

Another Neural Code?

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This paper presents the conjecture that functional integration may be mediated by the mutual induction and maintenance of stereotyped spatiotemporal patterns of activity (i.e., transients) in different neuronal populations. In contradistinction to temporal and rate coding models of neuronal interactions, transient coding considers that transactions among neuronal systems use transient dynamics that are distributed in a structured way over both space and time. In contrast to synchronization models, transient coding does not depend on interactions at the same frequencies, in different parts of the brain, but involves covariations among *different* frequencies and can therefore be considered a more general form of coding. Using an analysis of the correlations among the spectral density of neuromagnetic signals, measured at different cortical regions, this hypothesis was confirmed. For example high (gamma)-frequency oscillations in the prefrontal cortex are associated with low (20 Hz)-frequency oscillations in the parietal cortex. The results are consistent with transient coding and suggest that transient dynamics endure for at least 40–200 ms. Transient coding means that correlations (rate coding) and coherence (synchrony) are neither complete nor sufficient characterizations of neuronal interactions. Although temporal coding, rate coding, and synchrony are important aspects of neuronal interactions, the results speak to further integrative neuronal mechanisms of a more general nature. © 1997 Academic Press

INTRODUCTION

This paper presents the idea that dynamic changes in the spectral density of neuronal activity may reflect an underlying “metric” or code mediating functional integration in the brain. Functional integration here refers to the concerted interactions among neuronal populations, and functionally specialized cortical areas, that mediate perceptual binding, sensorimotor integration, and cognitive processing. It pertains to the mechanisms by which, and constraints under which, the dynamics of one population influences the activity of others. It is suggested that a component of integration among neuronal systems proceeds at the level of tran-

sient dynamics. This transient coding hypothesis suggests that interactions are mediated by the mutual expression and induction of reproducible, stereotyped spatiotemporal patterns of activity that endure over extended periods of time (i.e., neuronal transients). If the temporal structure of neural transients shows a regional specificity, then the prevalence of certain frequency components in one cortical area will be associated with the expression of different frequencies in another area. This hypothesis has implications for existing measures of neuronal interactions (i.e., coherence and cross-correlogram analyses). In particular it means that frequency-specific coherence in electrical and biomagnetic signals, or oscillations in separable spike trains, may be incomplete characterizations of neuronal interactions.

A “neural code” is used here to mean a measurement or metric of neuronal activity that could participate in teleologically meaningful transactions among different parts of the brain. However, no attempt is made to discern the meaning or content of a putative code. All that we assume is that a code or measure must necessarily show some dependency when assessed in two interacting neuronal populations or brain areas. The problem of identifying possible codes then reduces to establishing which sorts of measures are mutually predictive or statistically dependent when measured in two parts of the brain.

To discuss the nature of these transient dynamics, in relation to other putative codes, a taxonomy of neural codes is used that includes *temporal coding*, *rate coding*, *frequency coding*, and *transient coding*. This is not meant to be an exhaustive list but tries to cover most of the important differences. The first distinction is between codes that can be measured at one point in time (i.e., temporal coding and rate coding) and those that have an explicit temporal domain, in other words can only be measured after a period of observation (i.e., synchrony coding and transient coding):

Temporal Coding

The distinction between temporal coding and rate coding (see Shadlen and Newsome, 1995) centers on whether the precise timing of individual spikes is

sufficient to facilitate meaningful neuronal interactions. In temporal coding the exact time at which an individual spike occurs is the important metric and the spike train is considered a *point process*. The term is used here in this restrictive sense, as opposed to designating codes that have a temporal domain (see below and von der Malsburg, 1985; Singer, 1994).

Rate Coding

Rate coding considers spike trains as *stochastic processes* whose first-order moments (i.e., mean activity) define a space in which neuronal interactions are enacted. These moments may be in terms of the spikes themselves or other compound events (e.g., the average rate of bursting; Bair *et al.*, 1994). The essential aspect of rate coding is that a complete metric would be the average firing rates of all the system's components *at one point in time*. Interactions based on rate coding are usually assessed in terms of cross-correlations, and many models of associative plasticity are predicated on these correlated firing rates (e.g., Hebb, 1949).

