Doctoral Thesis（要約）

Analyses on Nonlinear Dynamics with Multiple Time-Scales in the Brain

(脳における多重時間スケールを有する非線形ダイナミクスの解析)

Takumi Sase
(佐瀬 巧)

Supervisor: Professor Kazuyuki Aihara (合原 一幸 教授)

December 4, 2015

Department of Mathematical Informatics
Graduate School of Information Science and Technology
the University of Tokyo

To my beloved families

Abstract

We analyzed nonlinear dynamics with the multiple time-scales structure emergent from the brain, and mainly focused on the three distinctive time-scales: deterministic slow, deterministic fast, and stochastic fast oscillations, with the aim at understanding the dynamics generating macroscopic oscillatory phenomena, often observed as electroencephalographic (EEG) signals—which reflect huge information of cell assemblies in the brain and accordingly would involve higher brain functions such as consciousness.

First, we developed a novel nonlinear time series analysis method called time series dimension (TSD), which was derived from the conventional fractal dimension through a key approximation. Owing to this approximation, the TSD was a function of the level of dynamical noise behind time series, where the dynamical noise was defined in the sense of the Gaussian white noise so that this noise was the origin of the stochastic fast oscillations. Based on such a functional TSD, we succeeded in detecting the level of dynamical noise included in unknown dynamics behind time series, so as to analyze any signal composed of both the deterministic oscillations and the stochastic fast oscillations. Via applying the TSD to EEG signals, we revealed that the visual inputs can control the level of dynamical noise in the frontal lobe; this result suggests that temporal changes of the extracted dynamical noise level contribute to characterizing nonlinear oscillatory phenomena.

Second, we developed an extended discrete-time neural network model, comprising excitatory and inhibitory stochastic neurons with dynamic synapses, so as to analyze signals composed of the deterministic slow oscillations and the deterministic fast oscillations. Owing to the mean field approximation, a set of variables representing neurons was converted to a macroscopic variable resembling an EEG signal, and furthermore the stochastic model was transformed into a discrete-time dynamical system. Via the bifurcation analysis, we revealed that the interactions between the above two different networks can generate the two subtypes of phase-amplitude cross-frequency coupling phenomena, which were separated by the cyclic saddle-node bifurcation of a one-dimensional torus in a map, named MT1SNC bifurcation; this result suggests that the underlying dynamics of cross-frequency coupling phenomena effectively switches between the two submodes, depending on external environmental changes.

We believe that the aforementioned two mathematical analyses, namely nonlinear time series analysis and bifurcation analysis will help us approach the comprehensive elucidation of complex dynamics in the brain.

Keywords: deterministic and stochastic oscillations, slow and fast oscillations, EEG, nonlinear time series analysis, mathematical modelling, bifurcation analysis, dynamical noise level, time series dimension (TSD), discrete-time neural network model, mean field approximation, cyclic saddle-node bifurcation of one-dimensional torus in map (MT1SNC), phase-amplitude cross-frequency coupling

Contents

Chapter 1

Introduction

1.1 Motivation

Our most interest—which would be among many neuroscientists, and should be solved urgently—is to know the property of 'macroscopic' neural oscillations, occurring in huge complex neural networks in the brain. Fortunately, we can now easily observe or measure one realization of the macroscopic oscillations, as an electroencephalographic (EEG) signal with the high temporal-resolution. Analyzing the EEG signals may help us know, e.g. "what the consciousness is" [2]; this theme is a big problem for us beyond this thesis. Actually, many neuroscientists have believed that, the EEG signals reflect key properties concerned with consciousness, because the signals are formed from a collection of cell assemblies (neural networks) such that the signals involve macroscopic rich information. Furthermore, the EEG signals result from the interaction among various types of neurons; this interaction may be one origin of the process of consciousness generation. Thus, we have suggested that only one neuron does not include the component of consciousness, but neural networks involve it.

To address how to reveal higher brain functions such as consciousness, probably contained in EEG signals, we firstly have to analyze the EEG signals effectively, by using the time series analysis. The waveform of an EEG signal is characterized by oscillations, so that until now almost neuroscientists especially have focused on the frequency and the phase, both of which directly connect to the form of oscillations. This 'linear' time series analysis, based on the Fourier series, seems to be natural to analyze oscillations, but misses 'nonlinearity'.

In particular from the viewpoint of nonlinearity, a band-pass filter is a good example breaking dynamics underlying oscillations, although almost neuroscientists have used it as preprocessing to extract well-known delta, theta, alpha, beta, or gamma waves, because each of them has frequency-specific functional roles in the brain [3]. For several decades, the linear time series analysis has revealed little by little, that how the external information is coded in the frequency and the phase in EEG signals and accordingly, discussions given by this analysis naturally have been concerned with synchronized phenomena [4]; this

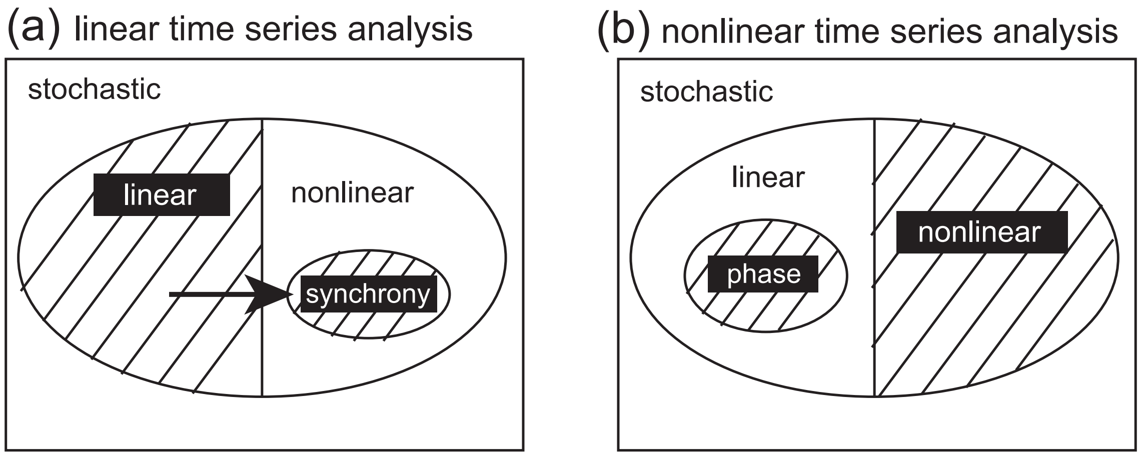

Figure 1.1. Relationship between the linear/nonlinear time series analysis and the extractable phenomena. (a) A case of the linear time series analysis. This analysis can extract a universal set of linear phenomena associated with the frequency or phase, but can view only synchronized phenomena through phases, where this phenomenon is a subset of nonlinear phenomena. (b) A case of the nonlinear time series analysis. This analysis can extract a universal set of nonlinear phenomena, but with the phase, which is a subset of linear phenomena, because even if a time series is embedded on a high-dimensional state space, the state space still involves phase information.

conventional linear analysis seems to be awkward because synchronization is actually a nonlinear phenomenon. If original EEG signals are separated into several frequency bands, nonlinearity will be also reduced, so that a question, whether the linear time series analysis can approach nonlinear dynamics which would reflect consciousness, occurs [Fig. 1.1(a)]. It seems that this conventional analysis can view only synchronization, not other nonlinear phenomena such as chaos, i.e., this approach implicitly has assumed that, consciousness is involved in synchronized phenomena. Perhaps this assumption has been out of mind for neuroscientists, but one should note that the linear time series analysis would be far from the elucidation of consciousness, because synchronization is very small subset of nonlinear phenomena [see Fig. 1.1(a)].

Besides there exists another linear aspect to analyze EEG signals, that is the averaging filter over multiple trials; this linear time series analysis aims at extracting very miniature components, called evoked potentials (EPs), in common contained in multiple EEG signals [5]. Typically EPs occur at the same timing over multiple trials, so that the averaging filter works well, but at the same time, this filter clearly reduces nonlinearity by considering it as background noise as well as the aforementioned band-pass filter, and therefore this type of linear time series analyses also views only synchronized phenomena; note that this synchrony comes from one electrode on the scalp, whereas the aforementioned synchrony comes from between more than two electrodes. Thus, the linear time series analysis, which we explained two cases, is restricted to extractions of only synchronized phenomena [Fig.

1.1(a)], so that a new type of time series analyses will be needed to bring us new insights in the neuroscience field and to approach the answer to a question: what the consciousness is.

