

Dynamics of Brain and Behaviour: Studies on Rat Exploratory Behaviour and its Neural Correlates

*A thesis submitted to the University of Hyderabad
for the award of a Ph.D. degree in Animal Sciences*

By
CHETAN KUMAR YADAV



Department of Animal Sciences
School of Life Sciences
University of Hyderabad
PO Central University, Gachibowli
Hyderabad 500 046
Andhra Pradesh (India)

Enrollment No: 05LAPH03

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To, my family.....

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BIBIOLOGY

Abbreviations

FFT	Fast Fourier Transform
PDF	Probability Density Function
Hz.	Hertz
Sec.	Seconds
SOC	Self-Organized Criticality
LFP	Local Field Potentials
nLFP	Negative Local Field Potentials
CA1	Cornu Ammonis
PSD	Power Spectral Density
IEI	Inter-Avalanche-Interval
cm.	Centi meter
mV	milli Volt
ms.	milli Seconds
Sec.	Seconds

Key Words

Behaviour, spatial information, home base, 1/f noise, power law, recurrence time statistics, Hippocampus, CA1, Local Field Potentials, Self-Organized Criticality, Avalanches

CHAPTER 1
GENERAL INTRODUCTION

1.1 Exploratory Behaviour in Rats

Animal behaviour is the output of various neuro-psycho-physiological processes in brain. This can be considered as a macroscopic system consisting of various elements or group of elements, e.g. neuronal activity in brain. The factors which can affect behaviour are not limited to physiology of behaving animal but various external factors like environment and socio-ecology are crucial factors contributing to behaviour at a given time. Psychological and physiological states of the animal are used to define a “behavioural state”. Scientific study of animal behaviour is called ‘Ethology’ (from Greek: ἦθος, ethos, "character"; and -λογία, -logia). Ethology is a sub-topic of ‘Zoology’. Although many naturalists have studied aspects of animal behaviour throughout history, the modern discipline of ethology is generally considered to have begun during the 1930s with the work of Dutch biologist Nikolaas Tinbergen and Austrian biologists Konrad Lorenz and Karl von Frisch, joint winners of the 1973 Nobel Prize in Physiology or Medicine (please refer to the official website of Nobel prize cited in “*bibliography*”). Ethology is a combination of laboratory and field science, with a strong relation to certain other disciplines — e.g., neuroanatomy, ecology, evolution. Ethologists are typically interested in a behavioural process rather than in a particular animal group and often study one type of behaviour (e.g. aggression or exploration) in a number of unrelated animals. Learning, emotions, communication etc. have been studied extensively in 21st century. A new branch of study in science has evolved which aims to study behaviour and its neural correlates in brain, it is known as ‘Neuroethology’. ‘Comparative Psychology’ is another discipline dealing with study of behaviour. This is more related and concerned about psychology of particular behaviour rather than its biology. Subjective and deep ecological thinking of famous scientists of times, Lamarck and Darwin are good examples of landmarks in natural sciences research. Their research was combination of ecology, evolution and ethology. Other researchers like Lorenz and Tinbergen worked on

behaviour and 'imprinting'. Niko Tinbergen (1951, 1953) addressed critical questions in paradigm, i.e. (i) Function — How does the behaviour affect the animal's chances of survival and reproduction? Why does the animal respond that way instead of some other way?

(ii) Causation — What are the stimuli that elicit the response, and how has it been modified by recent learning?

(iii) Development — How does the behaviour change with age, and what early experiences are necessary for the behaviour to be displayed?

(iv) Evolutionary history — How does the behaviour compare with similar behaviour in related species, and how might it have begun through the process of phylogeny?

