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Biology of brain waves: natural history and evolution of an information-rich sign of activity

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Abstract. Using "brain waves" and "EEG" broadly for ongoing electrical activity and stimulus- or event-related activity of organized masses of neural tissue as seen by wideband amplifiers and macro-, micro- or semi-microelectrodes within or in electrical contact with the central nervous system, I consider the character of these signs in animals of many phyla, by various descriptors, emphasizing local field potentials, pregnant questions and research opportunities.

We still have inadequate or hardly tested ideas of why most invertebrates, large and small, have inconspicuous slow waves (<50 Hz) and conspicuous spikes. They can, however, show slow waves under certain conditions, somewhat reminiscent of spinal cord, cerebellum or retina.

We have even less tested explanations of the strong similarity of all vertebrates: fish, amphibians, reptiles, birds and mammals, large and small - with respect to the power spectrum of conspicuous slow and inconspicuous spikes (until hunted by microelectrodes). Amplitude is the only obvious difference among vertebrate classes, mammals being highest. This may come from an evolution of the prevalence of synchrony, attributable, if true, to a generally higher coherence between pairs of sites in reptiles, birds and especially mammals.

The strong similarity in the power spectrum, among taxa with and without a cortex, is only one of several reasons to believe that we have not found the most relevant measures to reveal the real structure of the time series, in space and time. Fine structure in the millimeter and fractional second domains, in the seemingly stochastic, wideband component of activity is probably widespread and greater in mammals than in fish. It has properties that are not obvious, such as nonlinear quadratic phase couplings and pseudo-periodicities, locally and episodically. Wavelet analysis, independent component analysis and other tools that might reveal nonrhythmic fine structure have not yet been applied to evolutionary studies.

A new tool, the Period-Specific-Average (PSA) can show real rhythms even when the power spectrum does not and shows absence of rhythms at some frequencies where the power spectrum peaks show Fourier components of irregular transients. The PSA shows that most of the spectrum most of the time in most human cortex is without significant rhythms. Special conditions bring out episodes of delta, theta, alpha, beta and gamma waves and their subtypes, usually only one or two at once, while most of the energy is wideband and seemingly stochastic. Between episodes of one or two rhythms there are major periods of time in normal human life without any significant rhythm in cortical surface (subdural) and depth electrodes. In spite of many kinds of sophisticated analyses, gross mappings, and models, with our present understanding, we cannot yet anticipate the character of scalp or subdural surface or macroelectrode depth recordings from microelectrode data or vice versa. Also lacking, so far, is any general understanding of the relation of slower, local field potentials and spike firing. Examples are known of strong positive correlations and others show no correlation. Communication among neurons by subthreshold, nonsynaptic routes is probably important in some evolving places and times.

The relative neglect of the basic biology, natural history, evolution, and system identification of local field potentials at different scales in different places is undeserved and a prime opportunity for new tools .

If a living organism moves or emits light, electricity, secretions, or sound - whether it sings

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or buzzes or ticks, if it squirts or flowers or lays eggs, *biologists ask three kinds of questions*: what, how and whence. The first question may be stated: what is the most adequate description of whatever is happening? The second question: how does it work? The third question is where did it come from - ontogenetically and phylogenetically? The task I set myself here is to look at what we neuroscientists have done and comment on the proposition that we haven't done much on any of these three fronts with respect to one form of action, the electrical activity of the nervous systems of humans and other animals.

Our descriptions of brain waves (a term which I will use as shorthand for ongoing electrical activity of the central nervous system, whether seen from the scalp, or on, or in the brain) have usually been in terms of the power spectrum. This may be about as adequate as describing an opera in terms of its power spectrum. Chaos analysis and mutual information and bispectrum and all the rest have surely not adequately described the fine structure in space and time and the cooperativity of the myriad electrical generators in the depths of the brain. Still less have we an understanding of either *how the brain waves are generated or what their roles may be* - that is, whether they are purely the noise of the engine or can sometimes in some places also act as causes, able to influence cells in a field.

I find in some current literature that the EEG is the summation of action potentials! More often it is considered to be the summed synaptic potentials. We certainly know a number of other *kinds of potentials* that are at least candidate contributors and we can suspect still others. Even farther behind is any big picture of the *evolution of brain waves* - who has them, what they are like and how come? I will make some remarks on each of these three areas, as seen by a comparative biologist.

The "how it works" question

First, let me deal with the how question - because there is little more to say. We think that most of the *generators are cellular or subcellular,* that is the cell membrane of one part of the cell changes its impedance or leakiness, relative to other parts of the cell. The impedances face standing potentials across the membrane, which may vary from place to place. This subcellular differentiation of one part from another, changing in time, is essential to explain the extracellular field activity, because if the whole cell stood or changed together we would have a closed system and could see nothing in the external field. We suppose that each of several kinds of membrane changes

contributes to the summed external field: all-or-none **action potentials** (as far as they can invade the somata, dendrites and axon terminals), graded **slow** (ca. 0.1-50 Hz), subthreshold and **infraslow changes** in the membranes, **pacemaker potentials,** both rhythmic and nonrhythmic, **local potentials, synaptic potentials, miniature,** even **quantal events** peculiar to axonal terminal arbors or to dendrites or somata.

Some neurons - perhaps quite a few - never or rarely have all-or-none action potentials - which I may hereafter call spikes. **Neuroglia** of several kinds are also candidate generators. We cannot exclude other sources such as **streaming potentials** at the walls of blood vessels and epithelial potentials at the ependymal and pial surfaces. Empirically we find that events contribute over a wide spectrum of durations, from fractional milliseconds to many seconds and even minutes. The cellular and subcellular generators act as dipoles or multipoles in the size range from a few up to at least dozens of micrometers and they have some more or less consistent orientations to help determine their contributions to the sum. The extracellular volume conductor is a complex configuration of interstices that cannot be assumed to be homogenous. Most of this is a guess and we might have a quite distorted idea of the true situation (Bullock 1988, 1989a, 1991, 1997, 1999; Bullock and Başar 1988) Of course, there is an enormous literature on brain waves; a great deal has been learned - mostly clinical correlations. Here we deal with general biological questions.

In particular I would underline that we have little basis to judge the *relative importance of spikes* and synaptic communication on the one hand and of nonspike, nonsynaptic communication between cells on the other - especially since their qualitative roles are no doubt quite different in the kind or meaning of the communications they mediate.

The diversity of kinds of neurons must have some role and consequence in the summed activity of organized assemblies. Uniquely among all the organ systems of the body, the nervous system has units with widely different or only slightly but importantly different receptive fields and projection fields as well as subthreshold behavior and spiking properties from never spiking to two kinds of spikes (Bullock 1980).