The 'nonlinear' time series analysis based on Takens' embedding theorem [6] has been dramatically studied, especially in physics field, and has a possibility to answer the above question because this type of time series analyses can reconstruct high-dimensional nonlinear dynamics only from time series. This analysis assumes that, a nonlinear dynamics exists behind a time series, so that purely stochastic time series such as colored noise (fractional Brownian motions) are out of the analysis [see Fig. 1.1(b)], but our interest in this thesis is of oscillatory phenomena, consisting of a variety of nonlinearity, and therefore such an assumption can be ignored. Here noise, in the sense of the Gaussian white noise, is usually contained in a time series even if its origin is a deterministic dynamical system, but the amount of actual noise is relatively less than deterministic components so that the reconstruction of dynamics can be achieved. In addition, the reconstructed dynamics includes rich information concerned with many nonlinear phenomena such as chaos and off course reflects synchronized phenomena [see Fig. 1.1(b)], and therefore this dynamics would also involves consciousness. However, commonly the dynamics is on a very-high-dimensional state space, so that it seems that it is difficult to extract brain functions such as consciousness. Actually, the Lyapunov exponents [7], the correlation dimension [8], or the causality [9] can be estimated from the reconstructed dynamics, but still these several quantities have not directly been connected to brain functions.

To overcome this issue, recurrence plots (RPs) [10] have been developed to visualize high-dimensional attractors, where a two-dimensional plane we can easily observe is produced. Although RPs are only 2-dimensional and composed of a set of only binaries, surprisingly almost information are included in RPs [11], so that brain functions would be also reflected in a pattern composed of black (one) and white (zero) colors. This pattern may characterize each of brain functions, but this approach has not been applied to EEG signals well, because RPs effectively work if and only if the reconstructed dynamics and its original dynamics are one-to-one. Clearly methods using RPs make the nonlinear time series analysis easier for neuroscientists, than methods using other techniques, but the existence of noise, especially dynamical noise is a big problem to reconstructing dynamics, where noise, hereinafter, is naturally supposed to the Gaussian white noise.

Commonly, noise is divided into two types from the viewpoint of dynamical systems, namely observational noise and dynamical noise; the former is added to signals observed from devices so that this noise does not affect a trajectory moving on an attractor behind the signals; the latter affects system's dynamics directly so that the time evolution of the system depends not only on a dynamical rule but also on dynamical noise. In the real world, both types of noise would influence systems, and therefore the aforementioned nonlinear time series analysis may not be suitable for such systems, called stochastic dynamical systems. If a trajectory changes with noise, nonlinear quantities such as the Lyapunov

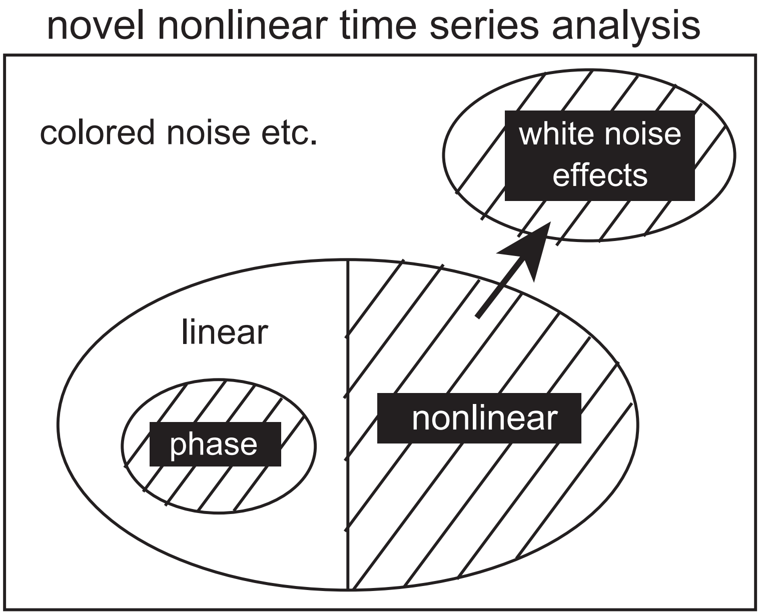

Figure 1.2. Relationship between a novel nonlinear time series analysis and the extractable phenomena. This analysis is an extended version of the conventional nonlinear time series analysis so that it can stll extract a universal set of nonlinear phenomena and a subset of linear phenomena, namely phase. In addition to such sets, the novel analysis can extract a subset of stochastic phenomena, called Gaussian white noise (dynamical noise) effects, where this noise drives variables constituting nonlinear dynamics so that the trajectory can change stochastically.

exponents cannot be estimated accurately. Off course we can assume that the level of dynamical noise is relatively less than that of deterministic components so that we can reconstruct dynamics, but in the brain, neurons themselves would generate noise, which will play a role of dynamical noise, and furthermore the resulting noise level possibly be very high so that the temporal evolution of EEG dynamics is dominantly stochastic. Thus, effective novel methods for analyzing dynamical noise behind time series should be developed urgently, because almost real-world systems are influenced by dynamical noise as mentioned above [see Fig. 1.2].

Actually, only the nonlinear time series analysis, which is one technology of our major called mathematical engineering, is not enough to understand nonlinear dynamics underlying EEG signals, because this analysis cannot reconstruct a mathematical model generating a phenomenon, rather, it mainly aims at characterizing unknown dynamics (models). Fortunately, another complementary technology is involved in mathematical engineering, namely mathematical modelling, which is to mathematically reconstruct dynamical models behind time series [Fig. 1.3], herein EEG signals. Perhaps, one may think that the combination between the nonlinear time series analysis and the mathematical modelling is enough to research EEG dynamics, i.e. experimental knowledge are not needed well,

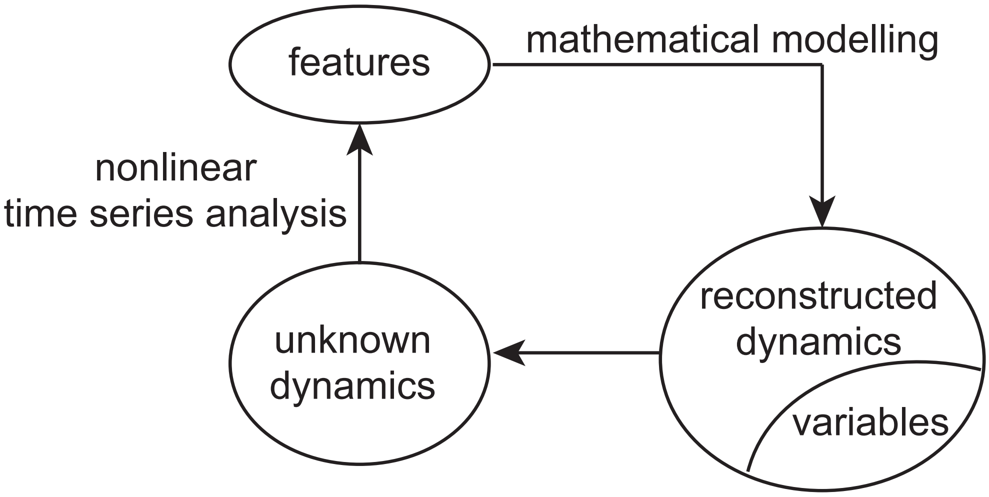

Figure 1.3. A complementary study using the following two technologies: (1) nonlinear time series analysis and (2) mathematical modelling. Technology (1) is to extract features characterizing 'unknown' dynamics behind time series, whereas technology (2) is to 'reconstruct' dynamics using the prior knowledge (features), where note that the reconstructed dynamics includes variables associated with the features. Until the properties of the variables and those of the features will be one-to-one, a cycle consisting of technologies (1) and (2) is repeated along the three arrows so that the reconstructed model can predict unknown phenomena perfectly.

because the former technology, nonlinear time series analysis, can characterize unknown models behind time series and therefore, someday it will be able to extract components of consciousness, while the latter technology, mathematical modelling, can reconstruct the dynamics—imagine here that a 'perfect' model is provided, i.e. a phenomenon originating from the model and the corresponding observed phenomenon are one-to-one. Based on this reconstruction, we can clearly predict various unknown phenomena by effectively changing parameters included in the model and accordingly, someday variables concerned with consciousness will be able to be included in the model depending on the prior knowledge, that are components of consciousness extracted by the nonlinear time series analysis described above [see Fig. 1.3].