Exploratory Behaviour in Animals:

Animals perform locomotion and various kinds of movements due to or for various reasons, e.g. for searching food, mating (nuptial flights in insects), search for safe habitat etc. There may be many reasons for change of place or position. Changes in geographical locations help in combating environmental or seasonal variations. Migratory birds or fishes in sea are good examples for this. Once the coordinates of location are learned they reach recurrently. In case, the location is no more secure they explore for other favorable options. Usually animals move is driven by their needs as well as curiosity. Different groups have studied exploratory behaviour in various organisms from invertebrates, i.e. insects (J.-L. Deneubourg et al., 1990; Chapman and Bernays, 1989; E. Bakchine et al., 1990) to higher mammals, i.e. rats and mice (Drai et al. 2001 & other cited references from Ian Golani's group at Tel Aviv University) and even humans (Nakamura et al., 2008). Much came for this through studies on mice and laboratory rats (wistar, long evans and kangaroo rats). Here it is worth mentioning the contribution of Prof. Ian Golani's

group at Tel Aviv University, Tel Aviv Israel. Prof. Golani and his associates not only studied behaviour and genetics of the behaviour but also the psychological aspects of the ethological considerations. Mice and Rats happen to be similar ethologically but their finer aspects differ. 'Navigation' is the commonly used term in relation to locomotion. There are various composite forms of locomotion (navigation), looping, priming, homing are some of these. Homebase is the location in spatial coordinates which is considered relatively safer and is visited again and again by the subject. Recurrent visits to homebase help the subject to relate other locations with home base. Spatial information gathered during exploration may be compared with home base and a complex computation in brain may decide further movements. Previous studies suggest that homebase establishment is an important event in rat exploratory behaviour (Tchernichovski et al. 1995; Alyan 1996; Draai et al. 2001; Geyer et al. 1986; Loewen et al. 2005). It is believed that home base behaviour represents the recruitment of several composite forms of navigation. Reut et al. (2006) suggested that shift from different exploratory behaviours, like looping to home base behaviour, is a part of the process of recruitment of navigation via a transition from sequential to parallel, and ultimately to continuous processing of spatial information. It is in general agreement that a home base exists to which animal returns with high speed ('running') after careful progressions with relatively lower speeds and in bouts.

Spatial Learning in Animals:

A subject gathers information about the space and its surroundings during exploration. The experimental space used for the study is called 'Arena'. The spatial information gathered is a set of information, e.g. distance, angle etc. relative to various 'landmarks' and home base. This information is, processed, consolidated and retrieved as per needs (further actions). The spatial information processing and organization in brain is not simple but complex. 'Hippocampus' is

the region of brain which deals with spatial learning and spatial information processing. Fundamental aspects of spatial learning became clear with discovery of 'Place Field Cells' or 'Place Cells' in hippocampus. Place cells are neurons in the hippocampus that exhibit a high rate of firing whenever an animal is in a specific location in an environment corresponding to the cell's "place field". These neurons are distinct from other neurons with spatial firing properties, such as grid cells, border cells, head direction cells, and spatial view cells. In the CA1 and CA3 hippocampal subfields, place cells are believed to be pyramidal cells, while those in the dentate gyrus are believed to be granule cells. Place cells were first described in rats by O'Keefe and Dostrovsky (1971). Place cells are dynamic cell clusters which reflect the dynamics of spatial information processing, so appear to be good candidates to study the spatial learning in the subjects. These kinds of systems are categorized as 'Complex Systems'. Complex systems usually evolve as 'emergent systems' and often exhibit 'self organization' of the building elements which interact with each other in various manners. These interactions drive the systems towards a 'Critical State' which acts as a landmark for the change in the behaviour of the system. The concept of 'Self-Organized Criticality' (Bak, 1984) has been adopted for describing various complex systems starting from but not limited to earthquakes (Bak & Tang 1989; Sornette & Sornette 1989), solar flares (Lu & Hamilton 1991), evolution of biological systems (Bak & Sneppen 1993), fluctuations in confined plasma (Politzer 2000), snow avalanches (Faillettaz et al. 2004), and rainfall (Peters et al. 2002). In this thesis the concept of 'Self-Organized Criticality (SOC)' is adopted as a happening phenomenon operating in rat brain in relation to spatial learning during exploration and spatial information processing during the same. We believe that this phenomenon could help us understanding mechanistic basis of spatial learning in brain.

