Monitoring Neuronal Oscillations and Signal Transmission Between Cortical Regions Using Time-Frequency Analysis of Electroencephalographic Activity

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Oscillatory states in the electroencephalogram (EEG) reflect the rhythmic synchronous activity in large networks of neurons. Time-frequency (TF) methods, which quantify the spectral content of the EEG as a function of time, are well suited as tools for the study of spontaneous and induced changes in oscillatory states. The use of these methods provides insights into the temporal dynamics of EEG activity in both humans and experimental animals, and aids the study of the neuronal mechanisms that generate rhythmic EEG activity. Further, the use of TF coherence analysis, which quantifies the consistency of phase relationships in multichannel EEG recordings, may contribute to the understanding of signal transmission between neuronal populations in different parts of the brain. We have used TF techniques to analyze the flow of activity patterns between two strongly connected brain structures: the entorhinal cortex and the hippocampus. Both of these structures are believed to be involved in information storage. By applying various frequencies of stimulation, we have found a peak in the spectral power in both sites at around 18 Hz, but the coherence between the EEG signals recorded from these sites was found to increase monotonically up to about 35 Hz. We have also found that long-term potentiation, a strong increase in the efficacy of excitatory synapses between these sites, either had no effect or decreased coherence.

NOMENCLATURE

Dentate gyrus: a major component of the hippocampus that receives extensive cortical input via the entorhinal cortex.

Electroencephalogram (EEG): a recording of the electrical activity of the brain through surface or implanted electrodes.

Entorhinal cortex: a cortical region surrounding the hippocampus which receives processed cortical information and sends it on to the hippocampus (dentate gyrus).

Gamma band: a frequency band for oscillatory components of the EEG that fall between 20 and 80 Hz.

Hippocampus: a brain structure that lies in the region of the temporal lobe of the brain and receives processed information from several different sensory systems.

Long-term potentiation: a long-lasting increase in the strength of synaptically induced neuronal responses due to the application of electrical stimulation to the input pathways.

Neuron: a cell in the nervous system that is organized to generate and transmit electrochemical signals.

Olfactory bulb: the brain structure that receives input from olfactory receptors.

Pyriform cortex: the area of the brain that receives input from the olfactory bulb; this area is also referred to as olfactory cortex.

Synapse: the connection between neurons, via which an electrochemical signal is transmitted.

Temporal binding: the linking of individual neuronal representations of different, local features of external stimuli by a common oscillatory pattern of discharge.

Temporal lobe: the part of the brain just adjacent to the side of the head; the pyriform cortex, entorhinal cortex, and hippocampus lie within this structure.

Theta band: a frequency band for oscillatory components of the EEG that fall between 4 and 12 Hz.

I. INTRODUCTION

One of the great challenges in neurobiology is the understanding of how sensory information is represented by spatiotemporal patterns of neuronal activity and how these representations are transmitted from one brain region to another during their further elaboration and processing [1]. The measurement of electrical brain activity, and its

correlates with behavior, can provide us with useful clues about these processes. Unfortunately, current technology does not allow us to record the individual activities of more than about 50 neurons at a time (and very few laboratories are able to record from more than three or four). With such small numbers of cells sampled, there is little that we can say about the nature of the networks of millions of cells that mediate cognitive functions.

The alternative to multiunit recording is the use of large electrodes to record the summed electrical activity of very large numbers of neurons (the EEG) [2]. EEG can be recorded from scalp electrodes in human subjects or from electrodes implanted in specific brain regions of experimental animals. While the spatial resolution of the EEG is poor, the temporal resolution is quite good and can provide us with some insights into the activity of large networks of neurons. Spontaneously occurring EEG can be used to monitor the activity of neuronal networks during naturally occurring behaviors [3], [4], and changes in EEG activity following the presentation of experimentally controlled stimuli can offer further insights into the processes of perception, learning, and memory [5]. Such stimuli could range from relatively normal sensory (e.g., auditory or visual) signals to the application of electrical stimulation directly to brain sites through implanted electrodes. Both spontaneous and evoked EEG activity can be oscillatory in nature, and EEG recordings are used extensively to monitor neuronal activation patterns, and the flow of neuronal signals between brain sites.