Therefore, it seems that because the aforementioned combinational methodology is closed in the field of mathematical engineering, this field does not need any feedback from EEG experimental knowledge, as long as the model is created once according to a prior experimental result. However, the model as mentioned above has been assumed to be pure, but actual models include some kinds of errors arising from discrepancies between the models and the corresponding actual dynamics so that a perfect prediction using such models cannot be achieved. Thus, interactive studies between mathematical engineers and experimental neuroscientists cannot be avoided, and hence the following four steps will be mainly recommended [see Fig. 1.4]:

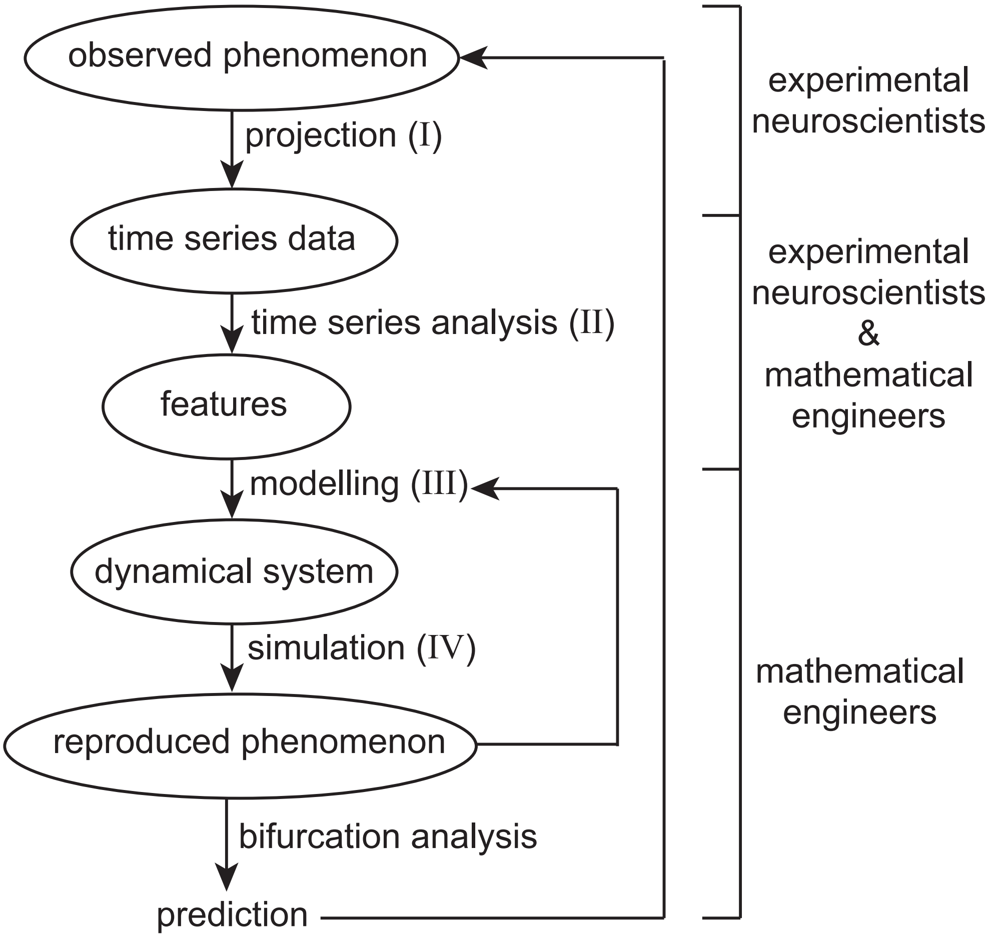

Figure 1.4. A flow from an observation to a prediction. The flow consists of the following four steps: (1) projection of the observation on time series data, (2) time series analysis for extracting features, (3) modelling a dynamical system based on the features, and (4) simulation for validation whether the observed phenomenon and reproduced one are one-to-one. After the validation at step (4) finishes, the bifurcation analysis may be performed to predict an unobserved phenomenon, and accordingly another validation whether such a predicted phenomenon can be observed in the real system is conducted. The study consisting of this flow will be achieved by a collaboration between experimental scientists and mathematical engineers.

(I) First, an experimenter observes a phenomenon as a time series, under a certain condition by using a controlled device, where a high-dimensional dynamics behind the phenomenon is converted to a one-dimensional signal, and furthermore the signal is formed as a time series with a certain sampling time. Perhaps, this time series may be a multivariate time series, especially for EEG recordings.
(II) Second, the experimenter characterizes the phenomenon with quantities such as frequencies characterizing EEG signals, where skills concerned with the time series analysis would be needed even for the experimenter, because if he has several techniques using not only the linear time series analysis but also the nonlinear time series analysis, the phenomenon can be quantified by many kinds of features comprising a variety of aspects, namely linearity and nonlinearity. These aspects provide us, for example not only the fundamental frequency, the power, or the phase locking value between two EEG signals, but also the Lyapunov exponents or the correlation dimension connected to chaos, or the causality between two signals. Furthermore, recently information flow using the technique called transfer entropy (TE) [12] has been becoming a key element little by little—this new type of techniques, TE, is actually out of linear or nonlinear time series analyses, because the TE is based on the Shannon entropy, the field of the information theory, not the time series analysis, but this new technology has been gradually approaching the time series analysis because information flow is similar to the causality; in addition, the quantification of information flow among several brain regions would be a remarkable feature towards modelling [13].
(III) Third, a modeler gets the above experimental condition including some parameters and a set of features characterized by the experimenter, where these parameters are used to model, but note that the experimenter cannot observe overall parameters such as the coupling strength between two EEG signals. Therefore, a given set of parameters would be a very small subset in a universal parameter set, controlling the phenomenon perfectly. Based on given parameters (condition), the modeler creates a model approximating the observed dynamics, where the model is commonly composed of some variables, parameters, and functions connecting the variables; such functions are either linear or nonlinear. Perhaps, a known model may be used for modelling in some situations, where only parameters will be tuned, but such a model would not be able to reproduce the desired phenomenon because the known model had been before used for reproducing another phenomenon.
(IV) Fourth, the modeler simulates the model on a computer and observes a time series, not a continuous signal because in the numerical simulation, differential equations are discretized for example by the Runge-Kutta method with a certain small sampling time so that we can get observation values with high accuracy, but a given observation value actually includes an error from a real value and furthermore, along the time evolution the error will expand—we have implicitly assumed here that modelling is achieved by differential equations, namely flow, because EEG signals we are interested in might be continuous signals. Based on the simulation, the modeler confirms whether a phenomenon emergent

from the model is qualitatively consistent with the actual phenomenon, by adapting features characterized by the experimenter. If these phenomena given by the experimenter and by the modeler are consistent, an integrated research—in which actual phenomena can be explained by mathematics—will be achieved. However, only one iteration from steps (I) to (IV) would not enough to finish this project, where the following two causes might hide: (i) validity of features characterizing phenomena and (ii) validity of models.
(i) Regarding the first cause, many experimental neuroscientists aim at finding new unobserved phenomena, so that the experimental skills are mainly needed rather than time series analysis techniques, and thus overcoming this cause seems to be very difficult, especially for the nonlinear time series analysis, which possibly be out of their minds. Fortunately, they are interested in the linear time series analysis, namely the frequency and the phase of EEG signals because it has been believed that the frequency characterizing e.g. alpha waves concerns brain functions, while the phase relates to information coding in the brain. Therefore, interactions between mathematical engineers and experimental neuroscientists are strongly needed even for a stage of the extraction of features characterizing phenomena, namely at step (II).
(ii) Regarding the second cause, recently a tendency can be seen, that is, models are created abstractly so that the bifurcation analysis—which is to reveal how a phenomenon changes to another one—can be easily conducted, and therefore if the bifurcation type between several phenomena becomes clear and if the control parameter inducing the bifurcation is identified, then we can facilitate or prevent to bifurcate systems. Thus, abstract models are useful to analyze the models themselves in detail, but some assumptions are commonly included in the models, for example concerned with coupling connections among neurons, where uniform connections have been often used recently, mainly towards the mean field theory. Thus, a probability that such abstract models can reproduce phenomena observed in experiment is very low, so that we have to turn from step (IV) to (III), and another model should be created towards an achievement of certain modelling.

Then, as well as the time series analysis, modelling also includes a problem whether the model is linear or nonlinear, where surprisingly even a 'perfect' linear model, namely the harmonic oscillator system can exhibit a waveform such as an EEG signal, owing to the effect of noise (Gaussian white noise). Note, however, that generating the waveform similar to real-world phenomena is not of our main focus, because even if such a 'linear' waveform can be given by a simulation, the underlying nonlinear phenomena such as chaos or even synchronization cannot be revealed. Nevertheless, several neuroscientists, especially experimental neuroscientists tend to not care how to model, i.e. they only care the similarity between the waveforms generated from a model and from the corresponding real phenomenon. Actually this notion is considerable from the viewpoint of the following proposition: "any phenomenon can be explained by mathematics", but only this thought might be very cheap for mathematical engineers, who aim at understanding the underlying phenomena of given time series through the bifurcation analysis in addition to the above