Synchrony Coding

The proposal most pertinent to this form of coding is that population responses participating in the encoding of a percept become organized in time through reciprocal interactions so that they come to discharge in synchrony (von der Malsburg, 1985; Singer, 1994). Frequency-specific interactions and synchronization are used here synonymously. It should be noted that synchronization does not necessarily imply oscillations. However, synchronized activity is inferred, operationally, by oscillations implicit in the periodic modulation of cross-correlograms of separable spike trains (e.g., Gray and Singer, 1991; Eckhorn *et al.*, 1992) or measures of coherence in multichannel electrical and neuro-magnetic time-series (e.g., Llinas *et al.*, 1994). The underlying mechanism of these frequency-specific interactions is usually attributed to phase-locking among neuronal populations (e.g., Sporns *et al.*, 1992; Aertsen and Preissl, 1991). The key aspect of this metric is that it refers explicitly to the extended temporal structure of firing patterns either in terms of spiking (e.g., syn-fire chains; Abeles *et al.*, 1994) or oscillations in the ensuing population dynamics (e.g., Singer, 1994).

Transient Coding

An alternative perspective on neuronal codes is provided by work on *dynamic correlations* as exemplified in Vaadia *et al.* (1995). A fundamental phenomenon observed by Vaadia *et al.* (1995) is that, following behaviorally salient events, the degree of coherent firing between two neurons can change profoundly and systematically over the ensuing second or so. One implication of this work is that a complete model of

neuronal interactions has to accommodate dynamic changes in correlations, modulated on time scales of 100–1000 ms. A simple explanation for these dynamic correlations has been suggested (Friston, 1995): It was pointed out that the coexpression of “neuronal transients” in different parts of the brain could account for dynamic correlations. This *transient code* hypothesis suggests that interactions are mediated by the expression and induction of reproducible, highly structured spatiotemporal dynamics that endure over extended periods of time (i.e., neuronal transients). Like frequency coding the dynamics have an explicit temporal dimension but, in this more general framework, there is no special dependence on oscillations or synchrony. In particular the frequency structure of a transient in one part of the brain may be very different from that in another, whereas in synchronous interactions the frequency structures of both will be the same (whether they are oscillatory or not).

If the transient model is correct then important transactions between cortical areas will be overlooked by techniques that are predicated on rate coding (correlations, covariance patterns, spatial modes, etc.) or synchronization models (e.g., coherence analysis and cross-correlograms). The aim of this work was therefore to confirm or discount the possibility of a transient code in the brain. The paper is divided into two sections. The first section presents the theory upon which we based our empirical analysis. In brief, if transient coding is present in the brain then one would predict that (i) the correlations between different spectral densities measured (over 100 ms or so) in two regions of the brain would be significantly high and (ii) these correlations would be asymmetric (i.e., high frequencies in one region would be associated with low frequencies in the other but not *vice versa*). The second section of this paper confirms these hypotheses using magnetoencephalographic (MEG) data obtained from a normal subject while performing self-paced finger movements.

THEORETICAL BACKGROUND

The Neural Basis of Transient Coding

From a neurobiological perspective the distinction between transient coding and synchrony coding could be viewed in the following way: Synchronization represents the direct, reciprocal exchange of signals between two populations, wherein the activity in one population has a direct effect on the activity of the second, such that the dynamics become entrained and mutually reinforcing. In transient coding the incoming activity from one population exerts a modulatory influence, *not on the activity of units in the second, but on the interactions* (e.g., synaptic or effective connectivity) *among these units* to change the dynamics intrinsic to the second population. In this model there is no neces-

sary synchrony between the intrinsic dynamics that ensue and the temporal pattern of modulatory input. A simple example of this may be the facilitation of high frequency gamma oscillations among nearby columns in visual cortex by transiently increased modulatory input from the pulvinar. In this example the expression of low-frequency transients in the pulvinar will be correlated with the expression of high-frequency transients in visual cortex. This phenomenon is distinct from broad-band coherence (e.g., Bressler *et al.*, 1993) in which synchronization is evident over many frequencies. In broad-band coherence the correlations between different frequencies are accounted for completely by correlations within each frequency band.

Why “Transients”?

The underlying mechanisms behind transient coding are speculative but are most easily framed in terms of nonlinear dynamics; where attractor-like transients evoke, and interact with, other transients among loosely coupled neuronal populations. These transients can be expressed in terms of firing rates (e.g., chaotic oscillations; Freeman and Barrie, 1994) or individual spikes (e.g., syn-fire chains; Abeles *et al.*, 1994, 1995). In nonlinear dynamics the term “transient” usually refers to the initial, self-limiting behavior of nonlinear systems that is observed before the system settles down into its attractor. The term is used in the same sense here to denote self-limiting patterns of activity. However, in the brain this period of “settling down” can be thought of as ongoing and continuous as the attractor changes from moment to moment (due to modulatory interactions among different populations). In other words, neuronal dynamics are not thought of as chaotic dynamics, played out on an invariant attractor, but as the succession of organized and structured transients that ensue as the attractor itself changes (due to activity-dependent changes and modulation of synaptic connections).