EEG time series usually contain multiple frequency components, which vary spontaneously and in response to experimental manipulations. Further, these data sets can be quite large, especially when multiple brain sites are sampled in studies of the relationships between EEG activity in connected regions of the brain. There is a clear need for effective techniques for the analysis of these large data sets. In this paper, we explore the application of time-frequency (TF) analysis techniques to the description of the genesis and propagation of oscillatory EEG activity in brain sites believed to be involved in information storage. We have used these techniques to monitor the responsiveness of particular brain sites to rhythmic stimulation. We have also used coherence analysis to measure the transmission of induced signals between brain sites, both before and after increasing the strength of synaptic connections in the pathways linking these sites.

II. THE NEED FOR TF ANALYSIS

Oscillatory states are the most striking feature of EEG activity, because they reflect not only the synchronization of massive numbers of neurons but also a temporally ordered rhythmicity of activation [6]. Different oscillatory patterns may be indicative of distinct information processing states, and it has been proposed that the oscillatory patterns play an active role in those states [6], [7]. According to this view, the rhythmic synchronization during oscillatory states can serve to enhance perception, learning, and the transmission of neuronal signals between different regions of the brain.

Traditional spectral analysis has been widely used to quantify the different oscillatory activities in the EEG [8], [9], but the statistical assumptions underlying these methods require the time series to be wide-sense stationary. In reality, the neural processes that generate the EEG are intrinsically dynamic over many time scales, and the EEG can be considered quasistationary only for periods of a few seconds under controlled conditions [10]. Indeed, it is often the nonstationary nature of the EEG that is of primary interest. Transient changes in the power or peak frequency of EEG rhythms can provide information about the dynamic and reactive properties of neuronal substrates that mediate those rhythms. Unfortunately, these transients are not quantified with traditional spectral analyses that do not include time.

TF analysis methods, describing the frequency content of a signal as a function of time, are able to quantify these transients. Indeed, these methods have a long history of application to the EEG [11]–[17]. The theory of TF distributions (TFD's) is well developed and there are both linear and nonlinear methods available for use [18], [19]. The linear methods include the *short-time Fourier transform* (STFT), which is a natural extension of the ordinary Fourier transform [20]. The nonlinear methods include the Wigner–Ville distribution (WVD), which is a bilinear TFD [18], [19]. Our primary interest in TFD's is in their use as a tool for "signal analysis." In this context, the WVD offers a higher resolution capability than the STFT, but it suffers from two serious shortcomings: 1) the generation of cross terms due to the presence of multicomponents in the signal and 2) the presence of "negative" energy contributions.

Most of the research results reported in this paper are based on the STFT, and some comparisons with the WVD are included. We also experimented with the pseudo-WVD that employs a window function. This calculation has the effect of attenuating the highly nonlocal nature of the WVD, with the result that the cross terms are suppressed to some extent [18].

These TF techniques have been applied to the study of oscillatory patterns and connectivity in various brain areas. Our primary focus has been on an integrative system that processes olfactory inputs.