1.2 Neural Correlates of Behaviour

A neural correlate of a content of experience is any bodily component, such as an electro-neurobiological state or the state assumed by some biophysical subsystem of the brain, whose presence necessarily and regularly correlates with such a specific content of experience. There may be many neural correlates for a particular behaviour. Basically it depends on what you want to look into and for what purpose. Electrophysiological activity of neurons in brain, local discharge and recruitment of various forms of neurons for specialized function may contribute as neural correlate of a behaviour. In addition to neural correlate of a psycho-behavioural state in general, much progress has been made in elucidating neural correlates of specific cognitive variables. Thus, Earl Miller and colleagues discovered prefrontal cortex neurons that represent perceptual categories (cats versus dogs in their experiments). The work of Richard Andersen, Steven Wise, Carl Olson, Jun Tanji, Apostolos Georgopoulos and other neuroscientists have illuminated neuronal correlates of motor planning, selective visual attention, motor sequences and spatial reference frames in which these entities are represented by brain cells. The progress in understanding neuronal correlates of motor planning has led to creation of brain-machine interfaces, the devices that translate neuronal activity into purposeful commands to artificial actuators. There are a number of approaches and ways to look into neural correlates of behaviour, i.e. anatomy, histology and electrical activity of specific parts of brain. The methods used are immuno-histochemistry (IHC), electro-encephalogram (EEG), magneto-encephalogram (MEG), local field potentials (LFP) and unit recordings. In our studies ‘Local Field Potentials (LFPs)’ are studied to look into neural correlates of rat exploratory behaviour. Our focus is on specialized neurons of CA1 region of hippocampus which respond with reference to spatial locations, i.e. ‘place cells’. LFPs provide local electrical information about the activity of

recording region. It is more precise than EEG but also the different cell type clusters could be characterized based on discharge properties of the cells. This method can be used in behaving animals with the help of remote controlled electrodes, hence is a suitable method to study behaviour induced modulations in electrical activity of brain. These factors provide an edge to this method above others.

1.3 Brain and Behaviour

Behaviour refers to the actions of an organism, usually in relation to its environment, which includes the other organisms around as well as the physical environment. It is the response of the organism to various stimuli, whether internal or external, conscious or subconscious, overt or covert, and voluntary or involuntary. Behaviour is affected or say governed in some cases by hormones, psychological state of subject or biology of the same. Brain is the principle regulatory organ in animal body hence all the parameters related to behaviour is enrooted through brain. It is most often believed that the complexity of the behaviour of an organism is related to the complexity of its nervous system. Generally, organisms with complex nervous systems have a greater capacity to learn new responses and thus adjust their behaviour. Behaviours can be either innate or learned. As described earlier, brains process the information during a particular behaviour (exploratory behaviour) and consolidate the same. This information is retrieved and used for further action making next component of the behaviour. Marken (1990) proposed a model which states that behaviour is amplified error signal generated by the comparator. Comparator compares the internal signal (intrinsic activity of brain) and external signal (through the environment) to produce the signal. This model appears to be more useful for addressing certain aspects of exploratory behaviour and spatial learning.

1.4 Methods for Studying Brain Functioning

There are various approaches developed in years for studying of brain. A few are listed below:

1. Molecular Biology based methods: Making knock outs and proteomics and genomics of brain cells and tissues. Knock outs are being popular to test behavioural states and finding genes/ proteins responsible for those.
2. Immuno-histochemistry: Histochemistry is studied using antibodies against target proteins, e.g. receptors and marker proteins.
3. Immuno-histology: this approach is similar to immuno-histochemistry.
4. Immuno-cytochemistry: here, the cells are studied for different levels of molecular expressions and identifying marker molecules.
5. Positron emission tomography (PET) - The fuel that nerve cells (and all other cells in the body) use to maintain their activity is glucose. Nerve cells that are active must take up glucose and burn it to produce energy. In PET, people are given radioactive glucose (with a short half-life, so they don't stay radioactive forever) and asked to perform an activity. Their brains are then scanned to determine the location of the radioactivity; this corresponds to the brain areas that were active during the task. (For example, if we were able to go PET scanning on you now, as you read this, we would expect the brain areas concerned with vision and reading comprehension to show the greatest activity.) PET has yielded much useful information about localization of function. Disadvantages of this method are the necessity to ingest radioactive material and the fact that the images of the brain obtained using PET are relatively low in resolution.