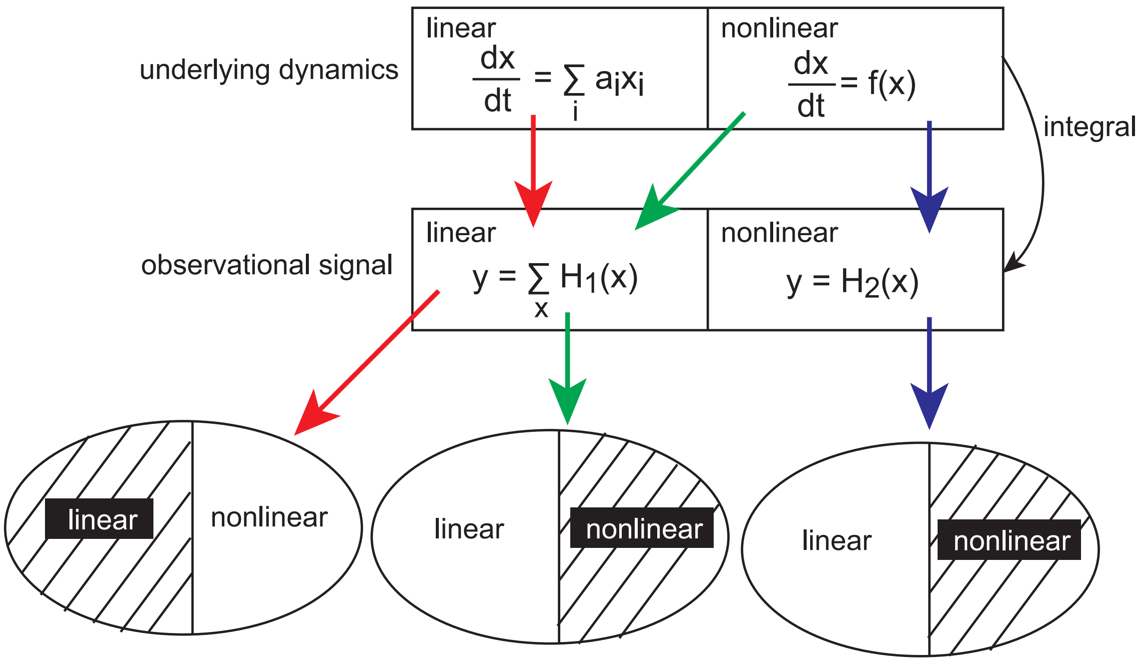

Figure 1.5. Relationship between modelling and the reproducible phenomena. Modelling includes the following two layers: (1) modelling an observational signal and (2) modelling the underlying dynamics, where each layer is constituted by either linearity or nonlinearity. The properties of linearity (nonlinearity) arising from layers (1) and (2) differ with each other and are connected via the integral. Towards modelling the following three cases are considerable: (a) If both layers are linear (red arrows), the reproducible phenomena show also linearity as a form of the harmonic oscillator system. (b) If layer (1) is linear but layer (2) is nonlinear (green arrows), the reproducible phenomena show nonlinearity owing to layer (2), where one can suppose that x and $f(x)$ are a phase and the Kuramoto model, respectively, while $H_1(x)$ is $\sin(x)$ so that this modelling exhibits an oscillator-based EEG model. (c) If both layers are nonlinear (blue arrows), the reproducible phenomena show also nonlinearity. Perhaps this case is more suitable to model than case (b) because modelling layer (1) in case (c) is constituted by only one element.

proposition. Therefore models should be created based on the prior knowledge given by real-world dynamics.

To return the topic that modelling also includes a problem whether a model is linear or nonlinear as well as a problem on the time series analysis, but modelling is more sensitive to linearity than the time series analysis, because if a 'linear' model is created, a phenomenon emergent from the model becomes also linear [see the red arrows in Fig. 1.5], whereas in the filed of the time series analysis, synchronized phenomena can be observed even if the analysis is perfectly linear [see Fig. 1.1(a)]. Furthermore, we should note that linearity arising from modelling is actually different from that arising from the time series analysis, because the former is a case on a differential equation, where a linear model means that the dynamical rule describing a dynamics is linear, but the latter is a case on a signal observed from a device (observation function) converting high-dimensional variables to a one-dimensional variable. Thus, we have to clearly understand such a discrepancy come from between the modelling and the time series analysis, to precisely discuss the necessity of nonlinearity based on both the modelling and the time series analysis; otherwise, perhaps one may discuss the nonlinearity of them on a common level, although nonlinearity arising from modelling occurs on a dynamical rule (differential equation), whereas that arising from the time series analysis occurs on the integral of the dynamical rule [see Fig. 1.5].

Now we focus on the modelling in terms of nonlinearity, but especially towards EEG dynamics modelling, a middle level actually exists, where this level of modelling is composed of both aspects of linearity and nonlinearity [see the green arrows in Fig. 1.5]. First, we shall introduce an example model, where an EEG signal is represented by a collection of many EEG oscillators such as delta, theta, alpha, beta, and gamma oscillators, as components of the EEG signal, and furthermore each EEG oscillator is described as the Kuramoto model [15]. Thus, this EEG model comprises both components of linearity and nonlinearity, i.e., the following two assumptions exist: one is that the model can be separated linearly into several frequency oscillators; another is that each oscillator is the Kuramoto phase oscillator. Here note that the Kuramoto model involves the Hopf bifurcation originating from nonlinearity of the coupling term so that there exist the following two dynamically distinctive regimes: one regime is the non-synchronized state, where the phases among respective oscillators are incoherent; another regime is the synchronized state, where the phases are definitely coherent. Because it has been strongly believed that an EEG signal might possess frequency-specific brain functions and that the amplitude of the signal would reflect the synchronization among EEG oscillators, the aforementioned two assumptions may be validated towards modelling. Furthermore, it is well known that modified versions [16, 17] of the Kuramoto model show a variety of nonlinear phenomena including chaos. However, the EEG model based on the Kuramoto model has explicitly comprised a concept of oscillations, as an aggregation of the frequencies so that a generation mechanism of such oscillations cannot be revealed.

Off course, we can model an EEG signal as a form of a more microscopic level rather than EEG oscillators, namely in terms of local field potentials (LFPs), where an LFP has been assumed to be the Kuramoto phase oscillator. However, the model based on LFP oscillators might be very similar to the above EEG model so that a problem how the oscillations appear still remains to be explored.

Besides, a phenomenological EEG model has been proposed, called neural mass model (NMM) [18] which is a 'perfect' nonlinear model [see the blue arrows in Fig. 1.5], that is, it has not been assumed that an EEG signal is a collection of EEG/LFP oscillators and furthermore, the dynamics of the NMM is described by several nonlinear terms so that we can answer the above problem: how the oscillations appear. In fact, the NMM can show a variety of oscillatory phenomena including alpha waves, where the mechanism of such phenomena indeed underlies the limit cycle attractor, generated due to nonlinearity involved in the NMM. By tuning parameters effectively, a diverse limit cycle oscillator with the various velocities emerges so that key parameters switching among several frequency bands can be identified. This NMM or the modified NMMs [19, 20] have been widely used in the neuroscience community because the dynamics within the models have been naturally expressed from the viewpoint of actual EEG dynamics. However, such models are very abstract, and therefore it seems to us that the process of consciousness generation we are strongly interested in, will not be revealed.

Although the NMM is a perfect nonlinear model in terms of both descriptions for the underlying dynamics and for its observational process [see Fig. 1.5], expressing the components of consciousness as a variable seems to be very difficult, and therefore another essential idea should be introduced. Herein we have to mention that the state of one neuron is not involved in the NMM as a variable, whereas a cell assembly—an aggregation of the neurons—is included in it as a variable. Thus, because the model has been created from the viewpoint of the cell assembly, not the neurons, their interactions (between cell assemblies and neurons) cannot be appeared as the resulting phenomena on the model. Here, a remarkable point exists, that is, the interactions between a whole and its elements; such interactions always can occur in the real-world systems, e.g. in the humans 'system' interacting in a room, in which each human interacts with other humans by speaking or acting so that the 'driven' human behaves according to an instruction of the 'driving' human (a case of an interaction from elements to a whole) and in contrast, the behavior of each human depends not only on his own mind but also on the atmosphere of the room, generated from the moods originating from all humans' minds (a case of an interaction from a whole to its elements). This analogical example can be directly applied to the interaction between a cell assembly and each neuron, and consequently we shall put forward a hypothesis that such interactions, especially from a whole to its elements, can generate consciousness [see Fig. 1.6] [21]. Hence, the use of the mean field approximation systematized in the field called statistical mechanics, which can convert a set of microscopic variables representing neurons to only one macroscopic variable representing an EEG or LFP signal, will be a straitforward way to modelling .

