

A method for the quantification of synchrony and oscillatory properties of neuronal activity

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Abstract

Interactions between neurones can be analysed by simultaneously recording from several cells and computing correlation functions between the respective activities. Recent studies have revealed that neuronal responses are often synchronous and exhibit an oscillatory temporal structure. These two properties are commonly assessed together from correlation functions. In order to evaluate these variables independently a method was devised for the quantification of a generalized Gabor function that was fitted to the correlograms. The performance of the method was tested on a large data set from cat area 17 and its stability was examined with respect to its dependence on the number of free parameters. The results demonstrate that the proposed fitting algorithm is robust in that it is rather independent of starting conditions and converges to optimal fits even with different settings of free variables. The fitted correlation functions allow for an automatic and independent classification of synchrony on the one hand and oscillatory firing patterns on the other.

Key words: Oscillation; Synchronization; Temporal coding; Correlation analysis; Visual cortex

1. Introduction

The classical approach to the investigation of neuronal interactions consists of cross-correlation analysis of neuronal activity recorded simultaneously from different neurones (Perkel et al., 1967; Gerstein and Perkel, 1969). The assumption is that the correlation functions are a direct reflection of the connections between the recorded neurones. In the mammalian neocortex the most frequently encountered correlation functions are characterized by a peak centered at zero delay, and this is usually taken as evidence for common input to the recorded neurones (Kimura et al., 1976; Lee et al., 1977; Abeles, 1982; Gerstein et al., 1985; Ts'o and Gilbert, 1988; Reinis et al., 1988; Krüger, 1990; Krüger and Mayer, 1990; Gochin et al., 1991; Schwarz and Bolz, 1991; Nelson et al., 1992; Toyama, 1992).

Recent experimental and theoretical studies have indicated, however, that synchronization of neuronal

discharges can also result from dynamic interactions within reciprocally coupled neuronal networks without requiring common excitatory drive (Engel et al., 1991a; Nelson et al., 1992; Schuster and Wagner, 1990; König and Schillen, 1991). It has been suggested that this dynamic synchronization can be used to tag the responses of neurones that need to be related with one another (Milner, 1974; Von der Malsburg, 1981, 1986; Shimizu et al., 1986) and data from the cat visual cortex are compatible with this view (Engel et al., 1992a; Singer, 1993). They have revealed that neurones can transiently synchronize their responses when co-activated with coherent stimuli (Gray et al., 1989; Engel et al., 1991b). An interesting feature of this synchronization phenomenon is that neurones tend to exhibit oscillatory firing patterns when they engage in synchronous activity (Engel et al., 1990; König et al., 1993). Thus, cross-correlograms computed during episodes where responses are synchronized show not only a center peak, but this peak is additionally flanked by troughs and satellite peaks reflecting an oscillatory temporal structure in the discharge. It has been argued that oscillatory activity could be instrumental for the establishment of synchrony by reciprocal coupling be-

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cause of the predictability of discharges in oscillatory time series (Engel et al., 1992b). Simulation studies have shown that cell groups can be synchronized even if they are coupled by slowly conducting connections or only indirectly via interneurons if the local groups have a tendency to oscillate with similar frequency (König and Schillen, 1991). In order to test the hypothesis that there is a relation between the occurrence of oscillations on the one hand and of synchrony on the other, it is necessary to define independent measures for the 2 variables. The goal of the present study was to develop methods which allow one to extract these variables from correlograms.

2. Method

Correlation functions were quantified by fitting to a generalized Gabor function with 8 parameters.

$$CF(t) = A \exp\left(-(|t - \phi|/\sigma_1)^\lambda\right) \cos(2\pi\nu(t - \phi)) \\ + O + B \exp(-t/\sigma_2)^2$$

