Have Brain Dynamics Evolved? Should We Look for Unique Dynamics in the Sapient Species?

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Ongoing “spontaneous” electrical field potentials of assemblies of neurons in the brains of diverse animal groups differ widely in character and amplitude without obvious explanation. There may be correlates with other measures of brain complexity, such as histological differentiation, but so far there are no known differences between the EEGs of humans and other mammals or between mammals and reptiles, amphibians or fish, apart from amplitude. The proposition is defended that further search for descriptors or statistical, probably nonlinear features of the time series will reveal consistent differences, meaning that we have so far missed major features of the natural history of EEGs, just as we have thus far relatively neglected the identification of features of the physiology of the brain relevant to its evolution of complexity through major grades of phyla, classes, and orders.

The outstanding differences between humans and other animals in behavior—the diversity of dances, the fuss over food preparation, the mess over morals, compulsion to creativity, interest in introspection, and passion for the past—make me believe, as a physiologist, that we should find differences in brain dynamics—at some level—between the human brain and that of taxa with less complex behavior, especially when we learn how conserved is the brain anatomy, the cellular physiology, and the molecular mechanisms.

Actually, I will not be satisfied to find some uniquely human physiological traits just as it will not be enough to find a uniquely human type of neuron (Nimchinsky et al., 1999). I am curious how the brain evolved through the drastic stages in complexity between medusae (jellyfish) and corals, flat and round worms, insects and lobsters, clams, snails, and squid, plus lampreys, frogs, and lizards, opossums, shrews, lemurs, and marmosets—and not necessarily in that sequence in time (Bullock, 1948, 1958b, 1959b, 1965, 1986, 1993). This is not anthropocentric. Repeated saltations in grade of complexity took place before humans or primates or mammals or vertebrates.

We know a lot about the neurons, including individually identifiable ones in every specimen in many invertebrate taxa (Bullock, 2000a; Leonard,
and in some fish, but the steps of advance in physiology are more elusive. It does not look as though the great leaps in brain development are due to sheer numbers or to more kinds of transmitters or modulators (Bullock, 1995; Tononi, Sporns, & Edelman, 1994). What else could it be?


Last, one must add the number of significantly different receptive fields and projection fields. Neighboring neurons have some degree of overlap but also some degree of nonoverlap that makes it possible to recognize distinct sets of fully equivalent neurons from other such sets (Bullock, 1980, 1993).
When we speak of the numbers of kinds of neurons, we should mean on all
these criteria.

My estimates, based on a few well-studied systems, such as the visual
system, and a lot of educated extrapolation put the number in the hundreds
in some simple worms, thousands in *Aplysia*, tens of thousands in more
advanced insects and crustaceans and in a fish like a carp, millions in a
rat, and billions in humans (Bullock, 1993)! This may seem out of reason
and is certainly at odds with a common view, such as that of Changeux
(1985), who said the number of categories of pyramidal cells in the cortex
is probably tens or hundreds. He neglected to consider their connectivity at
the level of receptive fields and projection fields and by “categories” meant
“classes.” I am asking how many species there are, on all criteria, including
distinguishably different connectivity fields.

I am talking about the evolution of nervous systems, from simple to
complex, and looking for relevant measurable variables. Relative brain size
or number of cells or of synapses or of impulses per second in the whole
system are doubtless relevant but imperfect and inadequate measures of
the machine (Bullock, 1995), just as numbers of distinct behaviors in the
whole ethogram, including brain states such as stages of sleep, arousal, and
attention, can represent an approximation to a measure of accomplishment
of the machine–complexity of behavior. But both neglect major variables
because they are difficult to count.

Stipulating the difficulty, I think it is worthwhile to recognize what we
would like to count in animals at different grades of evolution. In the brain,
one such desideratum would be the number of species of cells and their
synaptic and nonsynaptic connections—revising and correcting my crude
estimates. In the consequence domain, the behaviors mediated, one hitherto
untouched variable that would make a great difference if we could count
them would be the number of items of knowledge that an animal can ac-
cumulate and use. This means I lump together under the term knowledge
the number of individual neighbors it can distinguish—of audible signals,
different odors, levels of social hierarchy, relative values of alternative food
sources, kinds of sadness, and kinds of sensations, emotions, motivations,
goals, and memories. Difficult? Certainly! Tangible, definable, approach-
able in comparable packages from taxa far enough apart? Yes. We do not do
justice to the results of brain evolution if we do not at least mention such
measurable variables in behavioral evolution (much ethological literature
is relevant here).