1.2 Purpose

As mentioned above, the following two complementary technologies might be needed from the viewpoint of the field of mathematical engineering, namely (1) nonlinear time series analysis and (2) mathematical modelling, to analyze nonlinear dynamics generating the macroscopic oscillations such as EEG signals. In addition, the process of consciousness generation still remains to be explored. Therefore, hereafter we aim at developing the following two new tools associated with technologies (1) and (2), to approach the elucidation of consciousness:

(1) Regarding the nonlinear time series analysis, a novel tool for analyzing the dynamical noise, especially including in EEG dynamics and originating from stochastic neurons, will

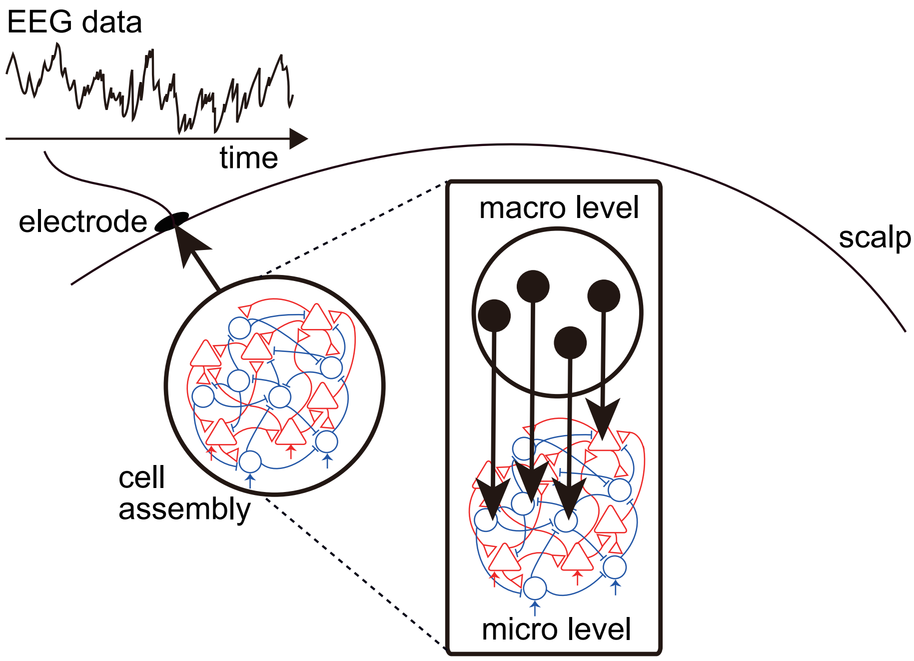

Figure 1.6. A hypothesis that the interaction between neurons (micro level) and EEG dynamics (macro level) generates higher brain functions such as consciousness and that the feedback from the macro to micro levels strongly connects to the process of consciousness generation.

be introduced in Chapter 2.
(2) Regarding the mathematical modelling, an extended stochastic neural network model will be introduced in Chapter 3, to understand the effect of the mean field approximation on the model; this model is a more realistic neural network model than the previous version [22] so that the model can reproduce a variety of macroscopic phenomena observed in EEG signals such as cross-frequency coupling phenomena, connecting between the macroscopic oscillations (EEG signals) and the microscopic neuronal firing [see the summarize of the purpose in Fig. 1.7].

Furthermore, we have to say that many kinds of nonlinear dynamics arising from this thesis will be analyzed in terms of oscillatory phenomena; this means that such dynamics comprise the multiple time-scales, from slow to fast oscillations and therefore, this study views the various nonlinear phenomena from the linearity [see Fig. 1.8]. Thus, the study sharing this viewpoint might play a key role that, someday many neuroscientists are going to be attracted to the world of the underlying nonlinear dynamics generating e.g. chaos.

1.3 Definitions of oscillations

Here we define oscillations in the sense of stochastic dynamical systems, so that oscillations emergent from the systems can be widely divided into the following two distinctive classes: (I) deterministic oscillations and (II) stochastic oscillations, both of which are

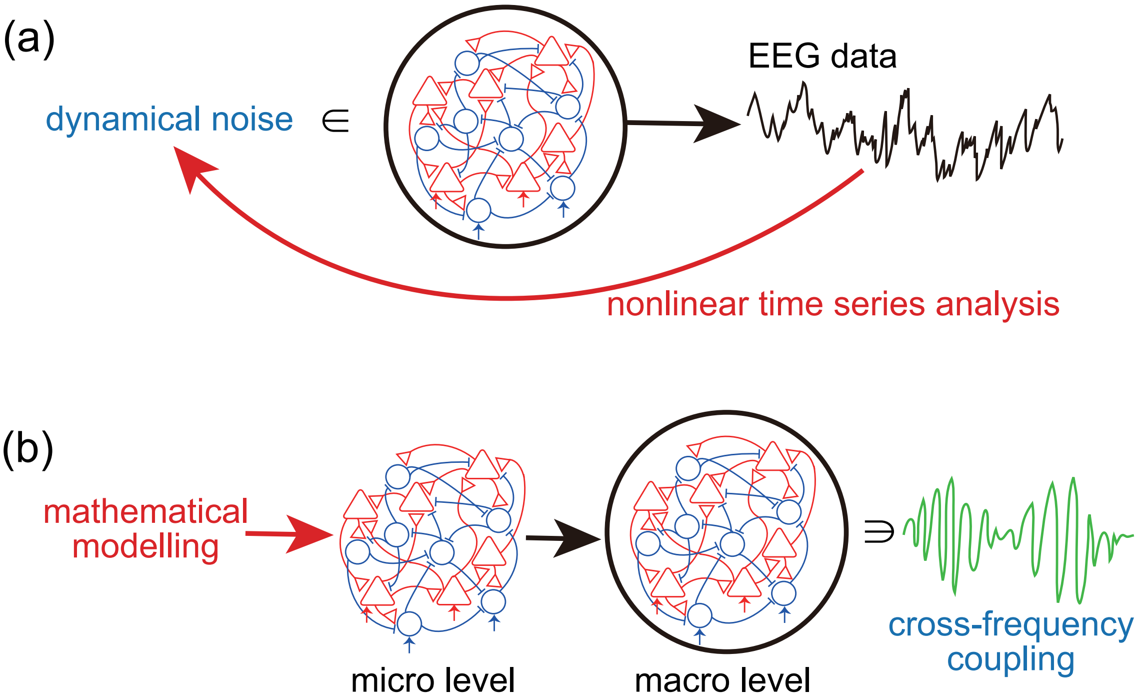

Figure 1.7. Two representative purposes arising from Chapter 2 for (a) and from Chapter 3 for (b). (a) The aim is to extract dynamical noise, driving variables constituting nonlinear dynamics, from EEG data, where a novel nonlinear time series analysis method is presented. (b) The aim is to understand the underlying dynamics of cross-frequency coupling phenomena, where an extended neural network model is presented, and furthermore the model is converted to a macroscopic model through the mean field approximation; this conversion from the micro to macro levels is possibly associated with the process of consciousness generation.

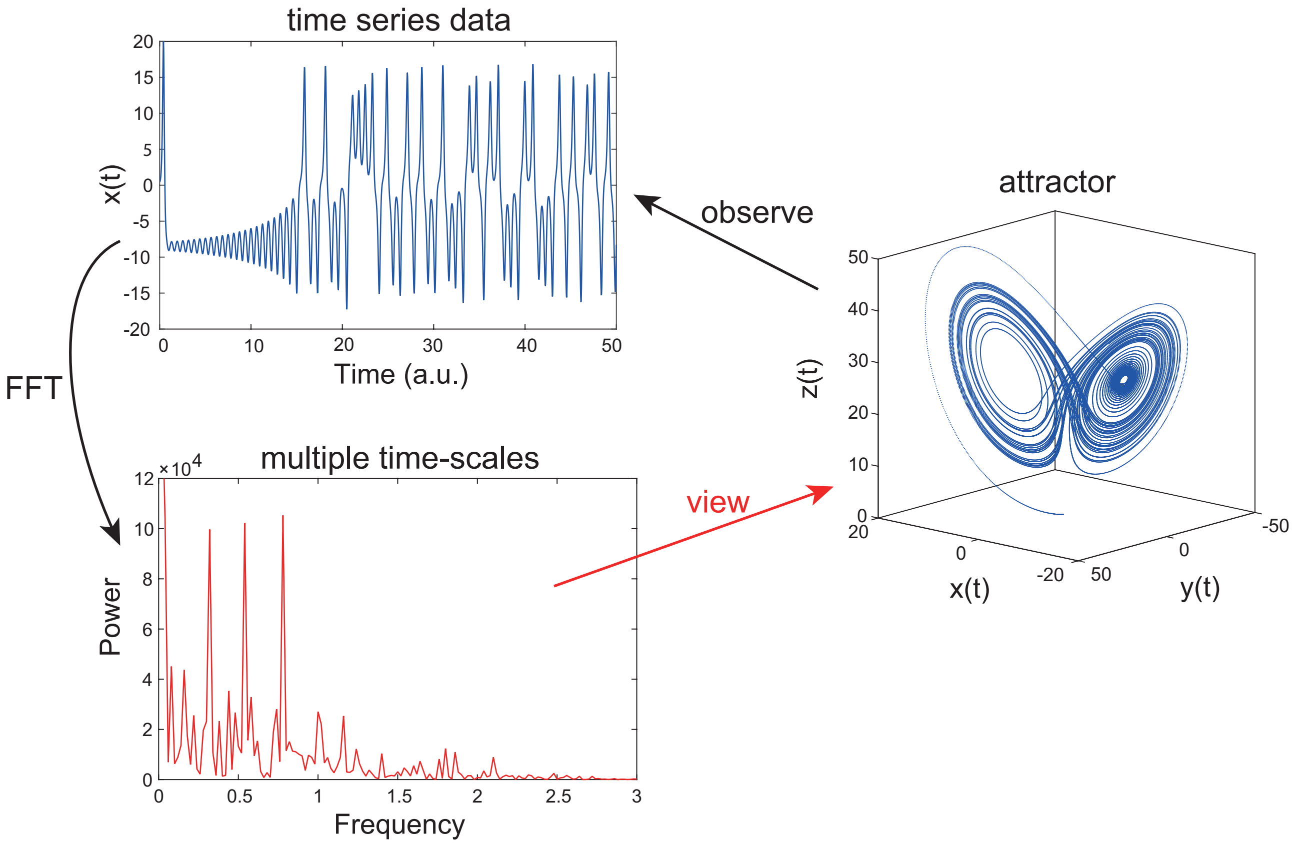

Figure 1.8. How to approach elucidating nonlinear dynamics in the brain. A variety of oscillatory phenomena is essential to form brain dynamics, so that the dynamics should be analyzed from the viewpoint of multiple time-scales the brain involves, i.e., the nonlinear dynamics generating oscillations is analyzed in terms of not only nonlinearity but also the frequency (linearity), ranged from the slow to fast oscillations and originating from the deterministic or stochastic process.