The parameters are: amplitude (A), decay constant (σ_1), frequency (ν), phase shift (ϕ), offset (O), exponent (λ), central modulation factor (B) and the width of a central peak (σ_2). In the above formula the different parameters can be described by their effect on the function. The ratio of the amplitude to the offset gives an estimate of the strength of the correlation. The decay constant is inverse proportional to the bandwidth of the oscillation. Frequency and phase shift determine the position and characteristics of the sinusoid in the envelope. Choosing an exponent different from 2 leads to a deviation of the envelope from a gaussian, with smaller values accentuating the central peak, while larger values lead to a box-like shape. The central peak is permitted to depart from the envelope by the last term in the sum. It describes an additional gaussian of height B and width σ_2 . When B is zero and the exponent λ is 2, the above equation describes a standard Gabor function. When either of these 2 conditions is not fulfilled, we call it a generalized Gabor function. This function accounts for the characteristic features of the experimentally determined correlograms and allows for a good fit. However, as the generalized Gabor function is non-linear for several parameters (σ , ν , ϕ and λ), an iterative fitting procedure has to be applied to find the parameters which give the best fit. The Marquardt-Levenberg algorithm which minimizes the χ^2 value was used for the fitting procedure (Press et al., 1986). Here, the benefit function is defined as the sum of the deviations between the fitted function and the correlogram, weighted by the error estimate of the correlation function. The error estimate of each individual value of the correlo-

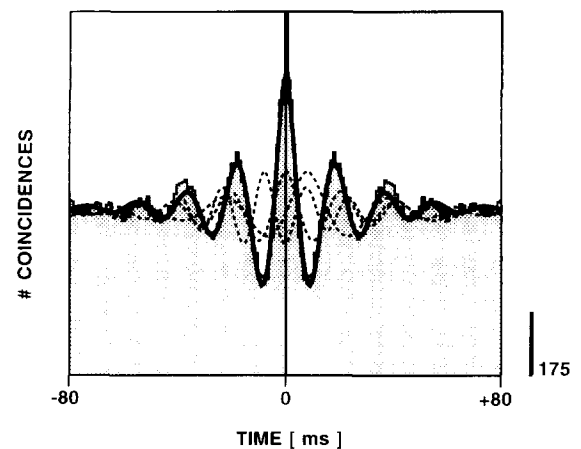


Fig. 1. Summed auto-correlogram computed from multiunit activity recorded in area 17 in response to a moving light bar (stippled surface). The ordinate shows the number of coincidences at each time shift. The various lines show the functions resulting from 3 sets of starting values (dotted) and the optimally fitted function (solid).

gram can be taken as the standard deviation of the correlation functions computed from the repeated stimulus presentations, which is approximately equal to the square root of the number of coincidences in each bin. This allows us to calculate analytically the χ^2 function as well as its first- and second-order derivative with respect to the parameters of the fitted function. The first-order derivative determines the direction of steepest descent, but gives no information on the amount of change in the parameters necessary to reach the minimum. Approximating the benefit function by a second-order Taylor expansion allows one to calculate directly the parameter set minimizing the benefit function. However, this approximation will be a good description of the true benefit function only locally. Therefore, the Marquardt-Levenberg method performs an iteration with a continuous shift from a steepest gradient method to an estimate of the minimum from a second-order model, leading to a rapid convergence. However, as it is an algorithm to search local minima, a suitable choice of initial values for the free parameters is important. We regularly use 9 sets of starting values covering a range of frequencies and phase shifts (see Fig. 1, dotted lines). The fitting procedure is run for each set of initial values until no significant improvement is found in 5 consecutive steps. Then the iteration for a particular set of starting values is stopped and the next set of starting values is tested. Usually several sets of initial values lead to the same and presumably globally optimal set of parameters of the fitted function (Table 1). The fit with the lowest χ^2 value is selected as optimal (Fig. 1, solid line). For successful fits the deviations between the fitted function and the correlogram are expected to be caused by noise, whose magnitude is described by the error esti-

Table 1

Values of the parameters and χ^2 value reached from the 9 different sets of starting values for the correlation function shown in Fig. 1 after convergence

<i>A</i> (sp.)	<i>t</i> (ms)	ν (Hz)	ϕ (ms)	<i>O</i> (sp.)	λ	χ^2	<i>i</i>
47.6	7.9	65	-7.7	450	0.1	2383	31
389.5	15.9	54	0.0	463	0.9	103	43
3.6	15.9	38	2.7	450	4.8	2179	5
389.5	15.9	54	0.0	463	0.9	103	8
389.5	15.9	54	0.0	463	0.9	103	6
389.5	15.9	54	0.0	463	0.9	103	12
47.6	7.9	65	7.7	450	0.1	2383	29
389.5	15.9	54	0.0	463	0.9	103	43
3.6	15.9	38	-2.4	450	4.8	2177	5

i denotes the necessary number of steps. As 5 of the starting values converged to the same good fit and the resulting χ^2 value (103) is of the same order as the degrees of freedom (81 independent data points minus 6 free parameters of the fitting function), it is assumed to be globally optimal.

mate of the correlogram. On average each independent data point should contribute 1 to the weighted sum of the deviations. Therefore, the number of independent data points of the correlogram minus the number of free parameters of the fitted function, called degrees of freedom, gives an estimate of the χ^2 value of a good fit. Furthermore, we requested that the χ^2 value should be at least 15% smaller than the variance of the data (Young et al., 1992). Once well fitting functions are obtained it is possible to extract from them descriptions for the correlogram by the few parameters of the fitting function.