Testing the Transient Coding Hypothesis

If the transient code hypothesis is correct there are some specific and testable predictions that are implied. In brief if one measures the spectral densities of many paired segments of activity, from two parts of the brain, then the coexpression of transients in these regions should be reflected in correlations among the spectral densities. We can therefore test the transient coding hypothesis by testing for the statistical dependence of these spectral density measures using standard multivariate statistical inference (in fact this turns out to be a test for the mutual information between the two sets of spectral density measures). This is a little bit like a coherence analysis but addresses not only the correlations at a particular frequency but also correlations among different frequencies.

Let $a(t)$ and $b(t)$ denote paired segments of length n , from two time series measured in different parts of the brain. Let $g(\omega)$ be the spectral density of $a(t)$. $g(\omega) = s(\omega) \cdot s(\omega)^*$, where $s(\omega)$ is the Fourier transform of $H(t) \cdot a(t)$ and $H(t)$ is a suitable (e.g., Hanning or Gaussian) windowing function. Similarly $f(\omega)$ is the spectral density of $b(t)$. Now assume that each segment contains a transient such that the i th transient from the first time series has spectral density $g_i(\omega)$ and the j th transient from the second time series has a spectral density $f_j(\omega)$. Note that if a transient is sampled half-way though, it is simply treated as a new transient (the precise phase relationships among transients and between the transients and sampling are discounted by the spectral density). Consider k paired, independent observations of $g(\omega)$, and $f(\omega)$ being drawn from the (large) sets of events $g_i(\omega)$ and $f_j(\omega)$ with probabilities p_i and q_j , respectively. In this formulation the null hypothesis of no transient coding suggests that the expression of the i th transient in the first time series is independent of the expression of the j th transient in the second. More exactly $p_{ij} = p_i \cdot q_j$ where p_{ij} is the joint probability of the i th and j th transients occurring at the same time. What implications does this have for the observed spectral densities? By direct calculation,

$$\begin{aligned} \text{Cov}\{g(u), f(v)\} &= E\{g(u) \cdot f(v)\} - E\{g(u)\} \cdot E\{f(v)\} \\ &= \sum \sum p_{ij} \cdot g_i(u) \cdot f_j(v) \\ &\quad - \sum p_i \cdot g_i(u) \cdot \sum q_j f_j(v), \end{aligned}$$

where $\text{Cov}\{\}$ denotes covariance and $E\{\}$ expectation. Now if $p_{ij} = p_i \cdot q_j$ this implies that $\text{Cov}\{g(u), f(v)\} = 0$ for all frequency pairs (u, v) . Let \mathbf{G} be the $(k \times n)$ matrix with one discrete estimate of spectral density $g(\omega)$ per row. Similarly let \mathbf{F} be the matrix of $f(\omega)$ estimates. Therefore under the null hypothesis of no transient coding $\text{Cov}\{\mathbf{G}, \mathbf{F}\} = 0$. $\text{Cov}\{\mathbf{G}, \mathbf{F}\}$ is the $(n \times n)$ spectral density covariance matrix with elements $\text{Cov}\{g(u), f(v)\}$. The transient coding hypothesis can now be tested using standard inferential statistics, in this instance, Wilk's λ , the likelihood ratio statistic for testing the independence of \mathbf{G} and \mathbf{F} (Chatfield and Collins, 1980, p. 167). Using appropriate distributional approximations (Chatfield and Collins, 1980, p. 149), one can calculate a P value using the observed spectral densities for any windowing function $H(t)$.

This statistical formulation of the problem allows one to test the transient coding hypothesis directly by showing that spectral densities in two brain areas \mathbf{F} and \mathbf{G} are indeed mutually predictive or dependent. If they were independent, then transients, and implicitly their spectral densities, could not be candidates for a neural code.