III. OSCILLATORY PATTERNS IN THE OLFACTORY SYSTEM AND TEMPORAL LOBE EEG

The temporal lobe is the part of the brain lying adjacent to the side of the head (temple). The structures of the temporal lobe, including the olfactory system, display a variety of oscillatory rhythms related to perceptual and cognitive activities. One role of these oscillatory states may be to synchronize the activity of spatially diffuse populations of neurons, so that they may become more effective in forming global neural representations of sensory input. Exposure to an olfactory stimulus activates olfactory receptors that transmit information to a structure called the olfactory bulb. An olfactory stimulus triggers a burst of gamma (20–80 Hz) activity in the olfactory bulb, which is then projected to other sites within the olfactory system
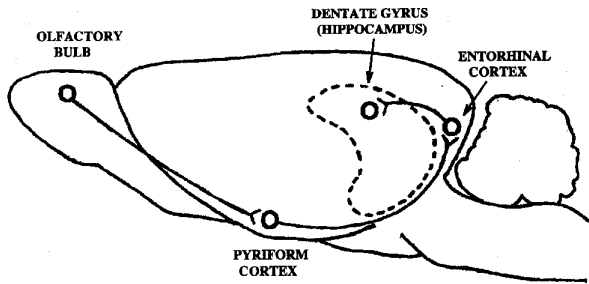
Fig. 1. The trajectory of the polysynaptic pathway tested in the experiments reported in this paper is shown above. This figure is a highly schematic representation of the rat brain as seen from the side. The information flow runs from olfactory bulb to pyriform cortex to entorhinal cortex to the dentate gyrus of the hippocampus (referred to in the paper simply as the hippocampus). In our experiments, bipolar *stimulating* electrodes were implanted into the pyriform cortex, bipolar *recording* electrodes were implanted into the entorhinal cortex, and hippocampal dentate gyrus.

[21], [22] (Fig. 1). The spatial distribution of gamma wave amplitude across the olfactory bulb changes gradually in a spatially ordered way in a task requiring the discrimination between different odors [23]. This suggests that gamma waves play an important role in spatial coding of olfactory stimuli. Similar oscillations have been recorded from the cat visual cortex [24], and from the human cortex using magnetoencephalography [25]. Neurons discharge rhythmically during gamma bursts, and the correlations between the firing of multiple neurons increases with the integrity of the stimulus driving the burst. It has been proposed that the gamma oscillations can serve to temporally "bind" the individual neuronal representations of different, local features of a stimulus [26].

Because of the time-varying nature of perception and the associated nonstationarities in gamma activity, TF techniques are appropriate for analyzing the temporal relationships between gamma activity and sensory stimulation. For example, during a visual performance task in which a monkey must discriminate between two visual stimuli, local EEG activities in a number of widely distributed cortical sites show increases in coherence for a brief period following the stimulus presentation [27]. Coherence between cortical sites increases not only at low frequencies but also in the gamma range within a few hundred milliseconds after the onset of the stimulus.

IV. SIGNAL TRANSMISSION IN THE CORTICAL PROJECTIONS TO THE HIPPOCAMPUS

The hippocampus is a temporal lobe structure involved in spatial memory and the integration of sensory information. Much of the information the hippocampus receives from cortical areas, including the olfactory (pyriform) cortex, is funnelled through the entorhinal cortex [28] (Fig. 1). The pathway between the entorhinal cortex and the hippocampus has been shown to readily support long-lasting increases in synaptic connection strength which are thought to contribute to memory formation [29]. Consequently, we have chosen to study the transmission of neuronal signals between the entorhinal cortex and the hippocampus (Fig. 1).

There were three primary objectives in this research: 1) to confirm that TF analyses are capable of resolving nonstationarities in the data set, 2) to determine the frequencies for optimal signal transmission from the pyriform cortex to the hippocampus via the entorhinal cortex, and 3) to determine the effects of enhanced connectivity between the entorhinal cortex and hippocampus on the flow of normal and imposed neuronal signals between these sites. The enhanced connectivity was induced by *long-term potentiation* (LTP) [29], which occurs in these pathways following the application of brief, high-frequency stimulation trains. Neuroscientists utilize this phenomenon to study the mechanisms of synaptic plasticity. In our experiments, LTP was induced by stimulating the pathway connecting the entorhinal cortex to the hippocampus.

Electrodes were implanted into the pyriform cortex, entorhinal cortex and hippocampus (Fig. 1). Following recovery from surgery, samples of EEG were recorded from the entorhinal cortex and hippocampus. The samples were analog-filtered (0.3–100 Hz), amplified, and digitized at 256 samples/s. The STFT was applied to 30 s sweeps of filtered EEG using a 2.0 s moving window (Hanning window) with a 1.9 s overlap between consecutive computations. This analysis was extended to the computation of a TF coherence function[1] [12] between the entorhinal cortex and hippocampal EEG. The TF coherence function provides a frequency-specific measure of the linear phase coupling between two signals as a function of time. Therefore, it can be used to measure the efficacy of the transmission of oscillatory signals from the entorhinal cortex to the hippocampus. A total of 15 sweeps of EEG were collected to obtain the TF coherence function; these sweeps were disjoint in time.