qualitatively different with each other, because class (I) originates from the drift term on systems, whereas class (II) originates from the diffusion term (dynamical noise) on systems. Furthermore, we define these classes such that the union between each class is equivalent to the original oscillations on a certain domain. Note that we do not care the existence of observational noise towards defining oscillations, because this kind of noise is out of the description of dynamics and only depends on the observational environment, mainly concerned with the property of observational devices.

We shall define the velocity of each class of oscillations relatively, in terms of stochastic dynamical systems so that the qualitative difference between classes (I) and (II) becomes clearly; the construction of this definition will be helpful to strictly define classes (I) and (II). To define the velocity, the following notion is needed, that is, because the diffusion term is generally expressed as the meaning of the Gaussian white noise, oscillations observed via the integrals of stochastic dynamical systems also reflect the property of the Gaussian white noise, more precisely that of the Wiener process, which is the integral of the Gaussian white noise. Thus, we define that the velocity of the stochastic oscillation is faster than that of the deterministic oscillation, because actually one realization of the Wiener process shows a very fast oscillation due to its definition. Off course, the drift term can make an oscillation faster, but even if the velocity of the oscillation becomes very fast owing to the formulation of the drift term, such an oscillation still contains more fast oscillatory components originating from the diffusion term, because one realization of the Wiener process contains the 'infinite' frequency. If and only if oscillatory components originating from the drift term include the infinite frequency, the velocity of the deterministic oscillation will be equivalent to that of the stochastic oscillation, but such a deterministic oscillation should be regarded as a stochastic oscillation, from the viewpoint of mathematical modelling.

Throughout this thesis, we use the term, "stochastic fast oscillation" instead of stochastic oscillation, to express more explicitly the property of this class of oscillations.

Finally, we shall introduce the definition associated with the following two subclasses: (i) deterministic slow oscillations and (ii) deterministic fast oscillations so that the union between these oscillations is equivalent to the original deterministic oscillation on a certain domain. As a simple case, we start to consider the oscillation observed from e.g. the coupled Stuart-Landau oscillators system generating the two-dimensional torus attractor—it has been assumed that this system is not affected by dynamical noise at all because now we are interested in pure deterministic oscillations. Clearly, such an oscillation involves the two representative frequency components so that it can be divided into the two subclasses (i) and (ii) on the frequency domain.

The objective towards analyses on Chapters 2 and 3 has been summarized in Fig. 1.9. In Chapter 2, signals composes of the deterministic oscillations (class (I)) and the stochastic fast oscillations (class (II)) will be analyzed, where class (I) is not divided into subclasses, i.e., the velocity of the deterministic oscillation is out of the purpose of Chapter 2. In

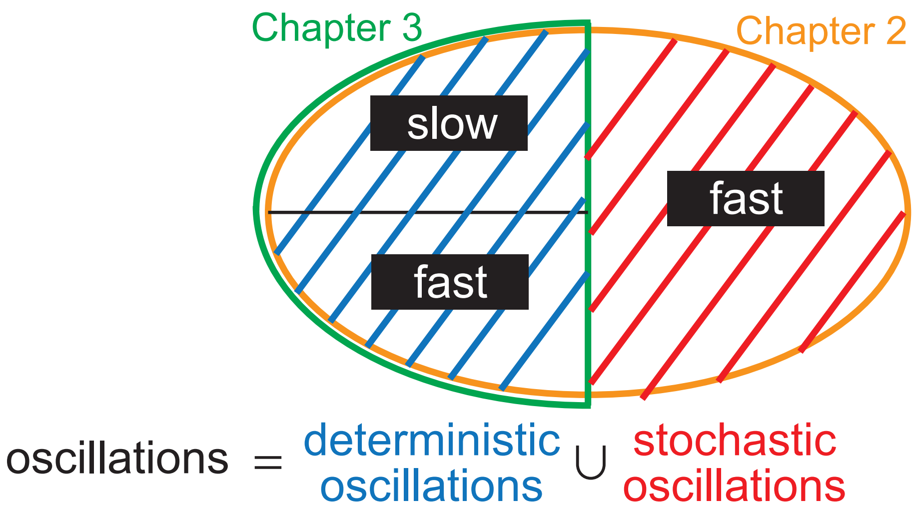

Figure 1.9. A set of oscillations is divided into the following two subsets: (1) deterministic oscillations and (2) stochastic oscillations in terms of stochastic dynamical systems. Subset (1) can be further divided into two sub-subsets: (i) deterministic slow oscillations and (ii) deterministic fast oscillations in terms of the frequency domain. In addition, subset (2) shows only the fast oscillation due to the Gaussian white noise (dynamical noise), so that we call this subset as stochastic fast oscillations. In Chapter 2, signals composed of subsets (1) and (2) are analyzed. In Chapter 3, signals composed of sub-subsets (i) and (ii) are analyzed.

contrast in Chapter 3, signals composed of the deterministic slow (class (i)) and fast (class (ii)) oscillations will be analyzed, where cross-frequency coupling phenomena emergent from the interaction between the deterministic slow and fast oscillations is observed.

1.4 Organization of the thesis

The rest of this thesis has been organized as follows:
In Chapter 2, the definition of a novel dimension is derived from that of the conventional fractal dimension, to analysis signals composed of the deterministic oscillations and the stochastic fast oscillations. Typically, it has been shown that this new type of dimensions, named after time series dimension (TSD), can detect the level of the underlying dynamical noise only from time series and can be applied to a variety of time series data, because the TSD does not require any information included in dynamics generating time series so that it can work as a model-free indicator, as we will explain in Chapter 2. Note that the TSD is one of the nonlinear time series analysis because it can characterize nonlinear dynamics driven by dynamical noise, but it dose not need embedding of a time series on a high-dimensional state space with delay coordinates, and therefore the TSD should be located in another world different from the conventional nonlinear time series analysis theory. In fact, the ability of the TSD has been demonstrated with the application of it to EEG

signals, and based on this application, a possibility whether the TSD—which works even if the dynamics behind a time series is filled with noise—can open the door where many features characterizing nonlinear phenomena strongly connected to noise are hidden, has been discussed. The contents of Chapter 2 will be published in Phys. Lett. A.

In Chapter 3, a realistic stochastic neural network model—which is suitable to be applied to the mean field theory so that the model can be transformed into a macroscopic model—is proposed to demonstrate whether the model can show cross-frequency coupling phenomena, connecting the macroscopic and the microscopic properties, through the mean field approximation. Note that this technology called mean field approximation would involve crucial roles for uncovering the process of consciousness generation if there exists the feedback from the macroscopic model to microscopic one, but the proposed model has been formulated as a feedforward model because our main purpose in Chapter 3 is to reveal the effect of the mean field approximation on the stochastic model. The proposed stochastic model has been created as a discrete-time model so that the errors arising from the numerical temporal evolution cannot appear, towards the application of the model to real-world systems, especially for EEG dynamics. Accordingly, the stochastic model has been converted to the corresponding discrete-time dynamical system, and therefore the property of deterministic oscillations has been intensively investigated through the bifurcation analysis, where the deterministic slow and fast oscillations, realized by a subnetwork composed of excitatory neurons and by that composed of inhibitory neurons, respectively, are analyzed. Furthermore, it has been assumed that only the torus attractor corresponds to real oscillatory phenomena, because the torus emergent from the proposed model can be interpreted as the limit cycle attractor or the torus attractor in the corresponding continuous-time dynamical system, but the periodic attractor perhaps corresponds to the equilibrium point, due to the failure of convergence by the Euler method. The contents of Chapter 3 was submitted to Frontiers in Computational Neuroscience.

Finally in Chapter 4, this thesis will be briefly concluded, in terms of nonlinear dynamics with multiple time-scales.