Let me turn to another extreme along the spectrum of efforts to measure
evolution in terms of its manifestations. What has it wrought? What differ-
ences have come about? I call this the natural history of brain traits. The
textbook lists—corpus callosum, six-layered cortex, corpora pedunculata,
nonspiking neurons, posttetanic potentiation, kindling, and the rest—must
be a small fraction of the traits that have evolved. It is time we aimed some
frontal assault on the frontier of complexity per se (Bullock, 1993), lest we
claim to study evolution while overlooking the saltations in complexity. Although most evolution is lateral radiation adapting species to different niches within the same general grade of organization, now and then new grades of more complexity appear on some twigs of the tree (Bullock, 1992). The overall span between the simplest levels of behavior and the most complex is a span difficult to overstate. The argument is very persuasive to me that this is not due merely to numbers of cells or synapses, although no one, to my knowledge, has put an upper limit on the consequences of differences in sheer number on qualitative or quantitative emergent properties. Emergent traits of anatomy and physiology have accompanied the unpredictable saltations, which were far from inevitable or linear and not obviously benefiting survival value.

I want to point here to just one domain of little-known physiological traits of central nervous systems. I bring it up because it is neglected. I’m thinking about the most information-rich measure of the living, working brain: the electrical activity seen by wideband amplifiers that record slow as well as fast activity (Bullock, 1997, 1999) from extracellular semi-microelectrodes at many loci at the same time, both on the surface and in the depths of the brain, with millisecond and millimeter resolution.

What should we expect if we compare the ongoing, not intentionally stimulated, but apparently spontaneous activity of *Aplysia* and a garden snail, a honey bee, lobster, octopus, shark, bony fish, alligator, opossum and human (Basar, 1999; Basar, Schütt, & Bullock, 1999). This is not an evolutionary ladder! I pick a list of living species, each at the end of some branch or twig, using the criterion of how intricate the brain looks histologically among invertebrates and vertebrates (Bullock & Horridge, 1965; Bullock, 1984, 1986).

First, let us look at the ongoing, apparently spontaneous background activity, itself a surprising discovery made during my lifetime. Later, we can look at the responses to stimuli and situations. Both the spontaneous, ongoing and the stimulus or state-related forms of electrical activity are rich in dynamical variables to measure (Bullock, 1984, 1986, 1995, 1997, in press; Bullock, Karamuelsen, Achimowicz, McClune, & Basar-Eroglu, 1994; Bullock & Terzuolo, 1957; Precht et al., 1998; Bullock & Achimowicz, 1994; Schütt, Bullock, & Basar, 2000).

The hypothesis we are testing—and rejecting (to spill the beans up front)—is that such background population activity of many or most places we can sample in the brain is a mixture of rhythms at many different frequencies plus some stochastic, information-poor, and entropy-high components. The bottom line as I predict it now (probably wrongly) is that our own EEGs have a lot of stochastic components plus a very few rhythms—now and then when the situation is just so and even less commonly more than one at a time, plus a significant proportion of the total mix in patterned sequences that are not rhythmic or sustained but spatially and temporally information rich, like speech in a crowded room.
This description is a risky and far-out extrapolation of meager knowledge, but perfectly compatible with prevailing views except for the common mental model of a wide spectrum of independent rhythms, as though the assumptions of the Fourier analysis were actually true. I think this kind of EEG has been achieved by evolution from simpler species whose EEGs are indistinguishable from stochastic pink noise, that is, a random mixture of unsynchronized, unpatterned spikes and slow waves of single neurons.