Synchrony among some proportion of the active cells, whether firing spikes or undergoing subthreshold fluctuations, due to intrinsic cellular spontaneity or to impinging input, must be a major variable. Probably several distinct kinds of synchronization coexist, largely by way of the phase

locking of slow fluctuations and thence of spikes or bursts.

Non-synaptic field effects are probably a major part of the communication between cells, besides the classical spikes and synapses, usually the only channel considered. Non-synaptic influences include direct electrical subthreshold interaction of slower fluctuations, some very slow and spoken of as "DC" or "infraslow".potentials (Bullock 1993, 1997; Ezrokhi and Voronin 2001).

The **infraslow potentials** are often greater in voltage than all the rest of the activity and almost certainly exert strong modulatory influences upon spiking frequencies of many cells (Aladzhalova 1958; O'Leary and Goldring 1964; Lickey 1966; Rowland 1967, 1968; Adey 1969; Speckmann and Elger 1987; Lang et al. 1992; Elbert 1993; Albrecht and Gabriel 1994; Bullock 1999; Devrim et al. 1999).

As already stated, we have no basis for estimating the relative importance of spike and synapse vs non-spike, non-synaptic information processing and communication in neuropile and gray matter. Long distance communication that depends on spikes is certainly important but may be the postal service to the more continuous, decisive, integrative communication within the board rooms, auditoriums, offices and homes of the neurons and the glia. I hope it is obvious by now that the aim is to lift up for attention some questions of broad general interest that have been relatively neglected and offer attractive opportunities for new research.

Neuronal integrative mechanisms

Instead of ***a*** code of the brain, *several or many codes*, including non-spike codes, operate in parallel. The long list of **integrative mechanisms**, cellular and subcellular, whereby converging influences upon a neuron, excitatory and inhibitory, are weighted, and facilitate over time or disfacilitate with shorter or longer time-constants, or both - this list is already well above fifty (Bullock 1993, p.16) and increases with nearly every issue of the journals. These integrative mechanisms *act at many levels:* protein synthesis, intracellular messengers, release of modulators of many kinds, gate opening and closing rates, transfer functions and non-linearities of many steps. Something similar probably happens with respect to small or medium populations of cells and more or less discrete circuits. By something similar I mean there are probably several levels of integration and parallel as well as serial operations. My guess is that the brain is a reservoir of unfamiliar principles of system organization, waiting to be discovered.

The operations of the brain and of its constituent parts, nuclei, laminae, and circuits are *not*

well understandable simply by unraveling the connectivity or hard wiring. We require also a major set of specifications of properties for each unit and site of interaction, mostly dynamical and plastic properties. I call them personality traits of the neurons and glia and sets of them. They represent formulae, equations and graphs of time dependence and state dependence, as additional determinants of output. The expression "circuits", even "local circuits" in the usual electronic engineering sense is a quite inadequate analog and terminology.

For this most complex of all systems, except systems of brains, we *lack appropriate familiar terminology* and analogs. Sometimes I find it heuristic to liken the organization of a brain to that of a complex human institution such as the government or a university. Many similar individuals perform a few similar acts - writing, speaking, filing and transporting materials, with many levels of integration, degrees of uniqueness and redundancy, plastic connectivity, serial and parallel. But, the analogy is limited.

Still speaking to the *problem of how it works*, the science cannot afford to wait for information about single cells and lower levels to accumulate sufficiently to permit bottom-up explanation or prediction of organized assembly dynamics. **Emergents** have already spiced up the history of brain physiology and are the only sure prediction in our science. Even hundred-channel recording of units, even if each channel were, as never before, wideband to allow both spikes and slow signals to be seen, is unlikely to make interpretation easier. Multichannel **unit** recording, with high resolution in space and time is certainly the wave of the future and a white hope for new insights, stipulating technical problems yet to be solved. But it will overlap with multiunit extracellular field potential, wideband recordings - which I am here advocating in spite of the relative neglect and low opinion of some physiologists who are still making important discoveries from unit spike recordings. Another outstanding need today is for models of the nervous tissue, realistic with respect to geometry of subcellular generators, volume conduction, both spike-like and subthreshold, slow activity - on which to test ideas about synchrony, rhythms, field effects and redundancy.

The "what" question - an adequate description?

This view of how it works does not give any clues to what we should measure or look for in the time series and their spatial distributions in various parts of the brain and different species to provide an adequate description of brain waves. Now that the brain is regarded as central to behavior

and mental life, we can not be satisfied with statistical measures of Gaussianity, Fourier analyses of energy at each equivalent frequency component, or estimates of dimensionality. Expecting nonlinearity and nonstationarity to be characeristic, except in special states, we do well to seek any evidence of microstructure, temporal as well as spatial.

Whether one considers the ongoing unstimulated background activity or the activity related to stimuli or to mental events or to changes in state, an array of extracellular, semimicro-probes, each detecting the wideband activity of a small volume overlapping with that of neighbors offers an **array of information-rich time-series** that challenges our ingenuity to find tools that might uncover nonrandomness potentially related to behavior or state. If the array is fortunately situated we may be able to recognize some of that rich information although it will in the general case be as difficult to interpret as would an array of microphones at a political convention in a foreign language; indeed, even more difficult, since the number of units in the brain is many times greater. One concept that embraces many approaches and relevant measures is called *cooperativity* - any aspect of the assembly considered as though it were an interacting group.

Fig.1 about here

Figure 1A shows one current state-of-the-art method of visualizing cooperativity of traveling brain waves in a plane by using voltage sensitive dyes and **optical recording** via an array of ca. 20 x 20 sensors. Without averaging, but confined to the near-surface plane, ca. 60 ms and 80 Fm temporal and spatial resolution is permitted in this favorable case by the optical noise reduction of replacing blood with corpuscle-free saline in a suitably tolerant species, the pond turtle.

Coherence is a first order, linear form of cooperativity measured for pairs of places at each frequency in the Fourier space. Although on the average it is high between electrodes a few cell diameters apart, in our measurements of rabbit cortex it is commonly low and varies widely second by second and pair by pair a few millimeters apart (Bullock and McClune 1989; Bullock et al. 1995a, b) . Average coherence falls rapidly with distance when recording with small electrodes - to chance level within ca. 10 mm. This is true for all frequencies, except for theta during episodes of high theta or for alpha during episodes of high alpha. The evidence of local fine structure and dynamic changes is *much less true with larger electrodes or with surface electrodes* on the pia or dura or outside the skull.