Chapter 2

Conclusions

In this study, a variety of nonlinear dynamics have been analyzed in terms of multiple time-scales the brain involves to form macroscopic oscillations shown in e.g. EEG signals, where it has been believed that the oscillations are associated with the facilitation of information processing by adaptively changing the properties of themselves. Thus, this study has been performed with both aspects of nonlinearity and linearity, i.e., nonlinear dynamics emergent from the brain has been analyzed from the viewpoint of frequencies—which are separated linearly—forming oscillations. Towards analyses of brain dynamics, actually a set of oscillations has been divided into the following two subsets: (I) deterministic oscillations and (II) stochastic fast oscillations, and furthermore subset (I) has been divided into the following two sub-subsets (Ia) deterministic slow oscillations and (Ib) deterministic fast oscillations, in terms of stochastic dynamical systems so that the dynamical noise has been defined in the sense of the Gaussian white noise.

In Chapter 2, signals composed of deterministic oscillations (subset (I)) and stochastic fast oscillations (subset (II)) have been analyzed, where a novel nonlinear time series analysis method had been strongly required because the conventional nonlinear time series analysis methods based on Takens' embedding theorem, in general, have been suitable only for deterministic dynamical systems, not for stochastic dynamical systems. Typically, it has been considered that the essential difference between the deterministic and stochastic dynamical systems is whether the dynamical noise drives variables in the state space so that the trajectory temporally evolves stochastically, although many conventional nonlinear time series analysis methods mainly have aimed at characterizing deterministic trajectories. Accordingly, a novel nonlinear time series analysis method, called time series dimension (TSD), has been developed to overcome the aforementioned drawback, where the novel dimension, TSD, enabled to detect the level of underlying dynamical noise only from time series data and furthermore, the TSD does not require any information associated with the dynamics generating time series and works even if the length of time series is very short so that there exist a possibility that the TSD can open the door where nonlinear time series analysis methods including the TSD have been broadly used in the neuroscience field.

In Chapter 3, signals composed of deterministic slow oscillations (sub-subset (Ia)) and deterministic fast oscillations (sub-subset (Ib)) have been analyzed, where an extended discrete-time neural network model, comprising excitatory and inhibitory stochastic neurons, has been introduced so that the corresponding macroscopic model can be derived through the mean field approximation. Now it has been considered that this mean field approximation is a key technology to approach the elucidation of the process of consciousness generation because it has been hypothesized that the interactions between microscopic elements (herein the stochastic model) and macroscopic ones (herein the macroscopic model via the mean field approximation) originate from consciousness. Note, however, that it has been investigated only in the case of the feedforward interaction from the microscopic to macroscopic elements, because to study the feedback interaction between them, prior knowledge resulting from experiments using an integration between EEG recordings and external stimulation inputs to brain dynamics—for example, the transcranial magnetic stimulation (TMS) or the transcranial alternating current stimulation (tACS)—should be needed to model, where the external stimulation (pseudo macroscopic element) plays a role of EEG dynamics and affects synaptic plasticity to get some evidences that the feedback interaction concerns consciousness. To return, through the mean field approximation, the original stochastic model has been converted to the corresponding macroscopic model, namely eight-dimensional discrete-time dynamical system so that this system can generate the deterministic slow and fast oscillations, each of which originates from the excitatory subnetwork and from the inhibitory subnetwork, respectively. It has been revealed that the system involves the following two kinds of phase-amplitude frequency-coupling phenomena: oscillatory state with two frequency components on two-dimensional torus (OS2T) and that with two frequency component on closed curve (OS2C) by use of the bifurcation analysis. Furthermore, it has been identified that these states can be separated by the cyclic bifurcation of a one-dimensional torus in a map (MT1SNC).

It has been believed that the aforementioned two kinds of analyses, namely (1) nonlinear time series analysis and (2) bifurcation analysis, make us approach the elucidation of brain oscillatory dynamics with multiple time-scales. In particular, analysis (1) will lead many neuroscientists to the world filled with nonlinear dynamics, while analysis (2) will be helpful to clarify functional roles of phase-amplitude cross-coupling phenomena, connecting between macroscopic and microscopic dynamics.

Acknowledgments

First of all, I would like to express my sincere gratitude to the journal of Physics Letters A, because the publisher Elsevier has permitted Chapter 2 to include major parts of the contents in Ref. [1]. In addition, the contents of Chapter 3 was submitted to the journal of Frontiers in Computational Neuroscience.

I would like to express my deepest gratitude to Professor Kazuyuki Aihara, who gave me very suitable environmental spaces to study with his laboratory members, including many postdoctoral researchers, especially belonging to the Aihara innovative mathematical modelling project through the FIRST program. All the discussions with them inspired my inquiring mind. In particular, I have remembered that Prof. Aihara gave me very critical some comments related to the relationship between the continuous-time and discrete-time dynamical systems. A simple example consisting of the logistic equation and the logistic map was very beneficial to model brain dynamics as a form of the discrete-time dynamical system. Furthermore, I have realized values of the torus attractors emergent from the discrete-time dynamical system.

In addition, I would like to thank Professor. Fumiyasu Komaki, Professor. Takayasu Matsuo, Professor. Yoko Yamaguchi, Professor. Hideyuki Suzuki, and Professor. Yoshito Hirata, each professor of who kindly received a role of the referee for my Ph. D program. Especially, the comments arising from Prof. Komaki were very kind to facilitate my understanding of the theory for the time series dimension (TSD).

In considering the creation of Chapter 2, I would like to express my sincere gratitude to Prof. Hirata, who gently accepted to work as a coauthor of my Ph. D study. All the discussions with him were very helpful to progress my mathematical thinking and English writing skills, needed for Ph. D graduation. I would also like to thank Dr. Keiichi Kitajo, who gave me some crucial suggestions concerned with neural oscillations in the brain. Discussions with him were so exciting for me.

In considering the creation of Chapter 3, I would like to express my sincere gratitude to Professor. Motomasa Komuro, who kindly taught me how to analyze bifurcations in discrete-time dynamical systems. Thanks to him, I could stand at the starting point of the bifurcation research. I would also like to thank Dr. Yuichi Katori, who motivated me to study the bifurcation analysis via mathematical modeling.

Further, I would like to thank Dr. Makito Oku, who was always supporting me, even if he was so busy.

Finally, I would like to thank all of the laboratory members, my friends, and my families both in Japan and in Malaysia. They warmly watched over the growth of me. In particular, I would like to express my deep gratitude to my mother and farther, who greatly supported me. Of course, I would like to express my deep gratitude to my wife, Nurul Liyana Binti Mohamad Zulkufli, who was always beside me, even if she was in Malaysia.

Bibliography

[1] T. Sase, J. Pena Ramirez, K. Kitajo, K. Aihara, and Y. Hirata (2016), Estimating the level of dynamical noise in time series by using fractal dimensions, Phys. Lett. A **380**, pp. 1151–1163.

[2] G. Edelman and G. Tononi, *A universe of consciousness: How matter becomes imagination* (Basic Books, New York, 2000).

[3] G. Buzsáki and A. Draguhn (2004), Neuronal oscillations in cortical networks, Science **304**, 1926.

[4] M. Kawasaki, K. Kitajo, and Y. Yamaguchi (2010), Dynamic links between theta executive functions and alpha storage buffers in auditory and visual working memory, Eur. J. Neurosci. **31**, 1683.

[5] B. C. Armstrong, M. V. Ruiz-Blondet, N. Khalifian, K. J. Kurtz, , Zhanpeng Jin, and S. Laszlo (2015), Brainprint: Assessing the uniqueness, collectability, and permanence of a novel method for ERP biometrics, Neurocomputing, **166**, 59.

[6] F. Takens, *in Dynamical Systems and Turbulence*, Lecture Notes in Mathematics Vol. 898, edited by D. A. Rand and L. S. Young (Springer, Berlin, 1981), p. 366.

[7] A. Wolf, J. B. Swift, H. L. Swinney, and J. A. Vastano (1985), Determining Lyapunov exponents from a time series, Physica D, **16**, 285.

[8] M. Thiel, M. C. Romano, P. L. Read, and J. Kurths (2004), Estimation of dynamical invariants without embedding by recurrence plots, Chaos, **14**, 234.

[9] Y. Hirata and K. Aihara (2010), Identifying hidden common causes from bivariate time series: A method using recurrence plots, Phys. Rev. E **81**, 016203.

[10] N. Marwan, M. C. Romano, M. Thiel, and J. Kurths (2007), Recurrence plots for the analysis of complex systems, Phys. Rep. **438**, 237.

[11] Y. Hirata , S. Horai, and K. Aihara, (2008), Reproduction of distance matrices and original time series from recurrence plots and their applications, Eur. Phys. J. Spec. Top. **164**, 13.

[12] T. Schreiber (2000), Measuring Information Transfer, Phys. Rev. Lett. **85**, 461.

[13] M. Kawasaki, Y. Uno, J. Mori, K. Kobata, and K. Kitajo (2014), Transcranial magnetic stimulation-induced global propagation of transient phase resetting associated with directional information flow, Front. Hum. Neurosci. **8**, doi: 10.3389/fnhum.2014.00173.

[14] O. Jensen and L. L. Colgin (2007), Cross-frequency coupling between neuronal oscillations, Trends Cogn. Sci. **11**, 267.