Correlation functions were obtained from 2 different data sets. When units were recorded simultaneously from different electrodes cross-correlation functions were computed between the signals from the 2 electrodes. When multiple units were recorded simultaneously from the same electrode, auto-correlation functions of the composite signal were calculated. In both cases the parameters of the central peak provide indications on the synchronicity of the recorded neurones and the parameters of the first satellite peak allow one to assess the rhythmicity of the neuronal responses. In order to obtain a measure of the size of the central and the satellite peaks their height over the offset was computed. The variance of these measures can be determined as follows. We computed the derivative of these expressions with respect to the parameters of the fitted function ($T \equiv (\delta\chi/\delta A, \delta\chi/\delta\sigma, \dots, \delta\chi/\delta O)$). Subsequently the covariance matrix (C), which is proportional to the inverse of the second derivative of the benefit function with respect to the parameters of the fitted function (hessian matrix) was obtained. The scalar value $T \cdot C \cdot T$ is then a measure of the variance of the respective features of the fitted function and was used for a test against zero on a 5%

significance level. If it passed this test we assumed that the feature contributed significantly to the quality of the fit. A significant central peak reflects a high probability of simultaneous discharges and was thus taken as the signature of synchronous neuronal activity. A significant satellite peak indicates that firing probability increases after a certain time lag and was therefore taken as the signature of an oscillatory temporal structure with a limited bandwidth. This method of analysis has been applied to a large data set in order to test its dependence on the choice of the fitting function and the number of free parameters.

3. Results

3.1. Fitting of experimental data

The performance and validity of the fitting and rating method was tested on a set of 312 auto- and 192 cross-correlation functions of multiunit activity recorded in area 17 of 8 anaesthetised cats. The correlation functions were calculated for time shifts ranging from -80 ms to +80 ms with a temporal resolution of 1 ms. As the auto-correlation functions were symmetric they had just one-half as many independent data points as the cross-correlation functions. Applying the algorithm to those functions, the average time to convergence for one starting set of parameters was about 23 iteration steps, each taking 24 ms of CPU time on a VAX Station 4000/60. Of the 9 sets of starting values, 3 on average converged to the same optimum. This proves that the fitting procedure is sufficiently independent of the exact choice of starting values. The set of starting values yielding the fastest convergence to the optimal parameter set required about 18.5 iteration steps, which is less than the average. This indicates that performance can still be improved if necessary.

The quality of the fit was judged with the help of the χ^2 value. However, as auto- and cross-correlation functions had different numbers of independent data points, not the χ^2 value itself, but the ratio of it and the number of degrees of freedom (number of independent data points minus number of free parameters of the fitting function) was used. This ratio is approximately independent of the range for which the correlation function is computed (-80 to +80 ms in our analysis) and takes into account the differences of auto- and cross-correlation functions. For a good fit, it is expected to be of the order of 1.0. If we were to fit with a horizontal function, then only the offset (*O*) would be variable and non-zero, and the ratio of χ^2 value to the number of degrees of freedom becomes equivalent to the weighted variance of the correlation function. In our data sample it amounted to 5.7. As this value is much larger than 1.0, the correlation

functions have a prominent structure which can not be described by a noisy distribution. The χ^2 value of the optimal fitting function was on the average only 1.4 times as large as the number of degrees of freedom. This demonstrates that a large part of the variance of the data could be explained by the fit and the experimentally observed correlation functions could be well described by a generalized Gabor function. For an unstructured (flat), noisy function the χ^2 value per degree of freedom is expected to be 1.0, only slightly lower than the respective value of the optimal fit.