Somehow the average coherence of local field potentials is able to rise to quite significant

levels on the scalp, even at separations as great as 40 mm between electrodes - each of which "sees" a large cone of active tissue overlapping with its neighbors. Neither result, the fine structure at the micro level or the macro structure from the surface could predict the other. Finer microelectrodes within the cortex or most subcortical regions, apparently, on average, show relatively more energy at higher frequencies and less coherence at a given distance plus many sharp discontinuities of coherence between one pair of electrodes and another close by. As one *approaches the cellular level, one often finds high agreement but often finds the opposite.* There are large regional differences, even between cortical laminae, such as those of the optic tectum and of the cerebellum.- but we really know little about regional distribution and lack a solid body of data recorded and analyzed in the same way.

We have found fine structure in space and time also with the unrelated, nonlinear and higher order measures called **bicoherence and bispectrum,** which depend on quadratic phase coupling between nonharmonic frequencies in the same or in different channels (electrodes). They also show episodic, transient increases very locally, suggestive that these may characterize some states or places, in the domains of seconds and millimeters (Bullock et al. 1998b).

Other measures, such as partial coherence, mutual information, dimensionality and chaos, entropy, wavelet analysis, and the Fourier spectrum have been used, principally via scalp electrodes on humans, looking at large cones of brain tissue. Much needed are searches for wave or spike burst packages with a degree of complexity that recur now and then, permitting efforts to find their correlates. Quite possibly some programs might be useful from the libraries of he search for nonrandom patterns in radio frequencies from extraterrestrial sources.

Particularly promising is the recently introduced **Independent Component Analysis** (ICA) which allows searching for localized sources of distinct time series at the resolution of the spacing of electrodes (Jung et al. 2001). It has not to my knowledge been applied intracranially or to laboratory animals or non-mammals.

How much is local brain activity rhythmic?

At present my colleagues and I are exploring **rhythms** (= oscillations) in human subdural and depth as well as scalp recordings, non-human and non-mammalian and invertebrate recordings, with a new method that permits the *distinction between real rhythms and peaks of Fourier components* which may not represent rhythms but Fourier components of irregular transients

(Bullock et al. 1998a, 2000). It is an additive periodogram we call **Period Specific Averaging** (PSA), based on the method of Enright (1965); the time series sample is segmented at an arbitrary period and these are averaged; this is repeated at every possible period between chosen limits, at a resolution of <1% of the period. The variance of each average is plotted against the period. Periodicities can be revealed which are missed by the FFT as well as, more often, absence of periodicity revealed where the FFT has a peak. PSA is nearly independent of wave form or duration of a repetitive event. It can show up to several nonharmonically related rhythms anywhere in a chosen range, such as 2 - 50 Hz, even in brief sample epochs. It works even when the stochastic background is many times higher than the rhythmic signal, i.e. with a signal to noise ratio of 1/4 or 1/5. If the rhythm is sloppy or frequency-jittered by 10 or 20 percent it is still useful though less sensitive. The control is the same time series segmented with randomized phase or randomized start times, permitting peaks to be highlighted when they are 95% or 99% confident. Figure 2 shows a short sample of band-passed noise and the absence of confident rhythms at some periods with FFT peaks.

Fig.2 about here

The idea is to provide another descriptor potentially discriminating or characterizing places in the brain, or states, stages and species or taxa. So far this method has shown that: (a) much of the time most electrodes see no rhythm, (b) rhythms are often short lived - appearing in one 4 s epoch and not the next, (c) clear rhythms in the human are usually narrow-peaked, rarely sloppy or otherwise frequency modulated, (d) generally, if there is a rhythm at all there is only one that stands out or lasts for some time; but a second, third or fourth not harmonically related can occur, usually for a short time. The method has many limitations and the plots are not easy to read, as yet.

We see the classical rhythms - delta (1-3 Hz), theta (4-7 Hz), alpha (8-13 Hz), beta (14-29 Hz) and gamma (30-80+ Hz), with their subtypes, each under the special circumstances that conduce to their appearance (Lopes da Silva et al. 1976; Bullock 1992; Basar and Bullock 1992; Basar 1983; Gray 1994; Bullock and Achimowicz 1994). Those special circumstances are not present most of the time, so that most local fields seen with subdural or depth macroelectrodes are most of the time without any rhythm that is statistically confident. Figures 3 and 4 show samples of human EEG with PSA & power spectrum.

Figs. 3 & 4 about here

Even though much of the EEG, especially the **intracerebral local field potentials**, are largely the stochastic result of independent fluctuations of many cells, I posit that it also *hides nonrandom and nonrhythmic features* in time and space. The challenge, as I see it, is similar to deciphering voices from babble on the radio or in a cocktail party. A human listener is likely to be able to say within seconds: "I hear something that sounds like Japanese from over there and something that sounds like Russian from over here - although I do not know either language." You can tell classical from pop music - but we don't know how you do it - or how to tell a computer to search for a non-stochastic pattern of unspecified form, except by wavelet analysis. We recognize and discriminate voices, handwriting, faces, even caricatures. We have fast, parallel filters for biologically important complex stimuli. But how do we uncover more of the spatiotemporal structure in the EEG? We have hardly begun.

I imagine that two or three human listeners given suitably transposed audio versions of the independent components extracted from multichannel brain recordings might with some hours of training, learn to discern agreed upon differences among the parts of the brain and between states of the brain. The result seems likely to be vastly more informative than images of local blood flow or positron emission. Particularly interesting, because my intuition fails me, is the question whether local field potential recording from small volumes or from the pial surface or the scalp would be more likely to reveal patterned or unpatterned signals. A large step in the informative direction will be to estimate the volume of the independent sources, comparing two kinds of recordings, one being multiple semimicroelectrode arrays *within* the brain, and the other being macroelectrodes on the pia or outside the skull, in monkeys or cats where we can do both.

So much for the "what" and the "how" questions, a view of the *nature of brain waves* and a series of hypotheses posed as existence theorems, in short, physiological natural history. Any substantial departure from the view I have outlined, once compelled by the evidence, would be more of an advance in scientific understanding than a finding that is compatible with this view.

The question "whence"

The third question "whence?" is also descriptive but adds the dimensions of **evolutionary time and phylogenetic relationships**. I will here omit discussion of the ontogenetic dimension. Formulating the goal more modestly, until the day when we have a sufficient data base: what are brain waves like in some birds, reptiles, amphibians, fish and invertebrates of various phyla -

especially the molluscs, arthropods, and annelids because they have concentrated and differentiated brains?