Transients and Other Codes

In this section we show that both rate and synchrony coding can be seen as special cases of transient coding. This means that a significant P value is not sufficient to accept the transient coding hypothesis in its most general form. To do this we have to show in addition that $\text{Cov}[\mathbf{G}, \mathbf{F}]$ is significantly different from $\text{Cov}[\mathbf{F}, \mathbf{G}]$:

Rate Coding

Interactions based on rate coding would be expressed as a significant correlation between the two time series $a(t)$ and $b(t)$. In the above formulation rate coding can be considered a special and limiting case of transient coding, where the length of the transient shrinks to one time bin. Here $n = 1$, meaning $g(\omega)$ and $f(\omega)$ are only evaluated at the 0th frequency and therefore correspond to the activity at that time. The statistical inference above reduces to a univariate test for a significant correlation. This presents a problem in the present context because, in rejecting the null hypothesis of no transient coding, we cannot discount rate coding as the explanation. However if rate coding is extant there are specific constraints on the form of $\text{Cov}[\mathbf{G}, \mathbf{F}]$: If the two segments $a(t)$ and $b(t)$ are correlated then $a(t) \approx b(t)$ where \approx means equal apart from unspecified error terms. Similarly $g(\omega) \approx f(\omega)$. This implies that $\text{Cov}[g(u), f(v)] \approx \text{Cov}[g(v), f(u)]$ or $\text{Cov}[\mathbf{G}, \mathbf{F}] = \text{Cov}[\mathbf{F}, \mathbf{G}]$. In other words $\text{Cov}[\mathbf{G}, \mathbf{F}]$ should be symmetric about the leading diagonal. More intuitively although high frequencies in one region may be correlated with low frequencies in another; this is because *both* frequencies are expressed at the same time in both regions.

Synchronization

Synchronisation due to phase-locking can also be considered a special case of transient coding, in which the two transients comprise the same frequencies. Unlike rate coding this does not necessarily imply a correlation (e.g., dominant oscillations may be $\pi/2$ out of phase), but, like rate coding, synchronization implies that the spectral density of the dynamics in interacting populations are similar. In other words the phasic and reentrant (Edelman, 1993) exchange of signals among disparate neuronal populations would incur oscillatory dynamics at the same frequencies so that, again, $g(\omega) \approx f(\omega)$ and $\text{Cov}[\mathbf{G}, \mathbf{F}] = \text{Cov}[\mathbf{F}, \mathbf{G}]$. Note that this argument also applies to aperiodic transients that are due to nonoscillatory synchronous interactions.

In order to demonstrate transient coding, above and beyond rate coding or synchronization, it is therefore necessary to show that $\text{Cov}[\mathbf{G}, \mathbf{F}]$ is not symmetric (i.e., the spectral density of two coupled transients $g_i(\omega)$ and $f_j(\omega)$ are dissimilar). For example a transient comprising predominantly high frequencies in one neuronal

population is predictive of, and predicted by, a transient elsewhere with a different (i.e., a low) frequency structure. This is exactly what we observed.

AN EMPIRICAL ANALYSIS OF MEG DATA

Data Acquisition

MEG data were obtained from a normal subject during unilateral, self-paced movements of a joystick using a Siemens KRENKON 37-channel machine. These data were kindly provided by Klaus Martin Stephan, Andy Ioannides, and their colleagues. The subject was trained to perform movements, with the right hand, every 2 s or so. The data were acquired every millisecond for at least 64 movements.

Data Preprocessing

In order to enhance the spatial resolution, and to reduce spurious correlations among channels, we applied a V_3 transformation to the data (this is a Laplacian derivative or edge-enhancing-like operation) (Ioannides *et al.*, 1990). The V_3 transformation transforms data, obtained with axial gradiometers, to signals that have maxima (roughly) over the underlying source currents.

Two continuous time series were selected from a prefrontal and a parietal region (Fig. 1). These regions were selected because they are known to participate in the motor task used. The data were digitally bandpass filtered (4–125 Hz). Portions of the resulting time series are shown at the bottom of Fig. 1. In order to remove spurious correlations due to (i) poor spatial resolution, (ii) artifacts (e.g., cardiac or ocular), and (iii) common (e.g., thalamic) input, which would otherwise confound the analysis we replaced the second time series \mathbf{b} with \mathbf{b}' , where

$$\mathbf{b}' = \mathbf{b} - \mathbf{a} \cdot (\mathbf{a}^T \cdot \mathbf{a})^{-1} \cdot \mathbf{a}^T \cdot \mathbf{b}.$$

\mathbf{a} and \mathbf{b} are the large column vectors representing the two time series. This orthogonalization removes any component of the second time series that can be predicted by the first and implicitly discounts rate coding as a putative explanation for any significant results that obtain. Recall that synchrony coding does not necessarily involve correlations (e.g., if the oscillations are $\pi/2$ out of phase).