Once a good fit was achieved, the features of the correlation function could be analysed by the statistical tests as described in the method section. Of the 504 correlation functions 304 had a significant central peak and 222 a significant satellite peak. The following 4 examples demonstrate that the synchronicity and the oscillatory nature of the analyzed time series can be assessed independently. Fig. 2A shows an auto-correlation function of multi-unit activity that is both synchronous and oscillatory. The fit reduces the χ^2 value by 81% and the ratio of the amplitude of the central peak to its error (z score) is 10.5, well above the 5% significance level. Thus, at the present noise level, a modulation of the correlogram 5 times smaller than the one shown would pass the statistical test. Smaller modulations can be detected by obtaining more data and thus reducing the noise level. However, an absolute

limit is set by the requirement of 15% reduction of the χ^2 value. The z score of the size of the first satellite peak is 11 and thus also highly significant. Fig. 2B shows an example of activity that is synchronous (z score 4.5) but not oscillatory (z score 0) and the correlation function in Fig. 2C reflects oscillatory activity (z score 15.5) that is not synchronous (z score -1.1). The last example (Fig. 2D) shows a flat correlation function rated non-synchronous and non-oscillatory (z score 0). The central dip reflects the refractory period of the recorded neurones.

3.2. The influence of free parameters on fitting quality

In order to see if the list of free parameters could be shortened, the number of variable parameters (A , σ_1 , ν , ϕ , O , λ , B , σ_2) was varied for one example of an auto-correlation function. When only the offset (O) was variable and the amplitudes of the modulation factors (A , B) were set to zero, the function was independent of the time shift and the χ^2 value of the fit equaled the sum of the weighted variance of the data (Fig. 3, dashed line), in this case 628.3. For a good fit we would expect the χ^2 value to be in a similar range as the number of the degrees of freedom which in this case is 79. Obviously the correlation function is not a noisy flat distribution and is badly fitted by a straight line. When the number of free parameters is

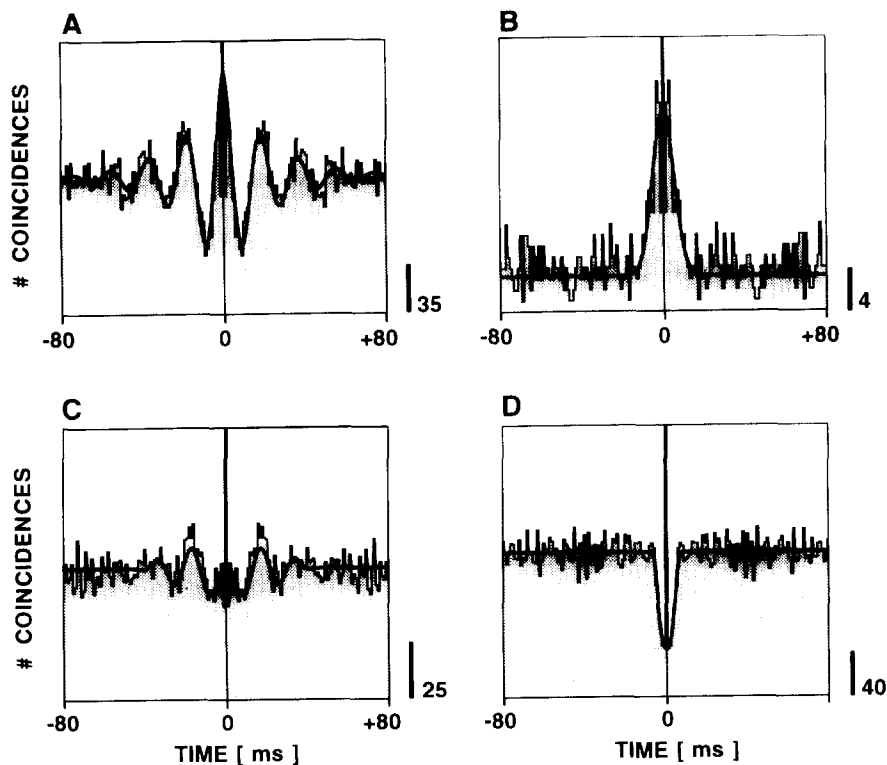


Fig. 2. Fit of auto-correlograms with different properties. A: synchronous and oscillatory; B: synchronous and not oscillatory; C: oscillatory, but not synchronous; D: flat, apart from a dip, reflecting the refractory period.