In spite of a paucity of studies (Adrian 1931; Adrian and Buytendijk 1931; Bullock 1989b, 1993; Bullock and Basar 1988), we know enough to raise basic and interesting questions. I will pose two in particular. (1) Firstly, what can be the relevant physiological or anatomical *differences between vertebrates and invertebrates* that explain a drastic difference in the EEGs from their respective higher brain centers - almost any recording from any species of either group? The major exception is the cephalopods which have EEGs more like those of vertebrates than those of other invertebrates. (2) Secondly, what can it mean that vertebrates, fish, frogs and man, show *essentially indistinguishable EEGs*, if we look at the midbrain tectum or the cerebral pallium or the cerebellum or the olfactory bulbs? I can be only a little more specific on each of these two puzzles in the space available. But I believe they are important and potentially illuminating differences.

(1) The first evolutionary puzzle I want to mention is what can it mean that a consistent *difference in the power spectrum* of the EEG appears to be general, comparing *any vertebrate with any invertebrate*, apart from the cephalopods, such as octopus and cuttlefish? The typical invertebrate record of ongoing electrical activity is spikey with single unit and compound spikes of one or a few milliseconds width, riding on slow waves that are usually inconspicuous (Figs. 5 and 6) . One doesn't have to hunt for spikes. In both surface and depth recordings, whether by microelectrodes or gross electrodes, from intact, behaving animals or isolated cerebral ganglia removed from the body, whether the subject is the brain of a snail, a slug, the marine tectibranch *Aplysia*, a cockroach, a bee, an adult moth or a larva (caterpillar), a crayfish, stomatopod (mantis shrimp), earthworm, or polychaete annelid, they all, except cephalopods, show omnipresent, simple or compound multiunit spikes overriding small slow waves.

Figs. 5 & 6 about here

In certain conditions - poorly understood - *slow waves can become prominent in the invertebrates* (Fig. 6, lower; Schütt et al. 1999a,b) whereas in all vertebrates and most regions of their brain, slow waves are omnipresent and relatively stronger; and spikes have to be sought by careful positioning. The power spectra are quite different. Vertebrates, as we just noted, almost invariably have a *maximum between 5 and 15 Hz* and fall off at higher frequencies typically more than a factor of two for each octave to about 1/10 at 100 Hz. In the invertebrates power commonly

stays up and even rises to a broad *maximum above 100 Hz.*

One wonders whether *two general differences* exist. One might be in the tissue **impedance** - vertebrates having more cell membranes and capacitance, tending to short out the high frequencies. The impedance has not been measured, to my knowledge, in the millimeter range.

The other candidate for a general difference is **synchrony**. This has been estimated in a preliminary way in our own sampling of coherence as a function of distance between pairs of electrodes referenced to a common and demonstrably inactive electrode. Averaging over many sample periods of 5-10 s and many pairs of electrodes of each separation, the means in mammals fall from ca.0.8-1.0 (perfect coherence) at 1-2 mm to a level indistinguishable from a stochastic control at a separation of ca.10-20 mm in rabbit and human (macroelectrodes on the pia or dura mater). This is true for all frequencies between ca. 2 and 50 Hz The more sensitive measure is the distance for mean coherence equal to 0.5 but it demands large scale averaging of many pairs with different separation, and is impractical in most preparations. I found, roughly, that it lies in the range of 5-10 mm in rabbit cortex; ca.3-4 mm in the lizard (*Gecko)* cortex, only 1-3 mm in a ray optic tectum (*Platyrhinoides*), and less than 1 mm in the gastropod, *Aplysia* (Bullock 1989b). It will require many more samples to establish whether this is a valid trend. For the present we can only suggest that there may be a significant *evolution in the degree and distribution of slow wave synchrony.*

(2) The second puzzle is this. The raw recordings and the power spectra look *alike in all the vertebrates,* (Fig. 5) except for the RMS amplitude, if we compare subdural surface recordings or intracerebral needle or fine wire recordings in the waking animal, between ca. 0.3 and 100 Hz. The main features are: (a) absence of spikes (except for certain places such as a deep layer in the cerebellar cortex and in other places if a fine electrode is micromanipulated through the tissue) and (b) a power spectrum falling quite steeply on each side of a maximum around 5-15 Hz (Fig. 5).

The presence of a **cortex** makes no generalized difference in the form of the power spectrum, as yet demonstrated and the same is true for the size of the brain and for its degree of microscopic differentiation. Amplitude is generally lower in the nonmammalian species but is doubtfully different among mammals, from mouse to dolphin - but we don't yet know what the key factors are. Many factors influence amplitude and selecting comparable samples is difficult.

Some *features that might be expected to play a large role* can be shown not to do so - for

example **lamination**. The cerebellar cortex has low amplitude slow waves. Species of fish and reptiles having highly laminated optic tecta show low EEG amplitudes - something like a third to a sixth of that of a mammal comparably recorded. Local field potentials of poorly or not at all laminated subcortical *mammalian* gray matter typically exceed the amplitude of any cerebral region of fish or reptiles or even the well laminated tectum. The wide *differences in EEG amplitude* that seem on the present data to be generalizable between mammals and fish or amphibians might possibly be understood if synchrony of slow waves is also generally lower in fish and amphibians. I return to this below.

Some evidence points to a lower coherence at the same distance between electrodes in reptiles than in mammals and a still lower coherence in teleosts and elasmobranchs. If this is borne out with a larger sample of species, we could attempt the generalization that degrees of synchrony tend to increase in the more complex brains.

The *large mystery I want to highlight* is the lack of other differences between the form, power spectrum and dynamics of the EEGs among the vertebrate classes, to parallel the great changes in brain anatomy and behavioral ethograms. Even the first order form and distribution of sensory evoked potentials (Prechtl et al. 1998) and event-related potentials (Bullock et al. 1990) in fish are surprisingly similar to those of mammals. I must conclude that we are missing major features in our description of EEGs - *features hiding in the temporal and spatial fine structure* of the time series, perhaps like the firing patterns of Abeles et al. (1993) or slow wave patterns of Lopes da Silva (1981). This is the most important take-home message and it seems not to have been noticed or to have attracted much attention heretofore. The challenge is tantalizing - what instructions can we give our high speed computers to seek dynamical features that distinguish a set of sample mammalian EEGs from a set of reptilian or teleostean EEGs, as generalizable as the six-layered cortex? I believe there are such features and that they are specific and measurable, not intangible or vague. They probably involve new integrative levels of complexity of the meaning of similar neuronal activity - like the meaning of “yes” pronounced by the chancellor of a university and by the principal of a small middle school.