I will give only a little space to that achievement, although it is full of surprises, in order to give more space to evidence for the high information content of the most evolved EEGs. To my surprise, it has turned out that most invertebrates, including worms, crustaceans, insects, snails, and slugs, have EEGs dominated by millisecond spikes, which do not require micro-electrodes or careful positioning. Slow waves, meaning waves below about 50 Hz, are inconspicuous except in some preparations and conditions. Most of the time there is little or no synchrony in *Aplysia* or in arthropods, as detected by coherence between recording electrodes only a fraction of a millimeter apart. It looks quite stochastic and very different from our own EEG, dominated by slow waves of high amplitude.

Another surprise is that fish, frogs, and reptiles have EEGs that look just like ours; only the amplitude is lower (Basar et al., 1999). The power spectrum has the same general shape: a maximum between 5 and 15 Hz and falling steeply above this.

We have several puzzles. First, why are spikes so much harder to see in all vertebrates than in almost any invertebrate? It is hard to dismiss this as due to cell size or packing density or the extracellular impedance or shunting of high frequencies by the proliferation of cell membranes in myelin and glia.

Second, why are slow waves so weak in the invertebrates most of the time and so strong in mammals and birds in many parts of the brain. This puzzle is more interesting because a first-blush explanation is that synchrony has suddenly become important in the vertebrates. Some evidence supports that—more coherence at a given distance in fish than in *Aplysia* and still more in reptiles and most in mammals.

Third, isn’t there something more than mere amplitude that is different in mammals with a good cortex? My bet is that we can find a measure of activity patterning that, like coherence, is higher in reptiles than in fish and highest in mammals—perhaps even graded within mammals, with primates having more than insectivores. Could it be that the power spectrum is not a good method for describing our EEG—perhaps losing the real character as it would if we described speech or music with FFTs?

The state of the art and the challenge for the future is that we need to learn how to filter for transient microstructure, like distinguishing babbling from speech. It should be easier to distinguish structure from nonstructure in the brain than in speech because in the brain, structure is sure to be spatial as well as temporal. Maybe an analog is the Tokyo fish market, where at 5:00 A.M., dozens of auctions are taking place simultaneously, a
few meters apart, each with 20 or 30 bidders responding in a time-locked fashion to their own auctioneer’s clues. My view of transient microstructure is that the brain does not have even quasistationary microstates as a general rule. As far as my limited understanding goes, wavelet analysis is not very promising except in special cases or by imposing simplifications. Similarly, mutual information or measures of entropy are not adequate measures of the dynamics of microstates.

I finish by mentioning three forays or exploratory excursions into measures that are elementary but have not been done heretofore. These are attempts to find descriptors of wideband time series that might discriminate among data sets—for example, between brain states or brain regions or classes of animals or disease or ontogenetic stages. They are estimates of the distribution and dynamics of coherence, of bicoherence, and of periodicity.

The first is coherence—a pairwise measure of correlation at each frequency between two simultaneous time series. I will only mention it as a function of separation between the pickup electrodes. This is the best estimator for synchrony so far. It tells us that the eye is a poor estimator—confusing amplitude with synchrony. There seems to be a difference between classes, with virtually no synchrony at any frequency in *Aplysia*, the sea slug, even at less than a millimeter and even for low frequencies. The fish we measured had significant coherence at 1 or 2 millimeters; turtles and gecko had a bit more and mammals still more.

We had no theoretical or empirical basis to guess what to expect. We found that when picking up EEGs from the brain surface on a smooth brain—the rabbit’s—the average of many pairs showed coherence of about .05 when the electrodes were about 3 to 5 mm apart, falling to chance level at about 7 to 10 mm (Bullock & McClune, 1989; Bullock et al., 1995a, 1995b). Human subdural recordings are about twice those numbers, but the electrodes are quite different, so we cannot claim that this is a fair comparison. We can emphasize that the distance for 0.5 coherence varies greatly from pair to pair, place to place, and moment to moment. The average is much greater in scalp recordings and smaller with intracortical microneedle recordings. All of these features underline the main finding: microstructure and widely varying dynamics in time and space. Other puzzles I will skip over here, such as the high agreement of different frequencies over the spectrum. Coherence is a simple, linear property, certainly quite inadequate as a descriptor. The phase spectrum is not useful except for frequencies that represent clear and stationary rhythms.

