Chaos and generalised multistability in a mesoscopic model of the electroencephalogram

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Abstract
We present evidence for chaos and generalised multistability in a mesoscopic model of the electroencephalogram (EEG). Two limit cycle attractors and one chaotic attractor were found to coexist in a two-dimensional plane of the ten-dimensional volume of initial conditions. The chaotic attractor was found to have a moderate value of the largest Lyapunov exponent (3.4 s⁻¹ base e) with

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an associated Kaplan-Yorke (Lyapunov) dimension of 2.086. There are two different limit cycles appearing in conjunction with this particular chaotic attractor: one multiperiodic low-amplitude limit cycle whose largest spectral peak is within the alpha band (8–13 Hz) of the EEG; and another multiperiodic large-amplitude limit cycle which may correspond to epilepsy. The cause of the coexistence of these structures is explained with a one-parameter bifurcation analysis. Each attractor has a basin of differing complexity: the large-amplitude limit cycle has a basin relatively uncomplicated in its structure while the small-amplitude limit cycle and chaotic attractor each have much more finely structured basins of attraction, but none of the basin boundaries appear to be fractal. The basins of attraction for the chaotic and small-amplitude limit cycle dynamics apparently reside within each other. We briefly discuss the implications of these findings in the context of theoretical attempts to understand the dynamics of brain function and behaviour.

1. Introduction

The term “generalised multistability” was first coined by Arecchi et al. [1] in order to distinguish “trivial multistability”, which can be considered as the coexistence of several stable fixed points (i.e., the dynamics here are point attractors) from “generalised multistability”, which can be considered as the coexistence of several nontrivial attractors (i.e., limit cycle and chaotic attractors). Generalised multistability was first discovered in an experimental nonlinear dynamical system by Arecchi et al. [2] in 1982 and in a computational setup by Arecchi et al. [1] in 1985. In neuroscience, one of the most interesting examples of generalised multistability is seen in the bursting molluscan neurone model by Canavier et al. [3] which was found to possess seven coexisting attractors (five limit cycles and two chaotic attractors).

In this paper we present evidence for the existence of generalised multistability in Liley’s theory of the electroencephalogram (EEG) [4]. To our knowledge, this is the first evidence of generalised multistability in such a theory. We show that a chaotic attractor resides in initial-condition space in partnership with a small- and large-amplitude limit cycle. Our current findings extend previous work in which parametrically widespread chaos, emerging through a Shilnikov saddle-node bifurcation, was found in the macrocolumnar reduction of Liley’s theory [5].

The work presented in this paper is an analysis of a novel parameter set which gives rise to the presence of multiple attractors in a two-dimensional plane of initial conditions. The finding of multiple coexisting attractors in a dynamical theory of the EEG has important implications for understanding brain function as it reveals how fluctuations in neuronal activity may enable transitions between one or more physiologically meaningful dynamical attractor states.
2. Theory

The model under discussion in this paper is a mesoscopic spatially homogeneous instantiation of Liley’s spatiotemporal theory of the EEG. A complete discussion of this theory can be found in Liley et al. [4]. The dynamical properties of the Liley theory have been widely explored, most notably in anaesthesia (see Bojak and Liley [6] and also Liley and Bojak [7]). The presence of chaotic dynamics in the Liley theory has also been widely investigated. Dafilis et al. [8] confirmed the existence of chaos in parameter space and additionally showed that the chaotic dynamics in parameter space has positive measure and exhibits fat fractal scaling. Additionally van Veen and Liley [9] further studied the parameter dependence of chaos in the Liley model and showed that, for a particular set of parameters, chaos is spawned by a Shilnikov saddle-node bifurcation, a route to chaos not previously seen in any other real world mathematical theory.

In brief the mesoscopic (macrocolumnar) instantiation of Liley’s theory considers two functionally distinct neuronal populations, excitatory and inhibitory, locally interacting by all possible combinations of feed-forward and feed-back synaptic connections. Each neuronal population is represented by a single RC compartment effective neurone into which all synaptic activity terminates. The time course of synaptic activity, based on extensive experimental evidence, is modelled by a critically damped oscillator driven respectively by the mean rate of incoming excitatory or inhibitory axonal pulses. For a single presynaptic pulse, modelled by a Dirac delta function, the modelled synaptic time course corresponds to a unitary postsynaptic potential (PSP). As a consequence our unitary PSP time course corresponds to that of the well known \( \alpha \)-function. On this basis the following model equations can be developed:

\[
\begin{align*}
\tau_e \frac{dh_e}{dt} &= (h_{er} - h_e) + \frac{h_{eeq} - h_e}{|h_{eeq} - h_{er}|} I_{ee} + \frac{h_{ieq} - h_e}{|h_{ieq} - h_{er}|} I_{ie} \\
\tau_i \frac{dh_i}{dt} &= (h_{ir} - h_i) + \frac{h_{eeq} - h_i}{|h_{eeq} - h_{ir}|} I_{ei} + \frac{h_{ieq} - h_i}{|h_{ieq} - h_{ir}|} I_{ii}
\end{align*}
\]

(1)

\[
\begin{align*}
\frac{d^2 I_{ee}}{dt^2} + 2a \frac{dI_{ee}}{dt} + a^2 I_{ee} &= Aae \{N_{ee}S_e(h_e) + p_{ee}\} \\
\frac{d^2 I_{ie}}{dt^2} + 2b \frac{dI_{ie}}{dt} + b^2 I_{ie} &= Bbe \{N_{ie}S_i(h_i) + p_{ie}\} \\
\frac{d^2 I_{ei}}{dt^2} + 2a \frac{dI_{ei}}{dt} + a^2 I_{ei} &= Aae \{N_{ei}S_e(h_e) + p_{ei}\} \\
\frac{d^2 I_{ii}}{dt^2} + 2b \frac{dI_{ii}}{dt} + b^2 I_{ii} &= Bbe \{N_{ii}S_i(h_i) + p_{ii}\}
\end{align*}
\]

(3-6)

where

\[
S_q(h_q) = S^\text{max}_q / (1 + \exp(\sqrt{2}(h_q - \theta_q)/s_q)), \quad q = e, i.
\]

The main state variables are the mean soma membrane potentials for the excitatory, \( (h_e) \), and inhibitory, \( (h_i) \), neural populations defined over a cortical territory corresponding approximately to a macrocolumn. The mean soma
membrane potential of the excitatory neuronal population provides the necessary link with experiment, as it is hypothesised that it will be linearly related to recorded EEG/ECOG/LFP. The \( I \) terms are expressions which model the mean synaptic “current” onto the neural populations due to population feedback and exogenous neural input. The subscripts \( jk \) denote synaptic activity of type \( j \) impinging on a population of type \( k \).

Parameters \( \tau_e \) and \( \tau_i \) are the membrane time constants for the modelled single compartment neural populations. The mean resting membrane potentials for the populations are denoted \( h_{er} \) and \( h_{ir} \), and the reversal potentials for the ionic species mediating synaptic activity, and which determine the amplitude of the PSPs for a given level of population activity, are denoted by \( h_{eq} \) and \( h_{ieq} \). Parameters \( a \) and \( b \) are rate constants that characterise the time scales for excitatory and inhibitory synaptic activity. In particular \( 1/a \) and \( 1/b \) are the times-to-peak for the respective PSPs. \( A \) and \( B \) are the mean peak amplitudes of excitatory and inhibitory PSPs. Parameters \( N_{jk} \) are the mean number of synapses from all neurones of type \( j \) terminating on neurones of type \( k \). The parameters \( p_{jk} \) represent exogenous input (principally thalamic) pulse densities of type \( j \) to populations of type \( k \).

The equations describing neuronal and synaptic dynamics are closed by a sigmoidal function which describes the proportion of neurones in a given neuronal population that are active at a given time for a given mean soma membrane potential. The parameters which determine the behaviour of the sigmoidal function in this model are \( \theta_q \) the mean threshold for the sigmoidal function, \( s_q \) a parameter proportional to the standard deviation of the firing thresholds of the modelled population and \( S_{max} \), the mean maximal neuronal population firing rate.

Numerical solutions to these equations have revealed a rich range of electroencephalographically plausible activity that include point attractor, limit cycle and chaotic dynamics [4, 5, 8].

3. Methods

3.1. Initial-condition space investigation

Equations (1)-(6) were solved numerically using the model parameters given in the caption to Figure 1. For the purposes of numerical integration, this system of six first and second order nonlinear ordinary differential equations was rewritten as a system of ten coupled first order nonlinear ordinary differential equations.