To emphasize this point, I will confess that a major disappointment in my career has been my failure to accumulate good digitized recordings from such a range of taxa, with adequately comparable conditions, including the state of the animal, the kind of electrodes and their placement

in equivalent regions of the brain, so that I could now push such data through the programs we have that can spit out comparative findings on many traits in the sadly neglected area of dynamical properties of organized assemblies of neurons.

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Legends for figures:

Fig. 1. **A.** Optically recorded visual evoked potentials from turtle dorsal cortex. *Upper*: 4 rows of 12 photographs of the brain surface, left to right, top to bottom, during 2.7 s of a video sequence of the stimulated membrane voltage changes. Each frame is a pseudo-colored image of 1.7 x 1.7 mm of the right visual area; rostral = right, lateral = up, white profile coming in from lower left = electrode. The moving visual stimulus starts in frame #30 (first of second row), causing a net hyperpolarization (dark blue) in frames 32-37, followed by depolarizations at a few loci which expand in caudal and lateral directions in frames 43-49; that is the figure shows a traveling wave. *Bottom left:* emission changes vs time from 3 loci indicated by the color-coded boxes in the enlarged frame #53, *bottom right*. The timing difference among the 3 plots reflects the spread of excitation. Responses imaged by epi-illumination with a CCD camera, 17 frames/s, after application of the fluorescent voltage-sensitive dye, RH795. Kindness of J.C. Prechtl (see Prechtl et al. (1997).
B. Raw data from 9 single sweeps of a similar preparation that shows the ON response, a "gamma" burst (ca. 20 Hz at 25EC), not time-locked and hence disappearing in an average - superimposed on a slow wave; no OFF effect. Turtle intracortical EEG; stimulus is a slowly moving visible stripe. Kindness of J.C. Prechtl.

Fig. 2. Power spectrum peaks (black) in 4 s of 1-100 Hz **noise** (upper panel) do not necessarily represent rhythms, by any common sense definition. The high-lighted peaks of the red trace mean average PSA (Period-Specific-Average) periodicities (red), i.e. chance sequences of waves in the brief noise sample that satisfy a definition of rhythms. Red dots = 99% confidence, blue diamonds = 95% confidence. The time series is segmented and averaged at each period shown. The variance of each average is plotted and normalized by dividing the control value into the data value. Control values (the expectation by chance) were computed in two ways: (i) the same time series was segmented with random starting times, and (ii) the phases of each segment were randomized. The resulting curves have nearly identical 95 and 99% confidence points. Note many power peaks that do not correspond to PSA peaks and some good rhythms occur where power is weak. Abscissa of

upper panel (data), at 256 samples per second, represents 4 s; abscissa of lower panel is in Herz. (Programs “Datgen” for generating artificial data, and “Periodity” for analysis by M.C. McClune.)

Fig. 3. Human subdural EEG data, 4 s in mid-seizure, during a strong theta epoch. As in the usual case, the power spectrum peak agrees with the periodicity peak - slightly less than 4 Hz. The periodicity analysis also shows smaller peaks at subharmonics just below 2 and 1.3 Hz, but this does not mean there are rhythms at those frequencies. To decide, we examine the averaged wave form at those periods.

Fig. 4. Human scalp EEG; normal subject looking at a target image (a classical illusion, the “non-Kanizsa square”; subject is instructed to count targets) among several visual stimuli that include the Kanizsa square, Kanizsa triangle, and non-Kanizsa triangle images. Electrode is the one placed at (O4). Data kindly provided by C. Herrmann et al. (1999) who showed brief periods of enhanced gamma activity at ca. 75-150 ms and 200-400 ms after stimulus onset. Here, analyzing the whole 2 s epoch, representing a single trial, without averaging, we see a significant gamma peak at 36 Hz where power is very low and a strong rhythm rhythm at ca. 16 Hz in both measures. Other power peaks do not represent rhythms. The upper time axis under the data is the elapsed time since the start of a stimulus series. Ordinate on the left is the PSA periodogram divided by the control from 200 randomized segment starts; 1.0 is the expectation from chance, given stochastic data with the same power spectrum.

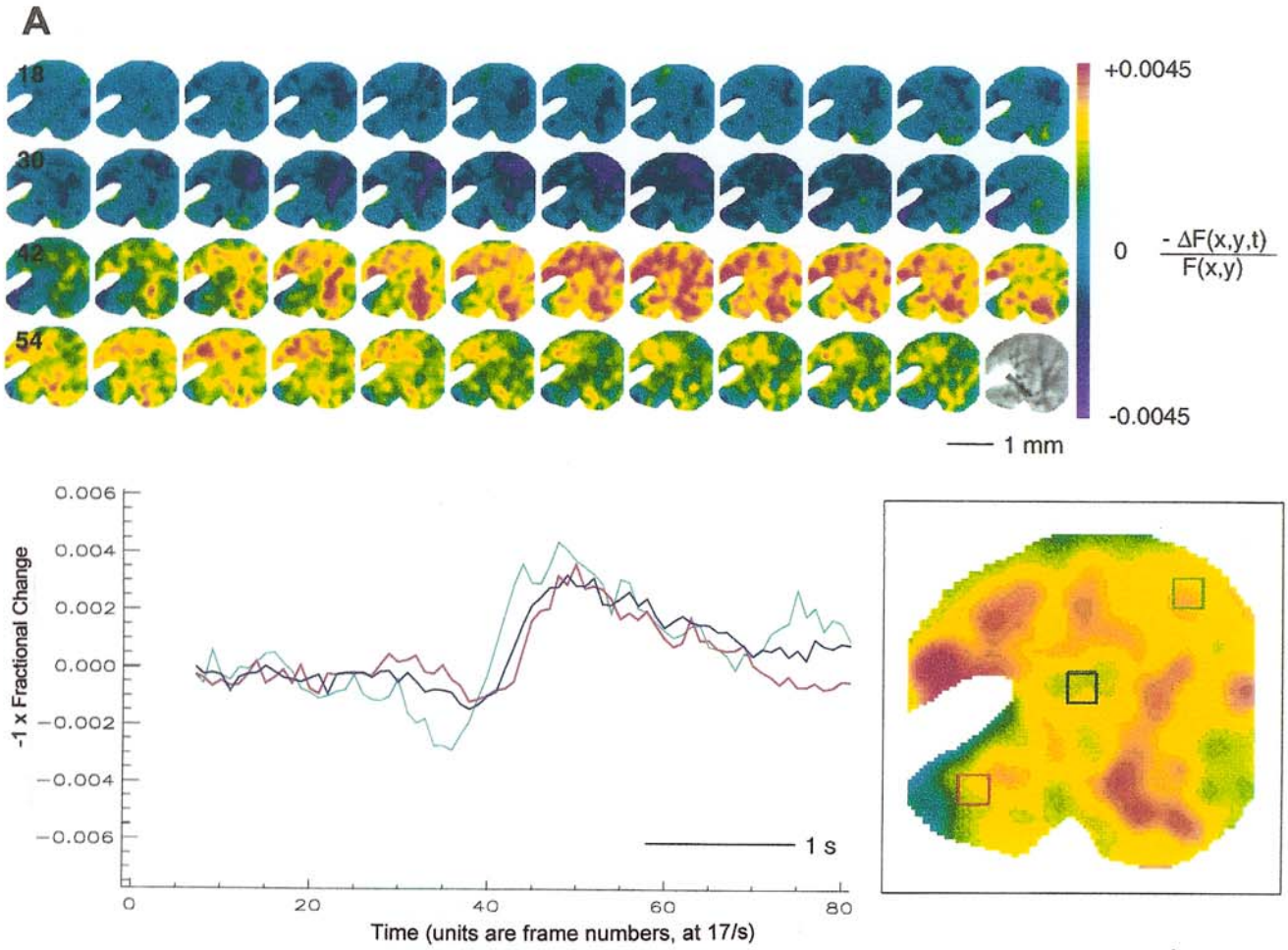
Fig. 5. Power spectra of EEG from various taxa. Upper three, vertebrates of different classes, with and without a cerebral cortex, share the pattern of maximum power below 10 Hz, steeply falling at higher frequencies. Note the ten-fold change in X-axis scale for the fifth trace, from crayfish. Octopus is closer to the vertebrate pattern.