Bicoherence is a nonlinear property not related to coherence. It is a higher moment of a form of phase coupling of pairs of frequencies, F1 and F2, and their sum, F3—a special case not found in purely linear systems or detected by purely linear analyses. It is not present above the chance level, for any pair of frequencies, in many EEG samples (Bullock, Achimowicz, Duckrow, Spencer, & Iragui-Madoz, 1996, 1998). Now and then for brief or longer episodes, peaks appear or elevated plateaus or mountain ranges in certain
portions of the 3D plot of coupling strength versus the intersections of F1 and F2. Here also we find microstructure and lability in space and time, possibly correlated with some state of the brain at that place and time.

The third measure is the most difficult: How strong is the periodicity at any frequency in the chosen spectral range? There is a tendency by authors to think of the Fourier spectrum of power at each frequency component as a display of rhythms and to think of the brain waves as the sum of many oscillators. But extremely nonperiodic time series, like an irregular succession of transients, have FFT peaks.

We have applied a simple, additive method that averages all the segments of the time series, segmented at all the periods between chosen limits. In our usual frequency resolution, there are 100 periods per octave, or 564 between 1 and 50 Hz. We plot the variance of the averages as a function of period, normalizing by dividing these values by the values of a stochastic control.

The main findings are that many EEG samples from different times and different places on the scalp or intracranial, subdural, or depth electrodes show no significant periodicity; others show one of the classical half-dozen rhythms, a few show two nonharmonically related frequencies, and still fewer may have three, four, or even five peaks in the range from 1 to 50 Hz (Bullock, McClune, & Enright, in press). I cannot list the difficulties and limitations of the method here, but one is that even when we use samples as short as 2 seconds, we cannot exclude that the rhythms are present for only a fraction of that time and may not be three, four, or five simultaneous rhythms. Microstructure is also clear by this measure in both time and space.

A long-lasting alpha or theta rhythm over a wide area is a special case. We have not enough experience with this measure to make statements about its correlation with brain states, regions, or taxa. It is surely a crude, first-order feature but points to the possibility that EEGs from small electrodes in the brain parenchyma are extremely local, nonstationary, and maybe as rich in nonrhythmic, phase-coupled 3D pattern as a political convention.

I conclude by underlining the extent of our ignorance about the evolution of the nervous systems of animals, especially in the intermediate integrative levels, the mesoscopic levels of small or larger assemblages of cells in systems between the subcellular, ionic channel, and molecular level and the behavioral level. The tremendous gaps between the complexity of the brain in a lower invertebrate and a higher invertebrate or a lower vertebrate and a higher vertebrate are apparently not principally attributable to sheer numbers of cells or to properties of neurons, synapses, transmitters, and modulators but to some organizational features that utilize the permutations of scores of integrative variables and thousands or millions of connectivity variables.

We are seriously lacking in knowledge of what the actual differences are between less complex and more complex brains, particularly in their physiology. Crude low-magnification histology tells us there are marked differences between taxa of several grades of complexity. The latest is a
spindle-shaped cell type in the fifth layer of cuneate cortex that has just been found to be peculiar to higher primates—humans, chimps, gorillas, and orangs.

But in spite of off-and-on claims of more speech cortex and prefrontal lobes in humans, we have no neural basis for the vast differences in behavioral complexity between humans and other species. If we found a difference in the EEG, it would not be a satisfying answer to the question, “What features in the brain account for our level of complexity?” but it would be a notable advance. It would be a notable advance to find relevant differences between Aplysia and squid, besides numbers of cells and percentages of them without axons or between alligators and cats, besides a corpus callosum and six-layered cortex.

Biologists, evolutionists, and neurophysiologists have too long overlooked one of the major biological, evolutionary, and neural aspects of the animal world: What specifically has evolution produced? In our concern for the how questions about evolution, a specialty with a good press and a lot of disciples, we tend to be satisfied with those differences between taxa that diagnose them or obviously concern their reproduction and we ignore the greatest reservoir of differences, the behavior machine, the brain, and that feature of brain evolution—its repeated saltations to more complex grades histologically and in behavior—not obviously improving survival value.

I am shamelessly beating the drum for comparative studies, for physiological studies in addition to anatomical and chemical, and for study of brain mechanisms of information evaluation, recognition, processing, and communication over and beyond spikes and circuits.

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References


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