A candidate chaotic parameter set was found via a Monte-Carlo search of the parameter space which was conducted in order to ascertain the types of possible dynamical behaviour the model is capable of supporting. Interactive examination of the dynamics of the parameter set for a variety of initial conditions (which was conducted via XPPAUT [9]) yielded information which suggested the candidate parameter set did indeed exhibit coexisting attractors (two limit cycles and a chaotic attractor) for different initial conditions for a fixed set of parameters.
In order to confirm the presence of chaotic dynamics we made use of the Christiansen-Rugh [10] algorithm for Lyapunov exponent determination, to see if the observed dynamics were indeed chaotic, via the presence of a positive largest Lyapunov exponent. The chaotic attractor is distinguishable by the presence of a positive largest Lyapunov exponent and the limit cycles (which have largest Lyapunov exponents equal to zero) may be differentiated on the basis of their oscillation amplitudes (see Figure 3). Using these two distinguishing characteristics in tandem, we were successfully able to discriminate between the three different attractors given a particular set of initial conditions.

Integration of the model equations in order to implement the Christiansen-Rugh algorithm for Lyapunov exponent determination was performed using the adaptive stiff solver CVODE [11], with the backward differentiation formula (BDF) method. The model equations were integrated for 20 seconds of simulated time which corresponded to the order of a few hundred oscillation periods which was sufficient time for the Christiansen-Rugh algorithm to produce a stable estimate of the largest Lyapunov exponent.

Initial conditions selected were those for the mean soma membrane potentials of the modelled neural populations ($h_e(0)$ and $h_i(0)$). The initial values of all the other variables were set to zero, and thus a two-dimensional plane through a ten-dimensional volume of initial conditions was investigated. Initial conditions for $h_e$ and $h_i$ were chosen for the exploration of attractor basin boundaries as these are expected to be the most easy to constrain experimentally and the most likely to be perturbed physiologically. A total of 1500000 randomly selected initial conditions (for $h_e(0)$ and $h_i(0)$) within the region of interest for our two-dimensional plane of initial-condition space was investigated.

3.2. Largest Lyapunov exponent and Kaplan-Yorke (Lyapunov) dimension

All chaotic attractors investigated to date arising out of the Liley theory have been found to have only one positive Lyapunov exponent with $\lambda_1 > 0$, $\lambda_2 = 0$ and $|\lambda_1| < |\lambda_3|$ where $\lambda_1 > \lambda_2 > \ldots > \lambda_j$ are the $j$ Lyapunov exponents of the system. Therefore in order to estimate the Kaplan-Yorke (Lyapunov) dimension of the system it is sufficient to only calculate the top three Lyapunov exponents. Using the methods specified above the top three Lyapunov exponents of the system were calculated by integrating an augmented system of 43 coupled ordinary differential equations. This system was integrated for 100 seconds in order to obtain accurate determinations of the Lyapunov exponents, and repeated 25 times using different initial conditions in order to average the estimates of the Lyapunov exponents over the attractor.

The full Kaplan-Yorke formula, which relates the Lyapunov exponents of the system to the dimension of the chaotic attractor, is given by Sprott [12]. For the case where the attractor has only one positive Lyapunov exponent ($\lambda_1 > 0$) with $\lambda_2 = 0$ and $|\lambda_1| < |\lambda_3|$, this becomes

$$D_{KY} = 2 - \frac{\lambda_1}{\lambda_3}$$  \hspace{1cm} (7)
4. Results

Figure 1 shows a representation of the initial-condition map of the system for the region of interest. The large area of initial conditions which lead to large-amplitude limit cycles surrounds a region which contains initial conditions which lead to chaotic dynamics, which in turn surrounds a set of disconnected regions which lead to small-amplitude limit cycles.

An interesting feature to notice is the overall extensiveness of the area of initial-condition space which leads to chaotic dynamics. This chaotic dynamics has a moderate value for its largest Lyapunov exponent (3.4 s$^{-1}$ base e, SD 0.1, N=25) and a Kaplan-Yorke (Lyapunov) dimension of 2.086 (SD 0.003, N=25). The dominant frequency of the dynamics of this chaotic attractor resides in the alpha (8–13 Hz) band of the EEG spectrum.

The set of initial conditions which leads to chaotic dynamics (subsequently referred to as “the chaotic IC set”), is in turn, broken up by bands of initial conditions which lead to small-amplitude limit cycle dynamics. This set of dynamics consists of a multiperiodic attractor with a dominant frequency also in the alpha band of the EEG spectrum. The mean neuronal population firing rates for both small-amplitude limit cycle and chaotic attractors are of the order of $\sim 20$ pulses per second, a level expected to be seen in a healthy awake brain.