Fig. 6. Comparison of invertebrate and vertebrate EEGs. *Upper panel*, crayfish and frog wideband recordings from the surface of the brain, using similar wire macroelectrodes. *Lower panel*, locust optic ganglia of the brain, adapted to moderate light; additional light at “ON” caused a local field potential oscillation at ca. 18 Hz, damping out in a few seconds. The two channels are low-pass and

high-pass filtered from the same wire recording macroelectrode. Invertebrates can show slow waves, probably manifesting synchrony of many neurons, under special conditions. See also Adrian (1931).

E N D

Fig. 1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54
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-0.0045
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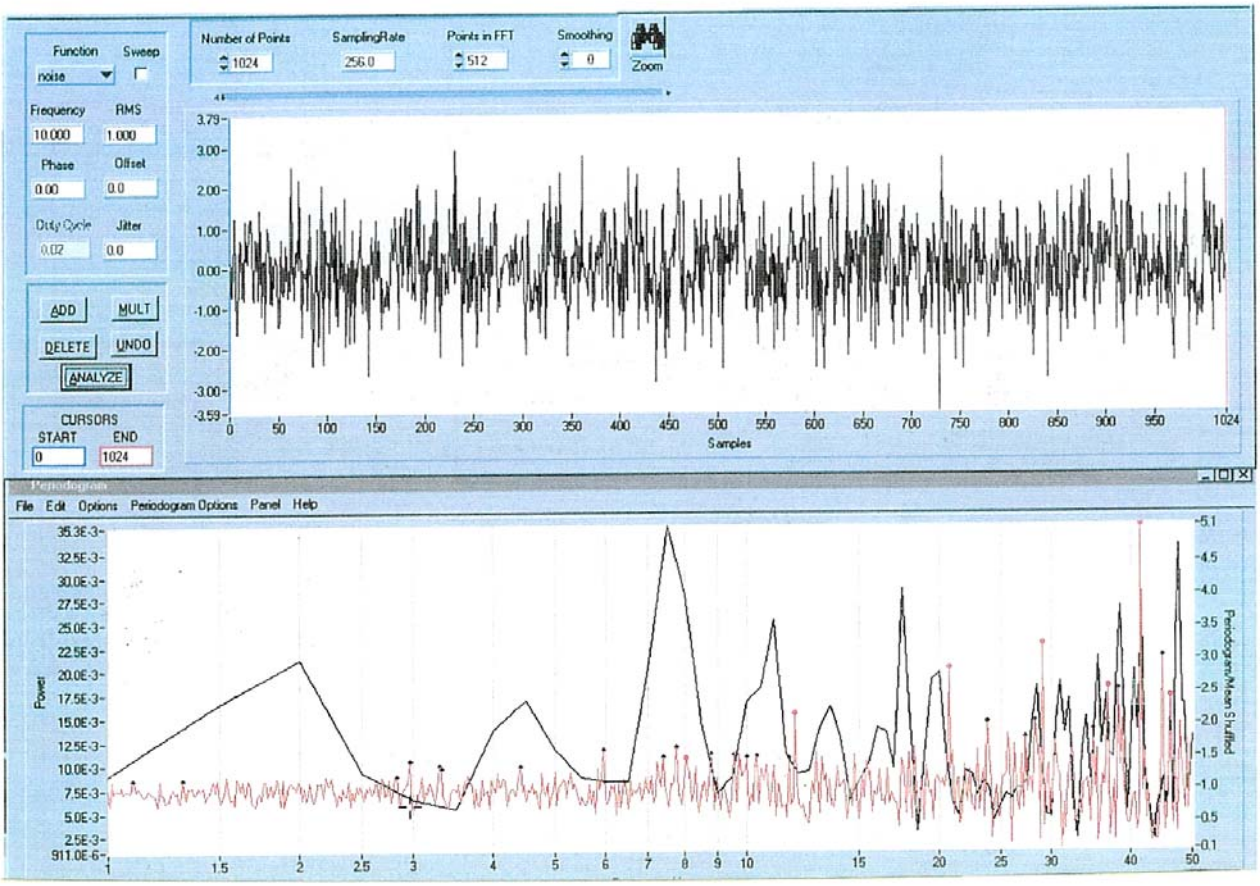
0.004
0.002
0.000
−0.002
−0.004
−0.006
-1 x Fractional Change
1 s
0
20
40
60
80
Time (units are frame numbers, at 17/s)
B
uV
Photodiodes:
stripe appears
disappears
200
0
-200
0
3
6
9
Seconds

