On the Detection and Measurement of Synchrony in Neural Populations by Coherence Analysis

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Christakos, Constantinos N. On the detection and measurement of synchrony in large neural populations by coherence analysis. J. Neurophysiol. 78: 3453–3459, 1997. This study considers the possibility of using coherence analysis for detection and measurement of synchrony (correlations) in large neural populations, applied to activities that are relatively easy to record in parallel. Mathematical analysis and computer simulations are used to examine the behavior of the coherence function between both unitary and population-aggregate activity (UTA coherence) and the aggregate activities of two populations (ATA coherence). The results indicate that for a large population showing partial correlations, the UTA coherence function is almost zero at all frequencies for the uncorrelated units. However, unless the synchrony is very restricted, its value is nonzero (i.e., statistically significant by common criteria) at each frequency of synchrony for the units that show correlations to other units. Moreover, this value is indicative of the strength of synchrony for any given unit. These properties enable the identification of the correlated units in a sample of unit/population activities simultaneously recorded in a series of experiments, and hence the detection of synchrony. The extent of synchrony can then be estimated as the fraction of such units in the sample, whereas the values of the UTA coherences in the sample can be used to estimate the strength and its distribution within the population. Similarly, the ATA coherence function is generally nonzero (significant) at the frequencies where there are correlations between members of two large populations. This enables the easy detection of such correlations from simultaneously recorded population activities. However, this function is a very sensitive index of synchrony and even shows saturation effects. It may therefore be used as a general measure of synchrony only under restricted conditions.

INTRODUCTION

The detection of synchrony (unitary correlations) within, or between, neural populations and the estimation of its extent and strength are important tasks in the study of many neural systems. However they present great difficulties when performed with traditional unit-to-unit (UTU) correlation analysis (Perkel et al. 1967), particularly if the populations are large in numerical size. The main difficulties relate to the simultaneous and independent recording of a large number of pairs of unitary activities, as required, and the appropriate and economical representation of the results of such analysis (which are originally in the form of a large number of cross-correlograms) for the quantification of synchrony. However, there is a more recent technique that deals with the latter difficulty (Gerstein and Aertsen 1985).

A different approach for analysis of population synchrony has been suggested by the results of a recent study (Christakos 1994; also see the appendix in Christakos et al. 1991). This approach uses as a tool the coherence function between unitary and population-aggregate activity (UTA coherence). In the following, the term aggregate activity represents the sum of the individual units’ activities in the population, such as the electrical activity recorded from a nerve.

On the basis of theoretical considerations and computer simulations of a uniform population, that study revealed a dual property of the UTA coherence function. Unless the population is small in numerical size (up to a few tens of units), this function is almost zero at all frequencies for the uncorrelated units. However, it is nonzero at the frequencies where there is synchrony for the units that are correlated to other units. As the results indicated, the value of this nonzero coherence at each frequency reflects the three features of synchrony: 1) its extent, i.e., the proportion of correlated units in the population; 2) its strength, i.e., the strength of the unitary correlations; and 3) the degree of similarity of the phases of the correlated units. The value of the UTA coherence also reflects the numerical size of the population, i.e., a parameter that is not related to synchrony. Finally, this coherence stays substantial within very wide ranges of values of these four parameters.

The properties of the UTA coherence function, as revealed by the simulations, suggested using this function as a tool for 1) identifying the correlated units in a sample of unit/population activities recorded in parallel in a series of experiments, and thus detecting population synchrony and estimating its extent; and 2) obtaining information on the strengths of the unitary correlations.

Subsequent mathematical analysis confirmed the results of the simulations and also furnished detailed predictions on the behavior of this function as a tool for detection and quantification of population synchrony. In addition, this analysis was extended to the behavior of the coherence function between the activities of two (sub)populations, i.e., of the aggregate-to-aggregate (ATA) coherence function. ATA coherence computations have often been used in certain areas of Neurophysiology (e.g., the EEG area) as a simple means of assessing population synchrony. However, detailed studies of the behavior and dependencies of this function were lacking. In other words, essential information for the correct interpretation of coherence estimates was not available.