The region which surrounds these dynamics, namely the large-amplitude limit cycle region, is very extensive. Examining the dynamics of this limit cycle, we note that it has a much larger amplitude and lower dominant frequency ($\sim 5$ Hz) than our previous exemplars. Because of the very high associated mean neuronal population firing rates (of the order of $\sim 300$ pulses per second) this leads us to conclude that the corresponding experimental concordance for this simulated signal may very well be some form of epileptic activity.

Whilst the structure of the set of initial conditions which leads to the small-amplitude limit cycle dynamics appears very complicated, as it comprises several disjointed disconnected bands of sets of initial conditions with rather an intricate structure residing within the chaotic IC set, we have neither evidence nor theoretical motivation to suggest that the boundary of this particular set of initial conditions is fractal.

Figure 2 shows exemplars of the different attractors found in the system. Part a) of the figure shows an example of the “epilepsy” limit cycle attractor for the model. Note the angular features indicative of a spiky waveform. Part b) of Figure 2 shows the multiperiodic limit cycle attractor. Note how each of the loops corresponds to a different part of the oscillation, leading to the multiperiodic nature of the waveform. Part c) of the figure shows an example of the chaotic dynamics in the system. Note how the aperiodic nature of the waveform leads to complicated geometry.

Figure 3 shows exemplars of the time series and power spectra for the different attractors. Parts a) and b) of the figure show the time series and power spectrum for the “epilepsy” attractor. The low frequency, high amplitude dynamics which are present are clearly illustrated in these figures. Parts c) and d) of the figure show the low amplitude, multiperiodic dynamics with the dom-
Figure 1: Initial-condition map for the parameter set under investigation. Large-amplitude limit cycles are depicted by light grey points, chaotic sets are represented by an intermediate grey shade, and small-amplitude limit cycles are represented by red points. Unshaded areas represent regions of initial condition space where no numerical integrations were performed but where only large-amplitude limit cycles are expected to exist. There are 594656 chaotic points (about 39.6% of the points sampled), 37815 small-amplitude limit cycle points (about 2.5% of the points sampled) and 867529 points for the large-amplitude limit cycle cases (about 57.8% of the points sampled) out of a total of 1500000 points sampled. The parameters for the model which generated this initial-condition map were 

\[ p_{se} = 9.43 \text{ pulses per millisecond}, \ p_{ei} = 8.742 \text{ pulses per millisecond}, \ p_{ec} = p_{ii} = 0, \ A = 1.22 \text{ mV}, \ B = 3.6 \text{ mV}, \ 1/a = 0.99 \text{ millisecond}, \ b = 7.06 \text{ millisecond}, \ h_{ei} = h_{ir} = -70 \text{ mV}, \ h_{ecq} = 45 \text{ mV}, \ h_{eq} = -90 \text{ mV}, \ \tau_e = 98 \text{ millisecond}, \ \tau_i = 34 \text{ millisecond}, \ S_{e}^{\max} = S_{i}^{\max} = 0.5, \ N_{ec} = N_{ei} = 3034, \ N_{ii} = 536, \ \theta_i = -49 \text{ mV}, \ \theta_i = -41 \text{ mV}, \ s_e = 4.75, \ s_i = 5.25. \]

Further details on the parameterisation of the model can be found in Liley et al. [4].

invariant frequency clearly within the alpha band of the EEG spectrum. Parts e) and f) illustrate the chaotic dynamics present in the model. Note the broadband spectrum and the aperiodic nature of the time series.

