type phenomenon, and only single-trial analysis can provide further understanding.

References