Statistical Inference

Seven hundred thirty-five paired and ordered segments 512 ms in length, separated by 256 ms, were taken from both time series (it is important that these segments were separated by 256 ms because this ensured that they represented independent observa-

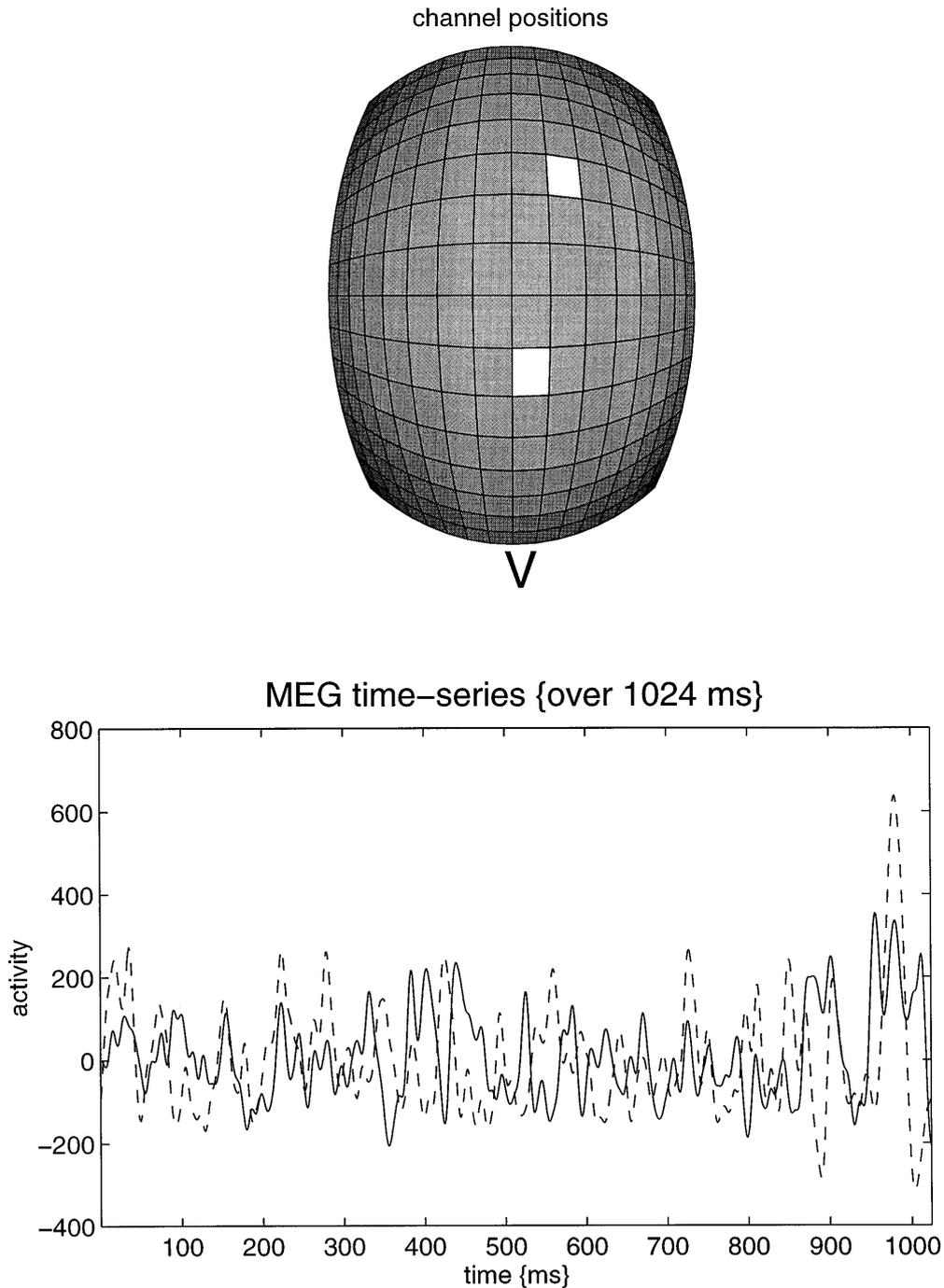


FIG. 1. (Top) Location of the two MEG time series chosen for the analysis. These data were selected after a V_3 transformation of 37-channel MEG data obtained during self-paced movements. The “V” denotes the nose and left corresponds to right. The lower square (channel 1) is over the medial prefrontal region. The upper square (channel 2) is over the left superior parietal region. (Bottom) Exemplar segments of the two time series. These data are the absolute values of the field vector following V_3 transformation and mean correction.

tions). Note that we performed no averaging or data selection on the basis of finger movements. In the absence of *a priori* information about the duration of transients we analyzed the segments using Gaussian windowing functions with a range of widths W from 16 to 256 ms (full width at half-maximum) in 16-ms steps.