Fig. 2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Jitter
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MULT
DELETE
UNDO
ANALYZE
CURSORS
START
END
0
1024
Number of Points
SamplingRate
Points in FFT
Smoothing
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256.0
512
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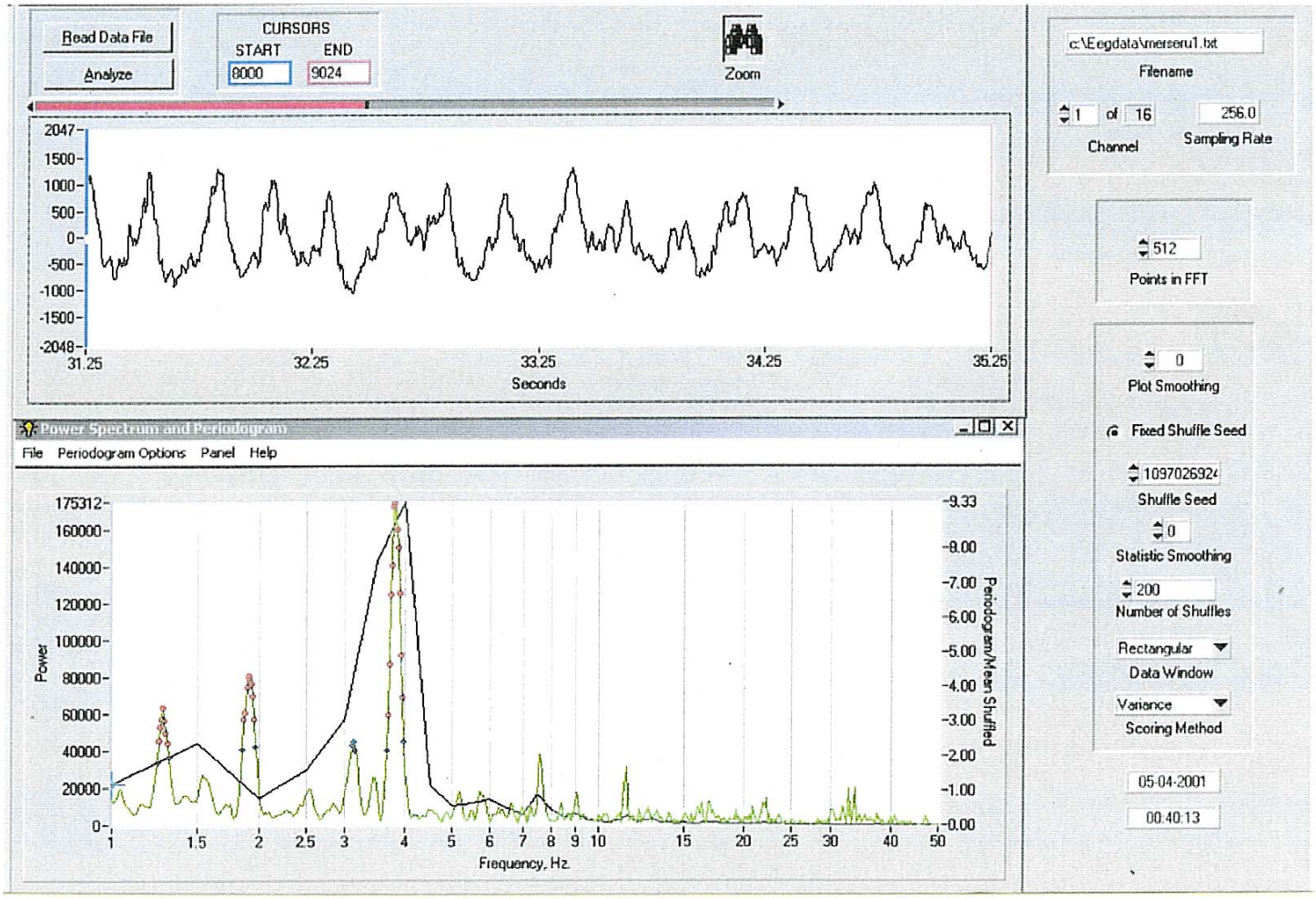
Zoom
Samples
Periodogram
File Edit Options Periodogram Options Panel Help
Power
Periodogram/Mean Shuffled

Fig. 3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CURSORS
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Channel
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Sampling Rate
512
Points in FFT
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Plot Smoothing
Fixed Shuffle Seed
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Shuffle Seed
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Statistic Smoothing
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Number of Shuffles
Rectangular
Data Window
Variance
Scoring Method
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2047
1500
1000
500
0
-500
-1000
-1500
-2048
31.25
32.25
33.25
34.25
35.25
Seconds
Power Spectrum and Periodogram
File
Periodogram Options
Panel
Help
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160000
140000
120000
100000
80000
60000
40000
20000
0
Power
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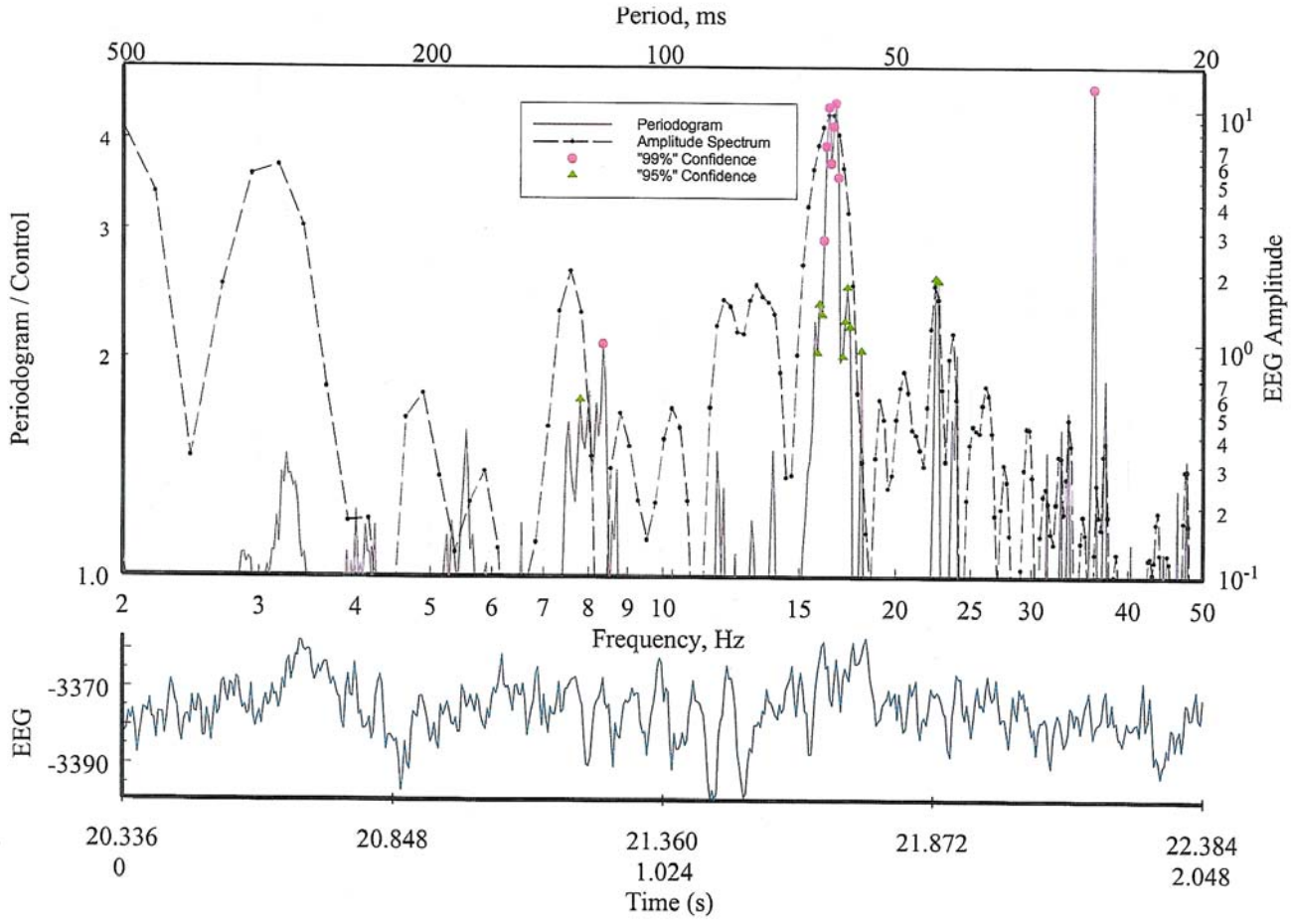
8.00
7.00
6.00
5.00
4.00
3.00
2.00
1.00
0.00
Periodogram/Mean Shuffled
1
1.5
2
2.5
3
4
5
6
7
8
9
10
15
20
25
30
40
50
Frequency, Hz