1) TF Analysis and the Detection of Nonstationarities: We applied the STFT and WVD to the characterization of two different nonstationary data sets. First, we collected samples of 8–10 Hz spindle discharges, which are obvious *spontaneous* transient events in the cortical EEG. Second, we experimentally imposed nonstationarities into the entorhinal cortex EEG by applying low-intensity stimulation trains to pyriform cortex. The EEG was recorded during stimulation with a train of pulses that was ramped from 1 to 40 Hz (50 μA, 100 μs pulses). Fig. 2 shows examples of both types of EEG trace and the results of two different types of TF analysis. As can be seen, the nonstationarities

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[1] Let $X^{(n)}(t, f)$ and $Y^{(n)}(t, f)$ denote the STFT's of the signals $x^{(n)}(t)$ and $y^{(n)}(t)$, respectively. The superscript (n) denotes the nth of N realizations (sweeps) of the two signals. The TF coherence function between the signals $x(t)$ and $y(t)$ is defined as follows:

$$\Gamma^2(t, f) = \frac{\left| \sum_{n=1}^{N} X^{(n)}(t, f) Y^{*(n)}(t, f) \right|^2}{\sum_{n=1}^{N} |X^{(n)}(t, f)|^2 \sum_{n=1}^{N} |Y^{(n)}(t, f)|^2}$$

where the asterisk denotes complex conjugation. Note that t refers to the time coordinate relative to the start of each sweep. Note also that for fixed t, the TF coherence function $\Gamma^2(t, f)$ reduces to the ordinary coherence function.
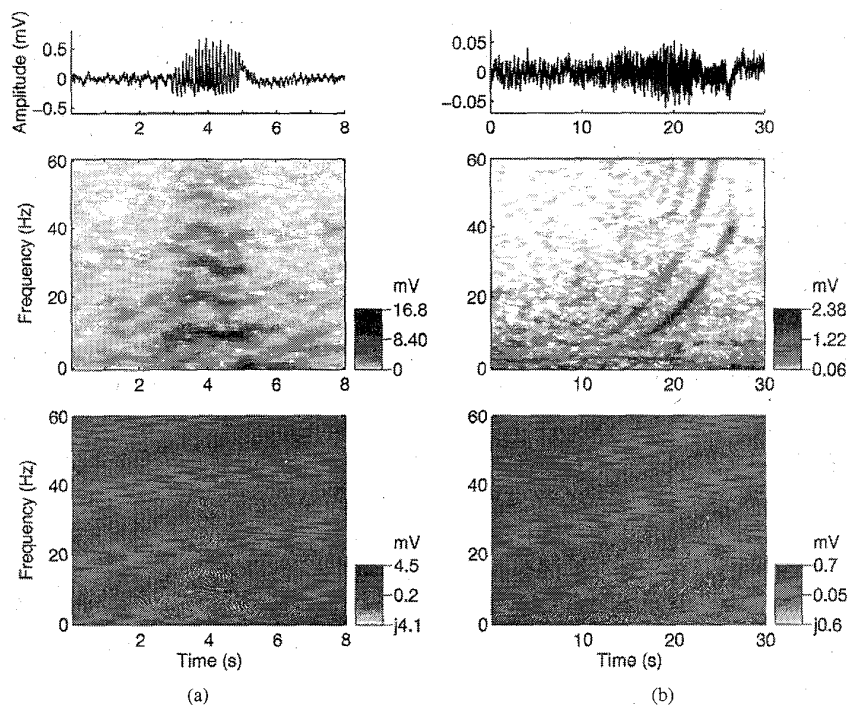
Fig. 2. (a) The spindle discharge in the upper left panel was recorded from the rat frontal cortex. It is a typical example of a nonstationarity in the *spontaneous* EEG. (b) The EEG trace in upper right panel shows a rather extreme form of nonstationarity, though of much lower amplitude, that is induced in the entorhinal cortex by stimulation of the pyriform cortex. The stimulation consisted of a train of pulses that was ramped from 1 to 40 Hz. The middle panels show the results of STFT analysis of these EEG segments. The lower images show the results of standard WVD analysis.

are well delineated by using these procedures. There are some striking differences between the STFT and the WVD images:[2] 1) the WVD exhibits a higher resolution than the STFT, both in time and frequency, and 2) the presence of the cross-terms in the WVD makes its interpretation more difficult [particularly for the spindle waves—Fig. 2(a)].