Each windowed segment was subject to Fourier transform and quadratic rooted, to give the spectral density matrices (**G** and **F**). The quadratic root transform ensures that the distribution of the residuals are approximately Gaussian (Gaussian distributions are assumed by the multivariate statistics employed). Wilk’s

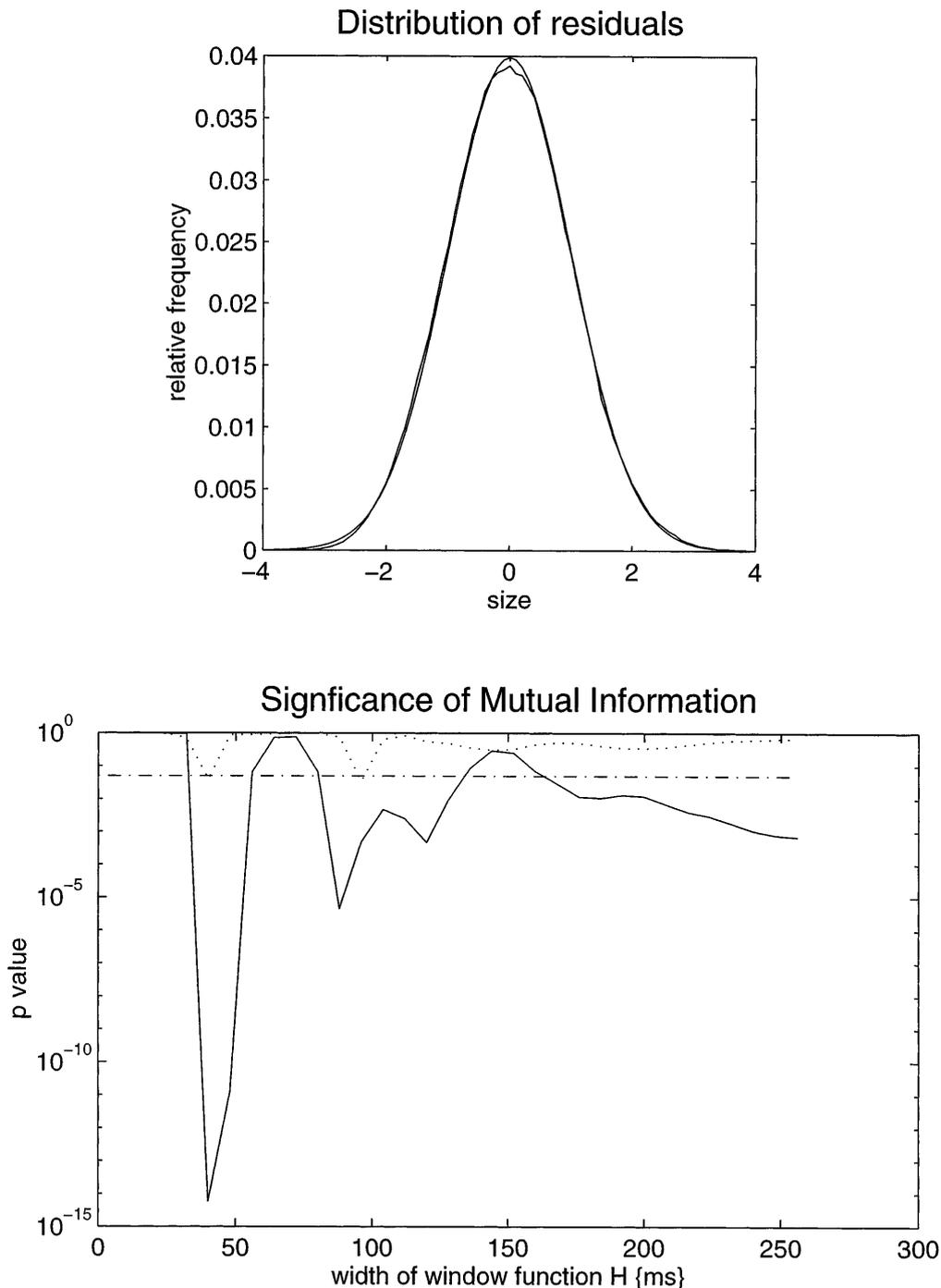


FIG. 2. (Top) Empirical and theoretical distributions of the error terms. (Bottom) P values testing the null hypothesis of independence between spectral densities expressed as a function of W , the width at half-maximum of the Gaussian windowing function $H(t)$ employed to estimate the spectral densities. Solid line—true analysis. Dotted line—null (phase-randomization) analysis. Broken line— $P = 0.05$.

λ was computed and the corresponding P value derived as a function of window length (W). To ensure the validity of these inferential results and the effectiveness of our data preprocessing, we performed a null, or control, analysis by repeating the entire procedure but randomizing the phases of one of the time series. These

data have exactly the same temporal autocorrelations and degrees of freedom as the real data but any true coupling between the spectral densities is removed.

The resulting P values are seen in Fig. 2 (bottom) as a function of W (effective length of the time series contributing to the spectral density estimates). It can be seen

that the dependence between the two sets of spectral density measures becomes profoundly significant at around 40 ms ($P < 10^{-14}$) and then again around 100 ms. Even at durations of 250 ms the mutual information is significant. P values that are not significant should not be overinterpreted because a failure to reject the null hypothesis does not imply it is true.

One can infer from these results that the temporal domain, in which transients exist, has a number of scales ranging from 40 to more than 250 ms, consistent with predictions from analyses of dynamic correlations (Vaadia *et al.*, 1995) and the duration of oscillatory dynamics [both empirical (Singer, 1994) and simulated (Sporns *et al.