increased with the amplitude, decay constant, frequency, phase shift and offset (A , σ , ν , ϕ , O) kept variable and the exponent (λ) set to 2 and the factor for the central modulation (B) to zero, the χ^2 value gets reduced to 264.4. Obviously the 3 additional free parameters led to a substantial reduction of the error and a much better fit (Fig. 3, dotted line), but the χ^2 value is still much larger than the number of degrees of freedom. The reason is the poor fit in the central region of the correlogram which is caused by the influence of the satellite peaks. However, when the central modulation factor B is allowed to vary in addition, the fit improves considerably (Fig. 3, solid line). The χ^2 value drops to 126.5 and the remaining deviations are mainly due to high-frequency noise in the correlogram which cannot be fitted by the generalized Gabor function. Evaluation of this fitted function results in a classification of the neuronal activity as oscillatory but not synchronous. The remaining parameters, as for example the exponent (λ) or the width of the central peak (σ_2) had no influence on the quality of the fit. When they were allowed to vary too, the χ^2 value was reduced only from 126.5 to 126.0, which did not lead to a change in the classification of the correlogram. A disadvantage of increasing the number of free parameters is the rise in computing time. An optimization strategy, which can easily be automated, is to fit the data with increasing sets of free parameters, until χ^2 reaches the order of the number of degrees of freedom. Flat correlation functions, e.g., can be described by a straight line and hence can be fitted with only 1 variable parameter. Therefore no computing time is wasted on unmodulated correlation functions.

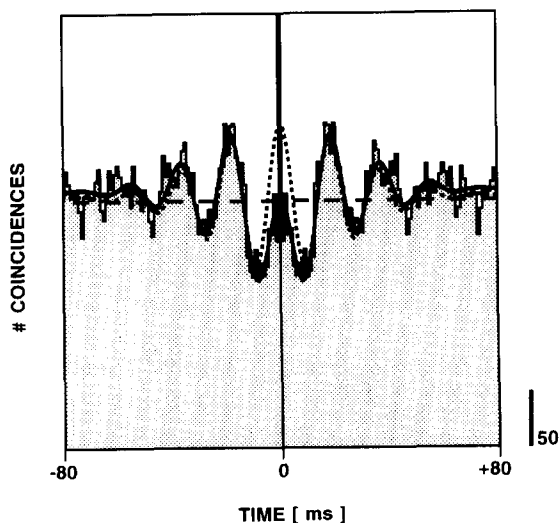


Fig. 3. Dependence of the fit on the number of free parameters. An auto-correlation function recorded from area 17 of visual cortex is shown. It is fitted by a function, which is independent of the time shift (horizontal dashed line), a Gabor function (dotted line) and a generalized Gabor function (solid line).

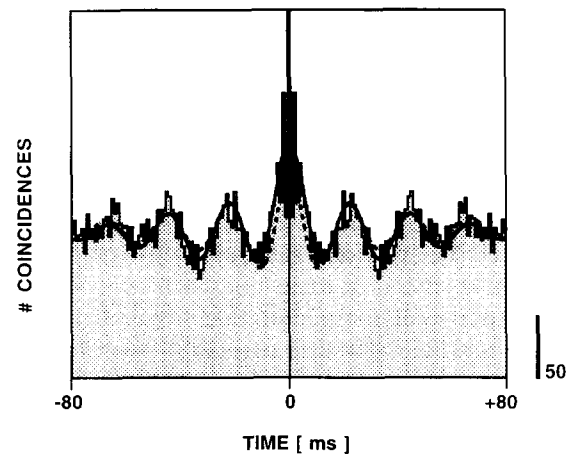


Fig. 4. Dependence of the fit on the set of free parameters. Fit with a generalized Gabor function with variable exponent (dotted) and a fit with the superposition of a Gabor function with an additional gaussian, described by the parameters B and σ_2 (solid).

