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Temporal dynamics of information flow in the cerebral cortex

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Abstract

The nature of information flow from one area of the cerebral cortex to another is poorly understood. Frequency-dependent measures of information flow, based on multivariate autoregressive modeling of field potential time series, have shown promise for understanding information transactions between cortical areas (Liang et al., Neuro Report, 11 (2000) 2875–2880). In the present contribution, a time domain measure of information flow between two areas, called the directed transinformation (DTI), is described and applied to investigate causal influences directly from the field potential time series. We show that the DTI, as a generalization of mutual information, can be measured in a rather natural way, such that the interdependence of two time series is the sum of flow from X to Y, flow from Y to X, and instantaneous flow. We demonstrate the usefulness of this technique on both simulated data and multichannel local field potentials from macaque monkeys. Comparison with the frequency-dependent measure is also made. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Information flow; Local field potentials; Bottom-up; Top-down; Cerebral cortex

1. Introduction

The question of neural signaling in the cerebral cortex has been the subject of extensive discussion. Interaction is a basic property of the cortical system, taking place at every level of the cortical hierarchy. In an attempt to understand dynamic interactions among multiple cortical areas, we have employed multivariate statistical

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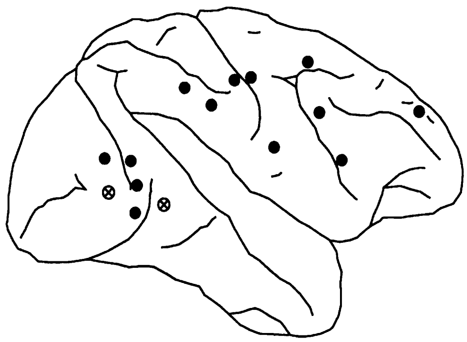

Fig. 1. Right hemisphere of monkey GE, showing positions of 15 cortical recording sites. Sites depicted by crossed circles, in striate and inferotemporal areas, are used to demonstrate application of the DTI to cortical LFPs.

measures of local field potential (LFP) time series. One such measure is called the short-time directed transfer function (STDTF), which determines causal influences between two cortical sites based on spectral analysis of multivariate autoregressive time series models. Although this technique has produced very promising results [5], we were also interested in exploring other methods that could characterize the temporal relationship between time series without the intermediate step of model construction. In this contribution, we describe the application of a measure called the directed transinformation (DTI) to the study of dynamic information transfer between different areas of the primate cerebral cortex.

Event-related LFP data from monkeys were used to test the DTI method. The LFPs, sampled at 200 Hz, were recorded transcortically (surface-to-depth) from bipolar electrodes at up to 15 unilateral sites (Fig. 1) in highly trained macaque monkeys performing a visuomotor pattern discrimination task [1]. They initiated each task trial by depressing a lever with the preferred hand. Data collection began about 115 ms prior to stimulus onset and continued until 500 ms poststimulus. The monkeys were required to discriminate between two pattern types (four dots as a line or diamond) in a set of four different dot patterns (left- or right-slanted line and diamond). No single dot could be used to discriminate between lines and diamonds. The discrimination was indicated by a GO or NO-GO response (release of the lever or maintenance of pressure). On GO trials, the monkeys were provided with a water reward at 500 ms poststimulus if the hand was lifted before that time. On NO-GO trials, the lever was depressed for 500 ms poststimulus, and released thereafter. A data set of 888 trials from one monkey (GE) balanced for response type (GO vs. NO-GO) was used in the analysis described below.

The validity of the DTI method was first verified through analysis of simulated time series. Application to cortical LFPs was then demonstrated. Comparison with the frequency-dependent STDTF measure was also made.

2. Methods

2.1. Directed TransInformation (DTI)

Mutual information analysis [9] represents a general method to measure the statistical dependencies between time series, and it can be considered as an alternative to the well-known correlation analysis. However, mutual information does not provide information on the direction of interaction since it is a symmetrical measure. A knowledge of the direction and amount of information flow can be useful and can give us an indication of which system (time series) is predominantly acting as a source. The DTI is a measure of information flow with such a direction. It is an information theory quantity that is an extension of Shannon's concept of mutual information to the idea of directional information flow. For simplicity, let two series X and Y be represented in the form

$$X = X^N X_k X^M,$$
$$Y = Y^N Y_k Y^M,$$

where

$$X^N = X_{k-N} \cdots X_{k-1},$$
$$Y^N = Y_{k-N} \cdots Y_{k-1}.$$

These are the past parts of X and Y, and

$$X^M = X_{k+1} \cdots X_{k+M},$$
$$Y^M = Y_{k+1} \cdots Y_{k+M}$$

are the future parts of X and Y.