Fig. 4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200
100
50
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Periodogram
Amplitude Spectrum
"99%" Confidence
"95%" Confidence
Periodogram / Control
EEG Amplitude
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EEG
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20.848
21.360
1.024
21.872
22.384
2.048
Time (s)

Fig. 5

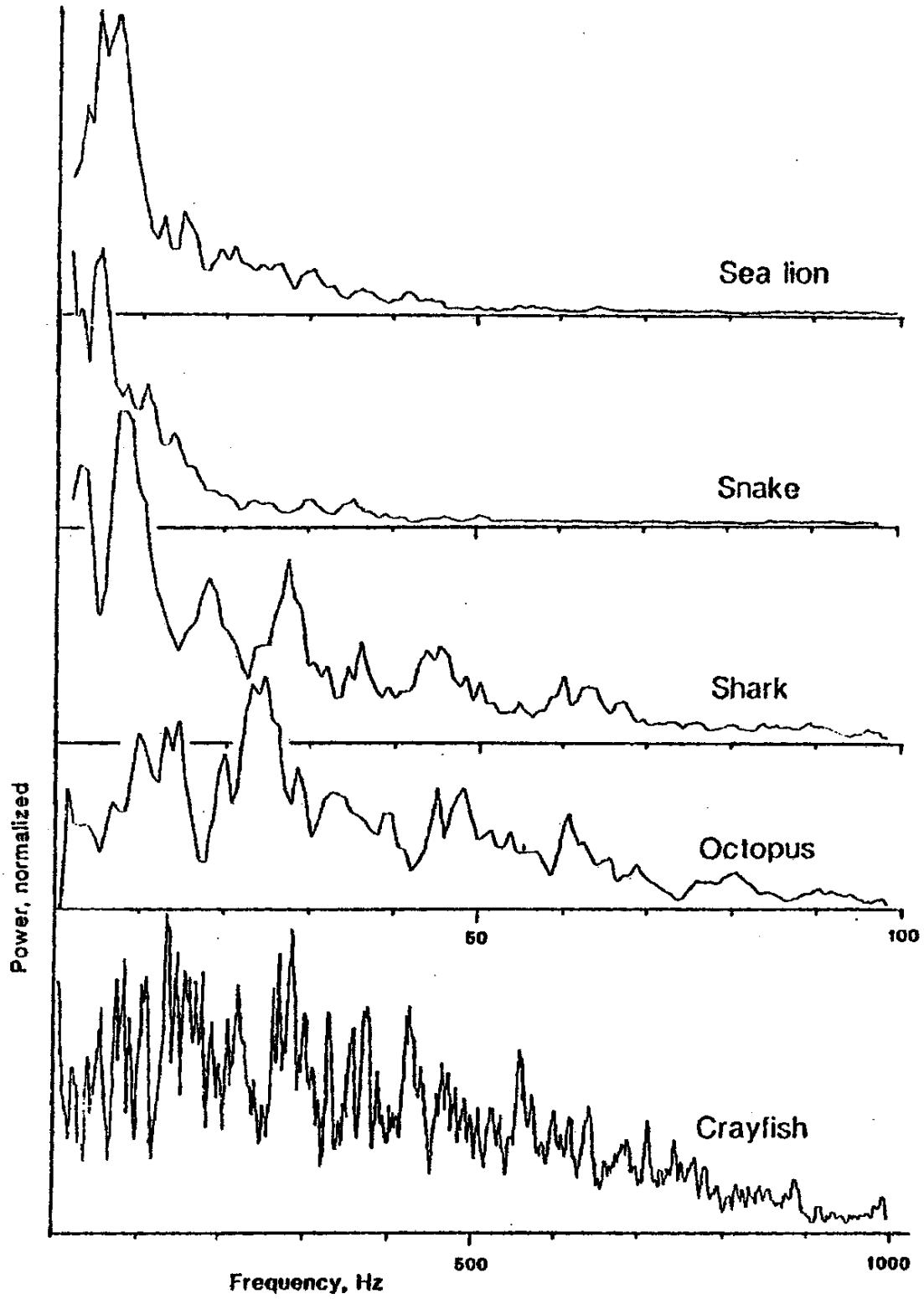
Sea lion
Snake
Shark
Octopus
Crayfish
Power, normalized
50
100
500
1000
Frequency, Hz

Fig. 6