[15] J. A. Acebron, L. L. Bonilla, C. J. Perez Vicente, F. Ritort, and R. Spigler (2005), The Kuramoto model: A simple paradigm for synchronization phenomena, Rev. Mod. Phys. **77**, 137.

[16] M. K. Stephen Yeung and S. H. Strogatz (1999), Time Delay in the Kuramoto Model of Coupled Oscillators, Phys. Rev. Lett. **82**, 648.

[17] Y. L. Maistrenko, B. Lysyansky, C. Hauptmann, O. Burylko, and P. A. Tass (2007), Multistability in the Kuramoto model with synaptic plasticity, Phys. Rev. E **75**, 066207.

[18] O. Davida and K. J. Fristona (2003), A neural mass model for MEG/EEG:: coupling and neuronal dynamics, Neuroimage **20**, 1743.

[19] R. C. Sotero, N. J. Trujillo-Barreto, Y. Iturria-Medina, F. Carbonell, and J. C. Jimenez (2007), Realistically Coupled Neural Mass Models Can Generate EEG Rhythms, Neural Comput. **19**, 478.

[20] O. David, L. Harrison, and K. J. Friston (2005), Modelling event-related responses in the brain, Neural Comput. **25**, 756.

[21] E. P. Hoel, L. Albantakis, and G. Tononi (2013), Quantifying causal emergence shows that macro can beat micro, PNAS **110**, 19790.

[22] Y. Katori, Y. Igarashi, M. Okada, and K. Aihara (2012), Stability analysis of stochastic neural network with depression and facilitation synapses, J. Phys. Soc. Jpn. **81**, 114007.

[23] H. Kantz and T. Schreiber, *Nonlinear Time Series Analysis* (Cambridge University Press, Cambridge, MA, 1997), p. 174.

[24] M. R. Muldoon, D. S. Broomhead, J. P. Huke, and R. Hegger, (1998), Delay embedding in the presence of dynamical noise, Dyn. Stab. Sys. **13**, 175.

[25] A. Serletis, A. Shahmoradi, and D. Serletis (2007), Effect of noise on the bifurcation behavior of nonlinear dynamical systems, Chaos Solitons Fractals **33**, 914.

[26] J. P. M. Heald and J. Stark (2000), Estimation of noise levels for models of chaotic dynamical systems, Phys. Rev. Lett. **84**, 2366.

[27] D. Orrell (2005), Filtering chaos: A technique to estimate dynamical and observational noise in nonlinear systems, Int. J. Bifurcat. Chaos **15**, 99.

[28] M. Siefert, A. Kittel, R. Friedrich, and J. Peinke (2003), On a quantitative method to analyze dynamical and measurement noise, Europhys. Lett. **61**, 466.

[29] A. N. Kolmogorov (1931), Math. Ann. **140**, 415.

[30] J. E. Moyal (1949), Stochastic processes and statistical physics, J. R. Stat. Soc. **11** 195.

[31] K. Urbanowicz and J. A. Holyst (2003), Noise-level estimation of time series using coarse-grained entropy, Phys. Rev. E **67**, 046218.

[32] T. Higuchi (1988), Approach to an irregular time series on the basis of the fractal theory, Physica D **31**, 277.

[33] P. Grassberger and I. Procaccia (1983), Estimation of the Kolmogorov entropy from a chaotic signal, Phys. Rev. A **28**, 2591.

[34] G. Benettin, L. Galgani, and J. M. Strelcyn (1976), Kolmogorov entropy and numerical experiments, Phys. Rev. A **14**, 2338.

[35] J. L. Hindmarsh and R. M. Rose (1984), A model of neuronal bursting using three coupled first order differential equations, Proc. R. Soc. London B **221**, 87.

[36] D. Hansel and H. Sompolinsky (1992), Synchronization and computation in a chaotic neural network, Phys. Rev. Lett. **68**, 718.

[37] B. B. Mandelbrot (1985), Self-affine fractals and fractal dimension, Phys. Scr. **32**, 257.

[38] T. Higuchi (1989), Toukeisuri **37**, 209.

[39] B. B. Mandelbrot, *The Fractal Geometry of Nature* (Freeman, San Francisco, 1982).

[40] W. Rudin, *Principles of Mathematical Analysis* (McGraw-Hill, New York, 1967), p. 83.

[41] K. Kitajo, D. Nozaki, L. M. Ward, and Y. Yamamoto (2003), Behavioral stochastic resonance within the human brain, Phys. Rev. Lett. **90**, 218103.

[42] K. Rektorys, *Survey of Applicable Mathematics* (Iliffe Books, London, 1969), p. 1125.

[43] A. K. Engel, P. Fries, and W. Singer (2001), Dynamic predictions: oscillations and synchrony in top - down processing, Nature Rev. Neurosci. **2**, 704.

[44] W. Klimesch (1999), EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis, Brain Res. Rev. **29**, 169.

[45] J. Csicsvari, B. Jamieson, K. D. Wise, and G. Buzsáki (2003), Mechanisms of gamma oscillations in the hippocampus of the behaving rat, Neuron **37**, 311.

[46] N. Kopell, G. B. Ermentrout, M. Whittington, and R. D. Traub (2000), Gamma rhythms and beta rhythms have different synchronization properties, Proc. Natl. Acad. Sci. U.S.A. **97**, 1867.

[47] M. Steriade (2001), Impact of network activities on neuronal properties in corticothalamic systems, J. Neurophysiol. **86**, 1.

[48] W. J. Freeman, L. J. Rogers, M. D. Holmes, and D. L. Silbergeld (2000), Spatial spectral analysis of human electrocorticograms including the alpha and gamma bands, J. Neurosci. Methods **95**, 111.

[49] A. Sirota, J. Csicsvari, D. Buhl, and G. Buzsáki (2003), Communication between neocortex and hippocampus during sleep in rodents, Proc. Natl. Acad. Sci. U.S.A. **100**, 2065.

[50] T. Tateno, A. Harsch, and H. P. C. Robinson (2004), Threshold firing frequency - current relationships of neurons in rat somatosensory cortex: type 1 and type 2 dynamics, J. Neurophysiol. **92**, 2283.

[51] H. Markram and M. Tsodyks (1996), Redistribution of synaptic efficacy between neocortical pyramidal neurons, Nature **382**, 807.

[52] H. Markram, Y. Wang, and M. Tsodyks (1998), Differential signaling via the same axon of neocortical pyramidal neurons, Proc. Natl. Acad. Sci. U.S.A. **95**, 5323.

[53] A. M. Thomson (2000), Facilitation, augmentation and potentiation at central synapses, Trends Neurosci. **23**, 305.

[54] Y. Wang, H. Markram, P. H. Goodman, T. K. Berger, J. Ma, and P. S. Goldman-Rakic (2006), Heterogeneity in the pyramidal network of the medial prefrontal cortex, Nat. Neurosci. **9**, 534.

[55] G. Mongillo, O. Barak, and M. Tsodyks (2008), Synaptic theory of working memory, Science **319**, 1543.

[56] Y. Katori, K. Sakamoto, N. Saito, J. Tanji, H. Mushiake, and K. Aihara (2011), Representational switching by dynamical reorganization of attractor structure in a network model of the prefrontal cortex, PLoS. Comput. Biol. **7**, doi: 10.1371/journal.pcbi.1002266.

[57] Y. Igarashi, M. Oizumi, and M. Okada (2010), Mean field analysis of stochastic neural network models with synaptic depression, J. Phys. Soc. Jpn. **79**, 84001.

[58] Y. Katori, Y. Otsubo, M. Okada, and K. Aihara (2013), Stability analysis of associative memory network composed of stochastic neurons and dynamic synapses, Front. Comput. Neurosci. **21**, doi: 10.3389/fncom.2013.00006.

[59] J. F. Mejias and J. J. Torres (2009), Maximum memory capacity on neural networks with short-term synaptic depression and facilitation, Neural Comput. **21**, 851.

[60] M. Tsodyks, K. Pawelzik, and H. Markram (1998), Neural networks with dynamic synapses, **10**, 821.

[61] K. Kamiyama, M. Komuro, T. Endo, and K. Aihara (2014), Classification of Bifurcations of Quasi-Periodic Solutions Using Lyapunov Bundles, Int. J. Bifurcation Chaos **24**, 1430034.

[62] A. Fisahn, F. G. Pike, E. H. Buhl, and O. Paulsen (1998), Cholinergic induction of network oscillations at 40 Hz in the hippocampus in vitro, Nature **394**, 186.

[63] E. O. Mann, J. M. Suckling, N. Hajos, S. A. Greenfield, and O. Paulsen (2005), Perisomatic feedback inhibition underlies cholinergically induced fast network oscillations in the rat hippocampus in vitro, Neuron **45**, 105.

[64] J. J. Chrobak and G. Buzsáki (1998), Gamma oscillations in the entorhinal cortex of the freely behaving rat, J. Neurosci. **18**, 388.