2) Frequency-Dependent Transmission of an Externally Imposed Signal: While theta activity (4–12 Hz) in the entorhinal cortex and hippocampus was the dominant rhythm and was highly coherent in the *spontaneous* EEG, the results of the STFT on the response to the ramped stimulation trains indicated increased power during higher stimulation frequencies [Fig. 2(b)]. We examined this more closely by applying a wide range of frequencies of stimulation to the pyriform cortex. The stimulation frequencies remained constant throughout each train, and the frequencies tested ranged between 2 and 35 Hz. This procedure enabled tight experimental control over the temporal characteristics of the input signal, and allowed the determination of the frequency response characteristics of both entorhinal cortex

and hippocampus. Although initiated electrically, the signal transmitted to the hippocampus was *synaptically* generated within the entorhinal cortex (as confirmed by postmortem analysis of stimulation artifacts which were small and well-filtered—Fig. 3). The stimulation trains were applied during the middle third of the 30 s EEG samples, and STFT representations were obtained for both the spontaneous and stimulus-driven segments of the samples. The stimulation trains were set to an intensity level that would trigger response amplitudes that were generally less than 10% of the asymptotic evoked response amplitude. These responses could seldom be seen in the time-domain above the background noise.

Power in the spontaneous EEG was concentrated at low frequencies between 1 and 10 Hz (Fig. 4). The theta rhythm was the dominant rhythm within this band in both of the tested structures. Power and coherence within the theta band increased during ambulatory activities [30]. Changes in EEG activity induced by the low-intensity stimulation were often more apparent in the TF images than in the time domain (Fig. 4). Power and coherence were increased at the stimulation frequency and its upper harmonics (Figs. 4 and 5).

When these measures were compared across different stimulation frequencies, we found the largest stimulation-dependent increases in power occurring at about 18 Hz in both the entorhinal cortex and hippocampus (Fig. 6).

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[2] In the STFT displays presented in Fig. 2, darkness is a measure of the magnitude of the STFT. In the WVD displays, darkness is a measure of the square root of the WVD. The reason for using amplitude, rather than power, as the z coordinate was merely one of providing a better contrast.