In the case of large populations (several hundred or more), the results of the mathematical analysis are simple and compact. A summary of these results is presented below,
together with an evaluation of the UTA and the ATA coherence approach for the study of synchrony in large neural populations. These findings have previously been reported in abstracts (Christakos 1995a,b). A general account, which did not include the present results for large populations, was presented in a book chapter (Christakos 1996).
number of the units (400 in this case). It should be noted strictly in extent and strength (extent
activities becomes available, particularly when the latter is a small fraction of one. More
only correlated with its own contribution to the aggregate introduced in METHODS (coherence estimate
has been shown (see Christakos 1994) that at frequencies ous traces in all plots).

The simulations showed such properties of the UTA coherence at any frequency of synchrony (20 Hz) and low coherences at other frequencies. Also note that peak UTA coherence is almost twice as large as the peak UTU coherence.

The mathematical result in APPENDIX A enables the sys-
tematic and efficient study of the value of the UTA coherence at any frequency of synchrony, and hence the determination of these conditions. In agreement with the results of the simulations (see Christakos 1994), the following parameters appear in the analytic expression of Eq. A4 for the UTA coherence: the UTU coherence, \( Q^2(\omega) \), representing the strength of synchrony in the uniform population; the number of correlated units, \( n_c \), and the total number of units in the population, \( n \), or equivalently, the extent of synchrony (\( n_c/n \)) and the numerical size of the population; and the three sums of cosines, \( 2A, 2B_1, \) and \( 2C_1 \), representing the influence of the units’ phases. The values of the various parameters can now be systematically varied and substituted in Eq. A4 to examine the properties of the UTA coherence function.

Note that because of the random character of the phases, the three sums of cosines in Eq. A4 are random variables. Therefore the UTA coherence is a function of three random variables. To simplify its study, sets of pseudorandom units’ delays are generated on the computer for a large number (50 to 200) of different seeds and the statistical moments (mean and standard deviation) of the UTA coherence are estimated under various conditions.

The examples of such computations in Fig. 2 show the following typical properties of the UTA coherence at any given frequency of synchrony, \( F \), for large populations and Gaussian units’ phases.

1) Its value reflects all three features of synchrony and also the numerical size of the population (compare the various traces in all plots).

2) This value is statistically significant by the criterion introduced in METHODS (coherence estimate > 0.05 or even 0.1), except possibly when both the synchrony is very restricted in extent and strength (extent < 20%, UTU coherence < 0.20) and the units’ phases are distributed over an entire cycle at 2\( \pi F \). For example, in Fig. 2B, for extent = 10%, the UTA coherence may with some probability be <0.05 only when the UTU coherence is as low as 0.1 and when the phases are distributed over an entire cycle.

3) The effects of the phases on this value are weak, except when the extent is very restricted, and those of the extent are also weak, except when the phases show a very limited similarity (cf. Fig. 2, B and C). In fact, the analysis revealed that for synchrony whose extent is not very restricted (>20% for 2,000 units, >25% for 1,000 units, or >30% for 500 units) and for a phase distribution that is not very broad (covering up to 75% of a cycle at 2\( \pi F \) for a population size of \( \approx1,000 \) or 50% of a cycle for a population size of 500), the UTA coherence is already close to a limiting value. This value is the square root of the UTU coherence, as can be seen in all traces of Fig. 2C and the top three traces of Fig. 2A. Indeed, under such conditions, \( n_c \) is large and the sums \( 2C_1 \) and \( 2A \) are very large and comparable. Thus the terms \( 2C_1Q^2(\omega) \) and \( 2AQ(\omega) \) dominate, respectively, the numerator and the denominator of the expression in Eq. A4 and hence the UTA coherence is \( \sim Q(\omega) \).