*, 1992)]. The absence of significant dependencies at short durations (i.e., 32 ms or less) should not be overinterpreted and probably reflects the decorrelation imposed upon the data by the orthogonalization above. The null analysis (dotted line in the bottom graph of Fig. 2) demonstrates specificity of the analysis.

Verification of the Gaussian Assumptions

Wilk's statistic is based on the general linear model and assumes that the error terms are identically and independently distributed according to the normal distribution. The error terms are given by $\mathbf{G} - \mathbf{F} \cdot \text{Cov}[\mathbf{F}, \mathbf{F}]^{-1} \cdot \text{Cov}[\mathbf{F}, \mathbf{G}]$. These terms were estimated and scaled to unit standard deviation for every frequency at each value of W . The pooled distribution is shown in the top graph of Fig. 2 and conforms almost exactly to Gaussian assumptions (the theoretical distribution is superimposed).

Testing for Asymmetric Correlations

The Z -transformed cross-correlation matrix $Z[\mathbf{F}, \mathbf{G}]$ corresponding to $\text{Cov}[\mathbf{F}, \mathbf{G}]$ for a window function H with width $W = 120$ ms is shown at the top of Fig. 3 in image format. The key point to note is that it is asymmetrical, suggesting that the transient coding model (in its most general form) is correct. This lack of symmetry discounts both rate coding and synchronization as explanations for the observed correlation. The most prominent correlation (after Fisher's Z transform $Z = 3.1$) was in the lower left quadrant, reflecting a high correlation between gamma (35–40 Hz) prefrontal frequencies and lower (18–20 Hz) frequencies in parietal cortex. It should be noted that there is evidence for possible synchrony at 10 and 20 Hz: The correlations are high on the leading diagonal at these frequencies and it is noteworthy that nearly all the correlations were positive (see the bottom of Fig. 3). In other words the expression of one frequency is associated with the expression of another but not the suppression of any particular frequency. This might be interpreted as a