We also experimented with the use of Hanning and Gaussian windows to perform pseudo-WVD [18] in the data. The results obtained by the latter method were very similar to those obtained using the standard WVD, except for the attenuation of cross terms in some parts of the WVD image.
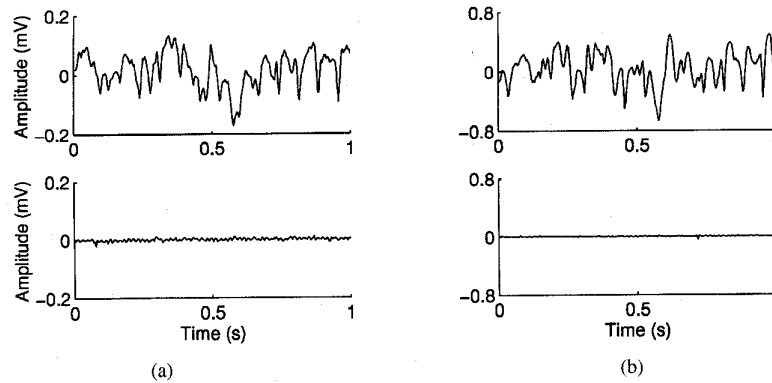
Fig. 3. Representative EEG traces recorded during the experimental tests are shown for the entorhinal cortex (a) and hippocampus (b) in the upper panels. EEG's recorded from the same sites 5 min after death from anesthesia are shown in the bottom panels. A 14 Hz stimulation train was applied to the pyriform cortex in both cases. As can be seen, the electrical artifacts from the stimulation trains are minimal.
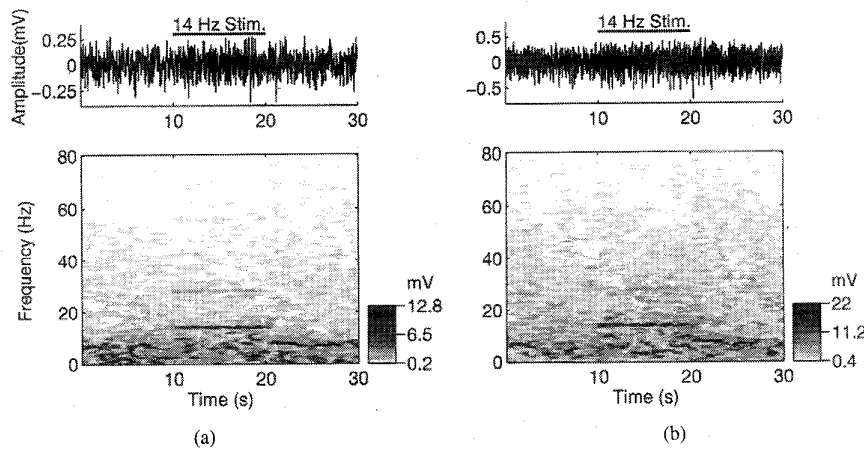

Fig. 4. The upper traces show examples of raw EEG activity in the entorhinal cortex (a) and hippocampus (b) during application of a low-intensity, 14 Hz stimulation train to the pyriform cortex. The lower panels show the results of STFT's of these traces.

In contrast, the coherence function did not fall off with stimulation frequency; rather it increased monotonically (Fig. 6). Thus although the neuronal signals above 18 Hz were reduced in magnitude, their phase coupling was even more consistent.

3) TF Analysis of the Effect of LTP Induction: Although increasing synaptic connectivity was expected to increase coherence between EEG's recorded in the entorhinal cortex and hippocampus, coherence was unaffected or even decreased (data not shown). This was the case for both spontaneous and stimulus train-driven EEG's. In retrospect, perhaps this result should have been anticipated. LTP effects are typically observed clearly only at high levels of activation [31], and the stimulation intensities used here were kept low to produce more normal polysynaptic patterns of activation. Consequently, these results suggest that strong enhancements in synaptic connectivity associated with LTP may not result in similarly strong changes in the transmission and phase relationships of more normal oscillatory activation patterns. TF methods like those used in this paper are essential to test for the occurrence of such changes.

V. DISCUSSION

TF signal processing techniques provide an effective tool for observing the time course of changes in oscillatory states in EEG activity. The correlation of these changes with relevant physiological and environmental stimuli, in turn, has aided the study of the functional significance of oscillatory states during perception, learning, and pathology. Further, TF coherence analysis methods have allowed the investigation of the temporal relationships between rhythmic activities in different regions of the brain. These methods provide additional tools for investigating the role that oscillatory states play in determining the flow of neuronal activity from one brain site to another.