Note that under the limiting conditions for the UTA coherence, this coherence only reflects the UTU coherence in a simple way. In addition it is higher than the UTU coherence, particularly when the latter is a small fraction of one. More generally, according to the results, the UTA coherence is
FIG. 2. Examples of estimated UTA coherence (mean ± SD) at the frequency of synchrony for the correlated subset, as a function of UTU coherence at same frequency. The 3 plots represent different combinations of extent of synchrony and numerical size of population. A: extent 50%, size 400. B: extent 10%, size 2,000. C: extent 50%, size 2,000. Different curves in each plot correspond to different delays’ ranges (i.e., ranges of units’ phases), as indicated at top. Note that unless both extent is very restricted, and the delays’ range is very broad, the UTA coherence is well above 0.05, and the various traces converge toward the trace that represents square root of UTU coherence.

higher than, or at least comparable with the UTU coherence, except when both the extent of synchrony and the phase similarity for the units are very restricted (e.g., Fig. 2). These are all useful properties with respect to the detection and quantification of synchrony (see DISCUSSION).

Computations for uniformly distributed units’ phases showed the same properties for this function as above, although within slightly narrower ranges of values for the four parameters. Note, however, that the present assumption of Gaussian phases is more realistic, in general.

ATA coherence between two uniform (sub)populations

As Eq. B3 shows, the parameters that influence the value of the ATA coherence are similar to those for the UTA coherence, namely the extent and strength of the synchrony between the two populations, the degree of similarity of the units’ phases in each population, and the numerical size of the populations.

The effects of these parameters are again easily studied with computer-generated sets of units’ delays for different seeds. The examples of such computations in Fig. 3 show the following typical features of the ATA coherence at any given frequency of synchrony, $F$, for large populations and Gaussian units’ phases.

1) Its value reflects the three features of the synchrony between the populations and also the numerical size of the populations (compare the various traces in all plots).

2) This value is generally significant by the 0.05 (or even the 0.1) criterion, except possibly when the synchrony is very restricted in extent and strength, and the units’ phases are distributed over almost a cycle at $2\pi F$ (see Fig. 3, except the bottom trace of Fig. 3B).

3) The effects of any of the above parameters on this value are weak, except when one or more of the other parameters have very small values (cf. Fig. 3, B and C). In fact, the analysis showed that for extent $>30\%$, UTU coherence $>0.3$, and a phase distribution that is not very broad (covering up to 75% of a cycle at $2\pi F$ for a population size of $\approx 1,000$ or 50% of a cycle for a population size of 500), the ATA coherence is already close to a limiting value of one. Indeed, under such conditions, $n_i$ is large and therefore the sums $2A_i$ and $2A_y$ are very large and comparable. They also dominate the terms in the numerator and the denominator of Eq. B3. Thus the ATA coherence is near one. Figure 3, A (top 3 traces) and C, shows this saturation effect, where the ATA coherence changes only slightly, staying near one, as the UTU coherence increases beyond $\sim 0.3$. They also make clear that the ATA coherence can be very high, even for a restricted synchrony (e.g., for extent $= 50\%$ and $Q^2 = 0.3$, its value is $\sim 0.9$).

Computations for uniformly distributed units’ phases showed the same properties as above, but again within a slightly narrower range of conditions.

DISCUSSION

According to the present results, in the case of a large uniform population, the UTA coherence is statistically significant at each frequency of synchrony for the correlated units, except, possibly, when both the synchrony is very restricted and the distribution of the units phases covers almost an entire cycle at the frequency of synchrony. In contrast, this coherence is nearly zero for the uncorrelated units in any situation. This dual property provides a criterion for identifying the correlated units in a sample of unit/population activities recorded in parallel in a series of experiments and hence for detecting synchrony. Note that even a single occurrence of a significant such coherence in the sample indicates the presence of a correlated subset to which the given unit belongs.

Information on the extent and strength of synchrony can be obtained from such a sample as follows. Generally, the value of any UTA coherence is indicative of the strength of
the correlations of the respective unit to the other members of the correlated subset. The reason for this is that the combination of the phases and the size of the population are common to all units (see Christakos 1994). Therefore a histogram constructed from the significant coherences in the sample contains information on the strength of synchrony and its distribution within the population.