The mutual information between times series X and Y is defined as [4,8]

$$I(X;Y) = \sum_k I_k(X;Y),$$

where

$$I_k(X;Y) = \underbrace{I(X_k;Y^M|X^N Y^N Y_k)}_{X_k \to Y^M} + \underbrace{I(Y_k;X^M|X^N Y^N X_k)}_{Y_k \to X^M} + \underbrace{I(X_k;Y_K|X^N Y^N)}_{X_k \to Y_k}.$$

This shows that the DTI between two time series X and Y is measured in a rather natural way such that their dependence is the sum of flow from X to Y, flow from Y to X, and instantaneous flow.

Using the relations $I(A;B) = H(A) - H(A|B)$ and $H(A,B) = H(A) + H(B|A)$, the DTI from X at time k to Y at time $k+M$ can be written in terms of joint entropies as:

$$I(X_k \to Y_{k+M}|X^N Y^N Y_k) = H(X^N Y^N Y_k Y_{k+M}) - H(X^N Y^N Y_k) - H(X^N Y^N X_k Y_k Y_{k+M}) + H(X^N Y^N X_k Y_k).$$

It is easy to show that, for n normally distributed random variables, their joint entropy is given by

$$H(z_1, \ldots, z_n) = \tfrac{1}{2}\ln\{(2\pi e)^n |R(z_1, \ldots, z_n)|\},$$

where $|.|$ denotes the determinant of the covariance matrix $R(z_1, \ldots, z_n)$, and e is the base of the natural logarithm. Hence, the above DTI equation can be rewritten as

$$I(X_k \rightarrow Y_{k+M} | X^N Y^N Y_k) = \frac{1}{2}\log\frac{|R(X^N Y^N X_k Y_k)||R(X^N Y^N Y_k Y_{k+M})|}{|R(X^N Y^N X_k Y_k Y_{k+M})||R(X^N Y^N Y_k)|}.$$

Similarly, other information quantities can be computed. We note that, although the DTI is given here for only two time series, it potentially can be extended to any number of time series.

2.2. Short-time directed transfer function (STDTF)

Suppose that $\mathbf{X}_t = [x_{1t}, x_{2t}, \cdot, x_{pt}]^{\mathrm{T}}$ are p channels of LFPs. The multivariate autoregressive (MVAR) model is given by

$$\sum_{k=0}^{m} \mathbf{A}_k \mathbf{X}_{t-k} = \mathbf{E}_t,$$

where $\mathbf{E}_t$ is uncorrelated noise with covariance matrix $\mathbf{\Sigma}$, and $\mathbf{A}_k$ are $p \times p$ coefficient matrices which can be obtained by solving the multivariate Yule–Walker Eqs. (of size mp^2) using the Levinson, Wiggins and Robinson (LWR) algorithm [7]. The model order m is determined by the Akaike information criterion (AIC) [6].

The transfer function of the MVAR model, $\mathbf{H}(f)$, can be written as [3]

$$\mathbf{H}(f) = \left(\sum_{j=0}^{m} \mathbf{A}(j) \mathrm{e}^{-\mathrm{i}j2\pi f} \right)^{-1}$$

The directed transfer function is defined as the magnitude of the matrix element $H_{ji}(f)$ which measures the causal influence from channel i to j. The STDTF is based on the AMVAR (adaptive MVAR) approach [2] involving adaptive estimation of the MVAR model coefficients with a sliding analysis window. Its usefulness for determining causal influences between cortical areas has been demonstrated in [5].

3. Results

A simulation study was first performed in order to test the mathematical formulations. Two stationary time series processes, X and Y, were generated by a simple model [8]:

$$x_t = z_{t-2} + a w_x,$$

$$y_t = z_{t-1} + w_y,$$

$$z_t = b z_{t-2} + w_x,$$

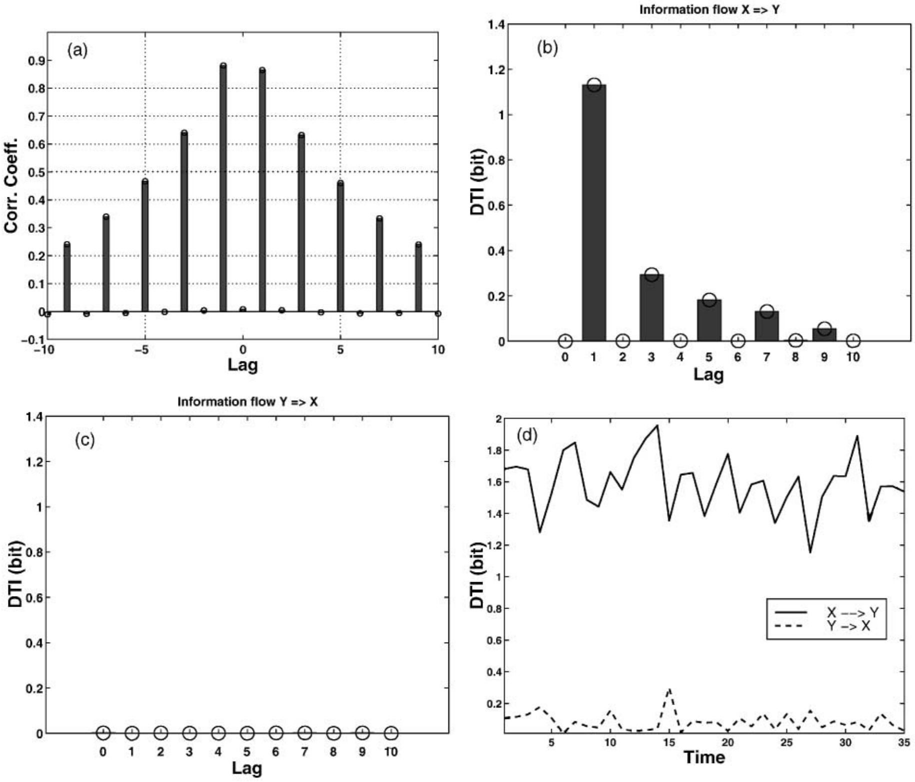

Fig. 2. Estimated cross-correlation (a), information flow profiles (b, c), and the total information flow at each time instant (d) for the simulation model. The occurrence of zeros at all even-valued lags is a property of the model. There are no negative lags for the DTI (b, c) because of its definition. Since the simulated processes are stationary, the variation of the DTI with time (d) is due to random fluctuation in the simulated time series. Note that the DTI from X to Y is appreciably higher than from Y to X for all times. (Time is in arbitrary units for the simulation model).

where w_x and w_y are zero mean white noise processes with $\sigma_x = 1$, $\sigma_y = 0.5$, and $a = 0.5, b = 0.8$. In this model, X leading Y through the intermediate variable z_t indicates the information flow from X to Y. Such information does not appear in cross-correlation analysis, since the cross-correlation function is almost completely symmetric with respect to zero lag, but is revealed by DTIs (Fig. 2). Fig. 2(a) shows the cross-correlation function averaged over an ensemble of sequences X and Y. Fig. 2(b) and (c) show DTIs from X to Y and from Y to X, respectively, which were computed with an 1 point long window. The total amount of information flow which was obtained by summing over the time lags at different time instant is plotted in Fig. 2(d) for both directions. It is clear that the DTI can reveal the direction of information flow which is not seen by the cross-correlation function.

Fig. 3 shows the total information flow from a striate to an inferotemporal cortical site, and the feedback flow from the inferotemporal to striate site. The DTI measure is

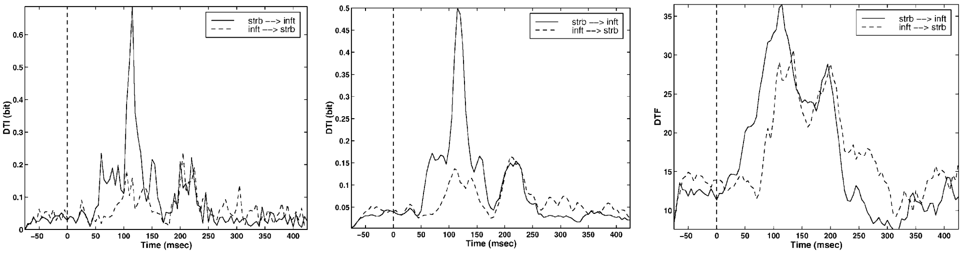

Fig. 3. Total information flows between a striate and an inferotemporal site computed with 5 ms (left) and 15 ms (middle) windows. The STDTF (right) shown has a similar profile as the DTI, although it may be somewhat smeared. The vertical dashed line indicates the stimulus onset.

shown in the left and center frames using windows of 5 ms (1 point) and 15 ms (3 points) length, respectively. The STDTF is shown in the right frame for comparison, using a 50 ms (10 points) long window. (All frequency components in the STDTF spectrum were summed to produce this curve). The DTI curve with 5 ms window offers the greatest temporal resolution, although the DTI curve with 15 ms window has a similar temporal waveshape. Both DTI curves have greater temporal resolution than the STDTF curve, which has greater temporal smearing due to the 50 ms window length. Nevertheless, some general features are quite similar for both methods: (a) the earlier onset of the striate-to-inferotemporal (bottom-up) influence as compared to the inferotemporal-to-striate (top-down); (b) the peak value near 120 ms poststimulus; (c) the greater magnitude of this peak in the bottom-up than the top-down influence; and (d) a secondary peak near 200 ms poststimulus.

4. Conclusions

In summary, use of the DTI technique, derived from information theory, may be a valuable approach to the study of cortical interactions. The DTI measure has several advantages, including the fact that it is model-free, and also that it may be used to reveal nonlinear relations between time series. However, it cannot be used to determine the frequency components that contribute to directional influences since it is based in the time domain. Therefore, the complementary use of DTI in the time domain and STDTF in the frequency domain is suggested as a viable approach for characterizing spectral–temporal interactions in the cerebral cortex.

Acknowledgements

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