3.3. The influence of free parameters on classification

As a next step the effect of fitting parameters on the rating procedure was estimated. Fig. 4 shows an auto-correlogram fitted to different functions. A standard Gabor function, with amplitude (A), decay constant (σ), frequency (ν), phase shift (ϕ) and offset (O) left variable, the exponent (λ) set to 2, and the central modulation factor (B) to zero, achieved only a reduction of the χ^2 value from 403.3 to 205.7 and thus left a large part of the variance unaccounted. Here the error occurred mainly in the central part of the correlation function. Therefore the central modulation factor (B) was allowed to vary in addition. This led to a reduction of the χ^2 value to 139.0, constituting a good fit (Fig. 4, solid line). Testing the significance of central and satellite peaks of this fitted function led to the rating of underlying activity as synchronous and oscillatory. In a subsequent fitting procedure the exponent (λ) was allowed to vary instead of the central modulation (B). This led to a different mathematical form of the fitted function with a sharp central peak and a slow decline of the envelope for increasing t . Nevertheless, the fit was comparable, as can be seen from the superimposed dashed curve in Fig. 4. The rating gave the same result as before. Finally, when both parameters (B and λ) were allowed to vary the fit improved only little further and the rating was again the same. However, there is one problem that needs to be considered. For correlation functions without satellite peaks both terms (B and λ) in the sum of the fitting function can validly describe the central peak. Therefore, the present parameter set is redundant for this type of correlograms and leads to a singular covariance matrix and to numerical instabilities. An easy remedy is again to start with a small set of free parameters and to increase it

only if the fit is not good enough as can be judged by comparing χ^2 values with the number of degrees of freedom.

4. Discussion

In this study a method is proposed which allows one to infer on the basis of strict statistical criteria from correlation functions of multi-unit activity whether the responses of the simultaneously recorded cells are synchronized and/or exhibit an oscillatory modulation.

When first introduced, correlation studies were regarded as a tool of functional anatomy to analyse synaptic connections between neurones (Perkel et al., 1967; Gerstein and Perkel, 1969). This approach was used to characterize the neurones physiologically and to demonstrate specific connections (Tanaka, 1985). Several criteria have been defined for the evaluation of correlation functions (Aertsen and Gerstein, 1985; Palm et al., 1988). Usually they are based on an estimation of the significance of a deviation of the number of coincidences from the expected rate at a particular delay. The common assumption is that coincidences above and below the expected values are indicative of excitatory and inhibitory interactions, respectively. If these deviations are offset from zero delay one cell is thought to excite or to inhibit the other. On the other hand, if the deviations are centered around zero delay, the analysed cell pairs are thought to receive a common excitatory or inhibitory input. When the deviations are short and sharply delineated, interactions are believed to be oligosynaptic while broad and shallow deviations are attributed to polysynaptic interactions. However, in the light of more recent investigations, these interpretations need to be extended. First, there is now evidence that correlograms with peaks centered around zero delay can result from reciprocal interactions between neurones and need not to be indicative of common input (Engel et al., 1991a). In other words, common excitatory or inhibitory input is not the only way to assure synchronicity of responses among spatially distributed neurones (König and Schillen, 1991). Second, simulation studies have demonstrated that cross-correlograms may fail to reflect existing connections between cell pairs because in networks such as neocortex, which are characterized by a high degree of convergence, the influence of a particular connection on the firing probability of a particular neurone depends very much on the actual level of background activity (Aertsen et al., 1989). Third, recent studies have revealed that correlations between the responses of simultaneously recorded neurones can change when stimulus conditions are altered: neurones having exhibited clear interactions with one stimulus configuration may no longer do so in response to another configura-

tion (Gray et al., 1989; Engel et al., 1991b). These results indicate that functional interactions between neurones may be highly dynamic, context dependent and non-stationary, in particular in structures such as neocortex. The implication is, that correlation analysis does not allow one to draw firm conclusions on the anatomy of connections as different connectivity patterns can lead to the same correlation patterns, and because a particular network can assume states with different manifest functional connectivity. On the other hand, correlation functions do reflect very well dynamic interactions among simultaneously recorded neurones. They allow one to detect dynamical states of networks such as transitory synchronization or oscillatory behaviour. It is therefore important to establish quantifiable criteria for the evaluation of correlation functions that go beyond the identification of significant deviations from expectancy values and permit inferences on dynamic properties of the network.

The algorithm presented in this study fulfils some of these requirements. It is robust with respect to the choice of the fitting function and the set of free parameters. Furthermore, it can easily be applied to any aspect of a correlation function as long as this can be expressed as a differentiable function of the parameters, i.e., if the first derivative (T) and the covariance matrix (C) of the function can be calculated with respect to the parameters of the fit. This includes tests of the width of the central peak, the appearance of central or satellite peaks and troughs etc. The source code of an implementation of the algorithm in VAX-Pascal can be obtained from the author.

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