For unitary correlations that have similar strengths, as was assumed in the preceding mathematical analysis, the histogram will be highly concentrated around the average coherence in the sample. The results of the analysis are then directly applicable to the situation. The extent of synchrony can be estimated as the fraction of significant UTA coherences in the sample. Clearly, the estimate is reliable, as long as the coherences in the histogram are not borderline significant. Otherwise, there may be inaccuracies in both directions. Note however that because the UTA coherence is in most cases higher than the UTU coherence, larger inaccuracies are expected if UTU coherence analysis is to be used instead. Furthermore, if the estimated extent exceeds 20–30%, then the average UTA coherence in the sample will be (at least) close to the square root of the common UTU coherence in the nearly uniform population (see results) and can be used for direct estimation of the latter. If the extent is small, the average UTA coherence can still serve as a general index of synchrony.

For unitary correlations that have unequal strengths, the UTA coherence will generally differ between units. However, the results of the mathematical analysis still apply in an average sense, as explained below. There are two particular issues in this case. First, there may be units in the correlated subset and the sample, whose correlations to other units are too weak to result in significant UTA coherences. This may therefore cause an underestimation of the extent of synchrony. Second, the strength of synchrony in the correlated subset has to be defined in terms of some average measure, such as the mean UTU coherence for this subset. Consequently, the UTA coherences will have to be related, if possible, to that measure.

This case of grossly different correlation strengths in large populations is presently under study. However, the results of simulations reveal analogous properties and relationships to those for the uniform population. A general observation for Gaussian-distributed correlation strengths is that unless the extent of synchrony and the phase similarity for the correlated units are very restricted, the UTA coherence is statistically significant even for units whose mean UTU coherence to the other correlated units is marginally significant. Thus a criterion similar to that for the uniform population can be used for identification of correlated units. A second observation, under the same conditions, is that the UTA coherence for any unit that lies at (or near) the center of the distribution is close to the square root of the common UTU coherence of this unit to the other correlated units. But the mean UTU coherence for such an average unit is a measure of the strength of synchrony in the correlated subset itself (it is equivalent to the mean UTU coherence between all members of this subset). Thus, with respect to the strength of synchrony, these average units have a UTA coherence that behaves like the one for the units of the uniform population.

Therefore, in the case of a broad histogram, which will be indicative of large differences in correlation strength between units, the steps are as before. The extent can be estimated as the fraction of significant UTA coherences in the sample. An error (underestimation) may occur, but this will be because of units whose UTU coherences to other units are not significant anyway. Furthermore, if the estimated extent exceeds 20–30%, then the average UTA coherence in the sample can again be squared to yield an estimate of the coherence that represents the strength of synchrony in the correlated subset.

Size differences between unitary contributions to the aggregate activity (such as the amplitudes of extracellularly recorded spikes) have not been considered in this study. The
reason is that the value of the UTA coherence for any member of the correlated subset only reflects the strength of the correlation of the given unit to the aggregate activity of this subset and also the magnitude of the latter activity, in comparison with that for the uncorrelated subset, which acts like noise (see Christakos 1994). Therefore this value is independent of the size of a unit, as was also verified by computer simulations.

Finally, the present approach for analysis of population synchrony has been developed on the assumption that none of the features of synchrony is known in advance. However, in specific situations, known constraints may exist regarding the distribution of the units’ phases (delays), which can facilitate the analysis. For example, if the frequency of synchrony is 10 Hz, then the distribution of the phases is narrow enough for the properties of the UTA coherence to hold (significance, square root relationship), as long as the range of delays does not exceed 75 ms width. This condition is obviously satisfied in the case of various neural populations.

Overall, considering the difficulty of the task, the proposed approach seems simple, as it uses two signals that are readily recorded simultaneously and its results are in a compact form. It also seems efficient, because it provides more information from much fewer recordings of single units’ activities, as compared with UTA correlation (coherence) analysis. Lastly, the proposed approach seems relatively reliable, because in most situations it can detect the synchrony for units whose correlations to other units are too weak to be detected as significant UTA coherence values. Finally, note that this approach is particularly suited for the study of synchrony of rhythmic activities. This applies especially to multiple rhythms, as the effects of such rhythms cannot be easily disentangled in a cross-correlogram.