The origin of the multistable dynamics can be explained with the aid of a one-parameter bifurcation analysis in the excitatory-excitatory pulse density \( p_{ee} \), using the continuation software AUTO [15]. This shows (Figure 4) that the system loses stability through a supercritical Hopf bifurcation (hb), which gives birth to oscillatory behaviour at \( p_{ee} \approx 6.9 \). As \( p_{ee} \) increases, a series of period doubling bifurcations (pd) for the periodic orbits occur, resulting in a cascade (pdc) which gives rise to chaos at \( p_{ee} \approx 9.387 \). There also exists a further subcritical Hopf bifurcation at very large values of the pulse density (not shown in Figure 4), from which an unstable cycle emerges. The continuation of the latter shows that, after a saddle-node point, this cycle becomes stable and heads
Figure 2: Delay-time-embedded representations of the $h_e$ time series of the model, colour coded according to the relative local rate of change of $h_e$ with respect to time. Red regions are where the dynamics changes relatively rapidly, green regions are areas of intermediate change, and blue regions are regions of relatively slower change. In total 105 seconds of simulated data were generated using XPPAUT, using a sampling rate of 1 millisecond, yielding a time series 105000 points long. The first 5000 points were discarded as a transient. The remaining 100000 points were embedded in three dimensions using the first zero of the autocorrelation function as the embedding delay. Tools from the TISEAN package [13] were utilised to generate the embedded time series and calculate the first zero of the autocorrelation function of the time series. Raw embedded time series data were converted to YWOM files using purpose built software. The attractors were then visualised using s2view, an application built with the S2PLOT library [14].

Figure 3: Time series and power spectra for the attractors investigated. Using the same $h_e$ time series as per Figure 2 time series were plotted, indicating the relative different amplitudes of the time series and showing the differences in the nature of the waveforms for the different dynamics. Power spectra were calculated using the ‘periodogram’ function of MATLAB using the entire time series. Note for panels a) and b) the time series is of a large amplitude and a low frequency and of a spiky, angular nature, which, as we have suggested, could broadly correspond to epileptic activity. Panels c) and d) show low amplitude activity with a dominant peak at approximately 10 Hz which corresponds approximately to the alpha band of the EEG spectrum. A further dominant harmonic occurs at approximately 20 Hz, which corresponds to the beta band of the EEG spectrum. Subharmonics and higher harmonics also exist. Panels e) and f) correspond to the chaotic dynamics of the system. Panel f) in particular clearly illustrates the broadband spectral features which are so familiar in chaotic dynamics, with dominant peaks at approximately 10 Hz and higher harmonics. Panel e) indicates the low amplitude, aperiodic nature of the time series.
Figure 4: One-parameter bifurcation diagram showing the absolute maxima of $h_e$ in terms of $p_{ee}$ for steady state (blue), low-amplitude periodic (red) and large-amplitude periodic (green) regimes. Stable (unstable) branches are continuous (dashed) and the vertical line indicates the value of $p_{ee}$ at which multistability occurs. Chaos (in black) ensues after a period doubling cascade ($p_{dc}$) of orbits originating from a supercritical Hopf bifurcation ($hb$) and is represented through a Poincaré section of the relative maxima and minima of $h_e$. Notice the stable large-amplitude orbits interspersed with chaos for $p_{ee} \approx 9.66$ (i.e. the black points that coincide at the top with the cycles in green) and the very small window of stability between a saddle-node ($snlc$) and a period doubling ($pd$) point for the same large-amplitude branch before it ends in a homoclinic bifurcation ($hm$).
back to the region of small $p_{ee}$. This periodic branch, which eventually ends in a homoclinic trajectory (hm), indeed contains the large-amplitude attractor depicted in Figures 2a and 3a) at $p_{ee} = 9.43$. On the other hand, the small-amplitude periodic attractor described in 2b) and 3c) is nested in the “sea” of chaos and its continuation is shown in Figure 5. Even though it crosses unstable segments of the fast orbits involved in the doubling cascade, it does not belong to any of them. Due to the stiffness of the system, it was not possible to conclude whether the branch is isolated or may be originated from a branch point for a cascading generation greater than the sixth (see Figure 5). Nonetheless, the existence of an isola of low-amplitude orbits is ruled out since the branch is not closed: after stability is lost through saddle-node (snlc) and period doubling (pd) points, the unstable segment terminates in a homoclinic bifurcation at $p_{ee} \approx 10.22$. It should be noted that, in terms of $p_{ee}$, the window of stability for the small-amplitude attractor is much smaller than the one for the large-amplitude counterpart, whereas the chaotic interval has a length which sits in between. In particular, for $p_{ee} = 9.43$, the absolute value of the maximum Floquet multiplier for the large-amplitude orbit is about a thousand times smaller than that of the small-amplitude orbit, which is about 0.74. All this is in agreement with the observed rates of occurrence for the three dynamical regimes reported in Figure 1, since the extent of the stability window and the strength of the maximum attractive eigendirection affect the likelihood of a random point of “picking” out the attractor and landing onto it.