As expected, we found that the dominant rhythms in the spontaneous EEG of the entorhinal cortex and hippocampus fell within the 4–12 Hz (theta) band. The TF methods used here allowed the description of nonstationarities in the power and coherence of these rhythms, and showed that the response of these structures to pulse trains occurred most strongly around 18 Hz. Further, coherence analysis indi-
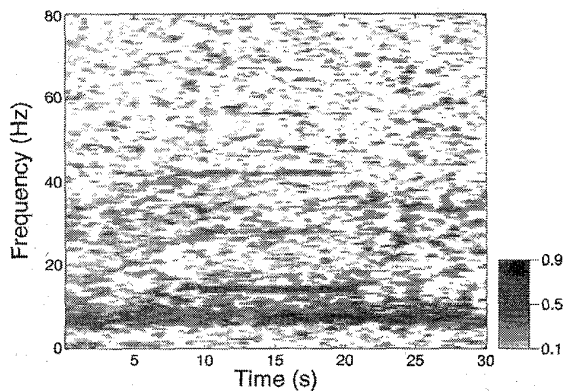
Fig. 5. TF coherence function for the entorhinal cortex and hippocampus data shown in Fig. 4. Note the enhanced coherence at 4–8 Hz (within the theta band) throughout the sweep, and the enhanced coherence at the 14 Hz input frequency and its harmonics during the middle 10 s.
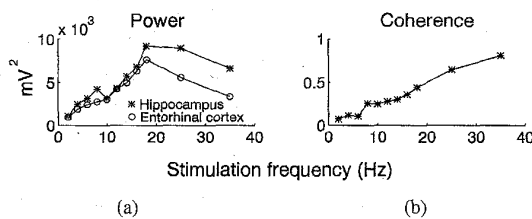

(a)   (b)

Fig. 6. Stimulation-related power in the (a) entorhinal cortex and hippocampus and (b) coherence as a function of pyriform cortex stimulation frequency. To determine the effects of stimulation, the total power at the stimulation frequency and its upper harmonics during the *spontaneous* EEG was subtracted from the measures during train delivery. For the coherence measures, the mean coherence in spontaneous EEG was subtracted from the coherence measures during evoked EEG.

cated that signal transmission between these sites peaked at even higher frequencies.

Background rhythms in olfactory cortex often peak around 40 Hz, so it was suprising to find peaks in the power occuring at 18–20 Hz in response to stimulation trains. Recently, Heale et al. [32] have found that certain odors do, in fact, trigger responses in the 18–20 Hz range. They conclude that these odors are activating systems that are tuned to respond to predator signals. TF techniques provide one means of tracking these signals through the brain sites that would most likely respond to biologically significant signals such as predator cues.

The experiments on LTP induction indicated no change or decreased coherence between the tested sites. In ongoing experiments, we have now found that the coherence measures based on strong sensory (olfactory) signals are also decreased after the induction of LTP in the tested pathways. We are currently investigating the basis for this decrease in coherence. One possibility is that inhibitory systems are potentiated along with the excitatory systems by the application of high-frequency trains. The information flow through the activated pathways would depend upon the balance between excitation and inhibition, and this balance

may be differentially affected at low and high activation levels. In support of this proposal, we have found that field potential amplitudes are often depressed at very low stimulation intensities following the induction of LTP. Using TF techniques, we can monitor the coherence between pathways at different intensities while manipulating the involvement of inhibitory systems pharmacologically. These experiments may lead to improved diagnostic techniques for evaluating the balance between excitation and inhibition in human neurological patients.

There are a number of other analytical techniques that could be applied to similar data sets. Rhythmic EEG patterns are nearly always nonsinusoidal. Consequently, particularly in the more extreme cases (e.g., seizure discharge, stimulation-driven activity), much of the power can be found in the upper harmonics rather than in the fundamental (Fig. 2). TF methods that collapse power within broad frequency bands (e.g., alpha, gamma) can obscure the relationship between higher-frequency components and their lower-frequency generators [33]. Upper harmonics can be linked to the generator of the fundamental frequency component by bispectral analysis [34], but to our knowledge there are no reports of TF bispectral analysis of the EEG. The *cross* bispectrum could be used to study the relationships between different frequency components in separate brain areas; but here again there are few reports of its use with EEG [35], and no TF applications. Another promising methodology is partial coherence. When EEG is recorded simultaneously from additional sites, the technique of partial coherence can be used to account for the common effects that other sites may have on the measured coherence between the sites of interest [36], [37]. We are currently exploring the use of these techniques for the study of signal transmission between brain sites.

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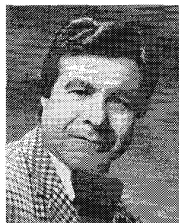
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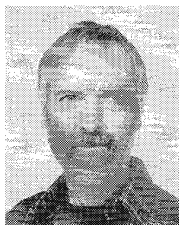
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