Coherence computations between unitary and population activities have been performed in a number of earlier studies, to demonstrate the existence of correlations between the two types of activity (see e.g., Elble and Randall 1976; Elul 1972). Certain principles of the described approach have been used in the study of correlations of dual fast rhythms in inspiratory activities (Christakos et al. 1991, 1994; Huang et al. 1996), dual fast sympathetic rhythms (Cohen et al. 1992), and motor unit activities during sinusoidal muscle contractions (Iyer et al. 1994).

Turning to the ATA coherence, the present results indicate that this function is very sensitive in reflecting synchrony between large populations and that it has significant values in almost all situations. It can therefore be used for easy detection of such synchrony, especially because it uses activities that are very easy to record in parallel.

With respect to the measurement of population synchrony, it is clear that in the general index provided by ATA coherence analysis at each frequency (see Bullock and McLune 1989), the combined effects of the three features of synchrony are lumped together with that of the population’s numerical size. According to the present results, such an index could therefore serve as a general measure of synchrony, for a given population’s size. However, a necessary condition for this is that the index stays outside the range of saturation, which is the case only when synchrony is restricted in extent and/or strength and the unit’s phases are broadly distributed.

Note that because of the high sensitivity of the ATA coherence in reflecting synchrony, this analysis can still give the misleading impression of a widespread and strong synchrony, in cases where the incidence and strengths of the unitary correlations are restricted. Moreover, size differences between units may cause additional complications in interpreting ATA coherence estimates (see Discussion in Christakos 1994). For all of the above reasons, this index of synchrony should be used with great caution.

In the previously mentioned studies of inspiratory rhythms, ATA (nerve-nerve) coherences have also been computed. In agreement with the present results, these coherences often gave an exaggerated picture of synchrony (see e.g., the nerve-nerve coherences for the medium-frequency oscillations in Christakos et al. 1994, Fig. 2).

Finally, the behavior of the ATA coherence in the case of nonuniform unitary correlations is presently under study.

APPENDIX A

Consider a uniform set \{x\} of \(n\) unitary processes in which a subset of the \(x_i\) is linearly correlated (\(i = 1, 2, \ldots, n\)) and the remaining \(x_i\) are uncorrelated (\(i = n + 1, \ldots, n\)). Let \(S_x(\omega)\) denote the autospectrum of any of the correlated \(x_i\), and \(S_{xx}(\omega)\) the modulus of the cross-spectrum of any two such \(x_i\), i.e.,

\[
S_x(\omega) = S_{xx}(\omega) \exp(-j\omega d_k), \quad \omega \neq 0
\]

where \(S_{xx}(\omega)\) is the cross-spectrum of \(x_i(t)\) and \(x(t)\), and \(S_x(\omega)\) and \(S_{xx}(\omega)\) are the respective autospectra. By setting \(i = 1\), for convenience, the cross-spectrum of any \(x_i\) to \(x(t)\) is given as (Jenkins and Watts 1968)

\[
S_{1x}(\omega) = S_x(\omega) + \sum_{i=2}^{n} S_{xx}(\omega) \exp(-j\omega d_k), \quad \omega \neq 0
\]

and its square modulus as

\[
|S_{1x}(\omega)|^2 = S_{x}^2(\omega) + 2B_1 S_x(\omega) + 2(\omega + 1 + 2C_1)S_{xx}(\omega), \quad \omega \neq 0
\]

where

\[
B_1 = \sum_{k=2}^{n} \cos \omega d_k
\]

is the sum of the cosines of the phase differences of \(x_i\) to all other correlated \(x_i\), and

\[
2C_1 = \sum_{k=2}^{n-1} \sum_{m=k+1}^{n} \cos \omega d_{m-k} = d_m - d_{m-k} = d_k - d_m
\]

is the sum of the cosines of the phase differences between all pairs of \(x_i\), excluding \(x_1\).

The autospectrum of the total aggregate activity \(x(t)\) equals the sum of all auto- and cross-spectra of the \(x_i\) (Jenkins and Watts 1968). On the assumption that the autospectra of the uncorrelated units are also \(S_x(\omega)\), this is written

\[
S_x(\omega) = nS_x(\omega) + 2AS_{xx}(\omega), \quad \omega \neq 0
\]

where
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