5. Discussion

The presence of widespread chaos in initial-condition space is broadly consistent with our earlier finding of extensive chaos in parameter space, however only chaos in parameter space has been shown to exhibit fat fractal scaling. Chaos in initial-condition space has not been shown to possess fat fractal scaling however chaos in this space is still “fat”. There is no evidence to suggest the presence of fractal basin boundaries. We cannot categorically rule out the presence of fractal basin boundaries in the Liley theory of the EEG as there may exist as yet undiscovered combinations of parameters which lead to sets of dynamics which possess such behaviour.

This finding of extensive chaos in a model of EEG (both in parameter space and in initial-condition space) accords well with Freeman’s assertions regarding the importance of chaotic dynamics for perception and cognition [16–18]. The chaos in the Liley model therefore accords with Freeman’s notion of a chaotic basal state, and the small-amplitude limit cycle attractor may be an attractor to which a transition occurs during the act of perception. Small changes in the initial conditions are required to transition between these two forms of attractors which may easily be provided by the sensory input to the brain during perception [16, 18, 19].

The large-amplitude limit cycle may correspond to some form of epileptic dynamics. Again the structure of the basins means that the system may be poised on the edge between chaotic dynamics and epileptic dynamics, and as
Figure 5: The periodic branch that corresponds to the small-amplitude attractor (blue line) is hidden in the chaotic region (black dots) and crosses the unstable segments of cascading orbits (red dashed lines). The branch then loses stability through a period doubling (pd) and a saddle-node point (snlc), terminating in two separate homoclinic bifurcations (not shown). The very limited window of stability for the orbits just includes $p_{cc} = 9.43$ (vertical line). The generation of cascading orbits is indicated in Roman numerals according to their appearance with increasing $p_{cc}$. Also note that, within a period, the small-amplitude orbits in the cascade have a number of maxima (or minima) that are always powers of two: this is not the case for the small-amplitude attractor which has six (see Figure 3) and thus cannot be directly generated through doubling.
such the system has the potential to transition between these two dynamical states, additionally with occasional transitions to a limit cycle. The transition between chaos and epilepsy may be akin to some form of dynamical transition where small changes dynamically lead to large changes in the observed dynamics.

The model predicts the possibility of several coexisting complex (limit cycle and chaotic) attractors in the EEG. However distinguishing the presence of these attractors in the EEG may be a difficult endeavour. Algorithms which determine the presence of several complex attractors from a time series of a system which exhibits such generalised multistability, to the best of our knowledge, do not as yet exist. However, it is a possibility that one may apply existing algorithms which are able to determine dynamical changes in a time series (for example the permutation entropy [20]) and interpret the results in such a fashion that the existence of many complex attractor states may be inferred. Such experiments remain an avenue for future work.

The brain is an inherently noisy environment. It is an interesting question to consider the effects of noise on a multistable system such as the one presented in this paper. Studies of such multistable systems in the presence of noise remains an active area of research. However we are able to mention at least one phenomenon which may be of interest in the context of the present study. This phenomenon is known as “attractor hopping” whereby the system’s dynamics is able to jump between the attractors of the system dependent on the noise input to the system [21]. Therefore noise may facilitate transitions between the attractors present for a given parameter set.

The findings in this paper are for a spatially homogeneous instantiation of Liley’s spatiotemporal theory of EEG. The complete spatiotemporal model consists of a system of coupled nonlinear partial differential equations. The additional complexity of this particular model, (which has as a special case the model discussed in this paper) may very well mean that the theory, when parametrically suitably constrained, is capable of exhibiting many more than three coexisting attractors, or even coexisting attractors with fractal basin boundaries.

6. Conclusion

We have presented evidence for chaos and generalised multistability in Liley’s theory of the EEG and that the basins of attraction albeit complicated, do not possess fractal basin boundaries. Models of the EEG that exhibit chaotic dynamics are consistent with Freeman’s ideas on the importance of chaos for cognition and perception.

7. Acknowledgements

The results presented in Figure 1 were confirmed by Dr Ingo Bojak in collaboration with Dr Lenmaert van Veen. We thank them for their expertise. We wish to thank Brett Foster for his careful consideration and comments on an
early draft of the manuscript, and assistance with the figures. We acknowledge the assistance of Dr David Barnes who provided the s2view application and the S2PLOT library which was used to visualise the attractors. The contribution of Paul Bourke, who provided the software to convert the attractor data into a format suitable for visualisation, is also acknowledged. MPD is supported by grant DP0879137 from the Australian Research Council.

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