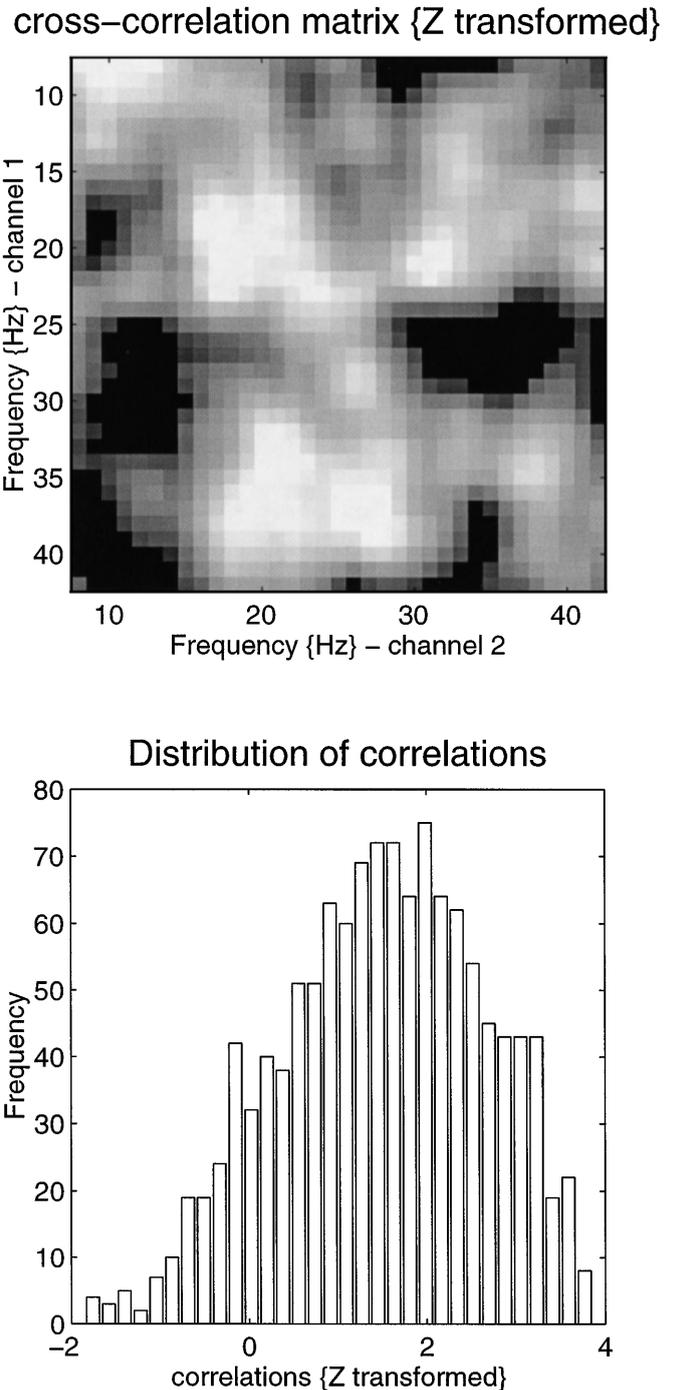


FIG. 3. Cross-correlation matrix (i.e., a normalized version of $\text{Cov}[\mathbf{F}, \mathbf{G}]$) shown in image format after transformation to the Z score using Fisher's Z transform. Black corresponds to $Z = 0$ and white corresponds to $Z = 3.1$. Channel 1 is the prefrontal time series and channel 2 is the parietal time series. These correlations were estimated using a window width W of 120 ms.

nonspecific modulation of power, at all frequencies, over time.

In summary the asymmetric form of the covariances between spectral densities in anterior and posterior cortical regions suggests that transient dynamics evi-

dence a long-range coupling and, crucially for prevailing models of neuronal interactions, these transients can have a very different frequency structure.

CONCLUSION

This work has tested the hypothesis that functional integration is mediated by the mutual induction and maintenance of stereotyped spatiotemporal patterns of neuronal activity (i.e., transients) in different parts of the brain. This transient coding hypothesis considers that transactions among neuronal subsystems use little packets or patterns of activity that are distributed in a structured way over both space and time. Through an analysis of the statistical dependence between spectral densities measured at different points in the brain this hypothesis was confirmed. The results were consistent with transient coding and suggested that these transients endure for at least 40–200 ms or so. The results presented here imply that correlations (rate coding) and coherence (synchrony) are neither complete or sufficient characterizations of neuronal interactions (for example high-frequency oscillations in the prefrontal cortex are associated with low-frequency oscillations in the partial cortex) and suggest that higher order, more general interactions may be employed by the brain. One implication of the transient coding hypothesis is that there is no teleologically meaningful brain process that exists below the temporal duration of a transient. This makes further characterization of neuronal transients a potentially important endeavor.

We have not attempted to characterize the nature of these transients here (this is the subject of current work). However, the results presented suggest that whatever their form or role in neuronal interactions, transients are an important candidate for furnishing the basis of a neural code.

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