6. Magnetic resonance imaging (MRI) - This technique provides high resolution images of "slices" through the brain in a variety of planes. Again, although brain structures are clearly visible using this technique, ordinary MRI images provide no information about brain function.
7. Functional magnetic resonance imaging (fMRI) - This method is a variation of traditional MRI as described above under imaging techniques. By adjusting the MRI, fMRI can detect areas that are most active while (or immediately after) a person performs a particular activity. With fMRI, there is no need to administer radioactive materials, and the images of the brain obtained have the high resolution characteristic of traditional MRIs. For this reason, fMRI is quickly becoming the method of choice for studying brain function.
8. Electroencephalography: Gross electrical activity in parts of brain is recorded. Usually an electrode is implanted at the scalp root and recordings are performed.
9. Magnetoencephalography: Here, the magnetic component of encephalogram is considered for investigating the brain activity.
10. Electrophysiological recordings: Unit recordings from neuron, Local field potentials recording from behaving, anesthetized and idle animals are being used for looking into electrical activity at precise scales. Also, brain slices, organotropic cultures and neuronal cultures grown on cover slips are used to study brain physiology at reduced scale, so called reduced systems.
11. Psycho-Behavioural Experiments, Lesion studies, NMR etc. are other methodological approaches which are used in neuroscience.
12. Statistical/ Computational analyses and Neuro-Bio-Informatics.

These methods/ approaches does not end the list but there are many more to name. This discussion is aimed to list a few which are popularly used and becoming vitals tools in study of brain in relation to behaviour and its fundamental aspects at cellular and molecular level. Psycho-Behavioural experiments and local electrical activity (Local Field Potentials, i.e. LFPs) from CA1 region of hippocampus (long evans rats) in awake behaving state as well as anesthetized conditions are used in our work.

Local field potentials (LFPs) are local electrical activity in brain, which is recorded using low impedance extracellular electrodes. These have advantage over classical methods like EEG, in a way that the electrodes are kept sufficiently close to a group of neurons so that the origin of electrical fluxes can be characterized, i.e. dendritic synaptic activity. A more detailed introduction to LFPs is provided in introduction of chapter 3. These data are usually preffered to study synaptic activity and to avoid action potential content from the gross electrical signal. Also, it has been used extensively in characterizing cell types in brain, e.g. “place field cells” and “grid cells” etc. based on their discharge properties. We have analyzed LFPs from CA1 region of hippocampus.

1.5 Awake and Anesthetized Brain

Awake or behaving brain exhibit cognitive functions which can be studied with the help of certain tools like EEG, fMRI and local field potentials. There is no or minimal cognitive activity of brain during anesthetized conditions. Anesthetized brain is a good control to study cognitive functions of brain. Both conditions exhibit different distinguished dynamics of neurons, which is reflected in their electrophysiology. In case of exploratory behaviour the behaving brain is capable of gathering the spatial information through visual and somato-sensory cues, processing

it and organizing the same. Idle brain and anesthetized brain are used as controls for the behaving brain where idle brain exhibits spontaneous neuronal activity, whereas anesthetized one exhibits diminished cognitive activity.

1.6 Time Series Analyses in Behavioural Neuroscience

In behavioural neuroscience data is acquired through various methods, e.g. behavioural experiments, electrophysiology, telemetry etc. These data are dynamic and appear as a series of data points as a function of time. This series is called ‘Time Series’. For example instantaneous velocity data used in this thesis are behavioural data recorded as a function of time. Obviously any time series is represented as function of time, e.g. $V_i(t)$ instantaneous velocity changing every i -th instant as a function of time. Consequent chapters illustrate time series data with their graphical representations.

Once the time series data is obtained, the next thing is to classify it as stationary or non-stationary time series. A stationary time series is a time series whose statistical central tendencies does not change with length of the series, i.e. mean, standard deviation etc. On the contrary, these quantities change in case of non-stationary time series. There are different approaches which are adopted to study both kinds of time series.

Wavelet based methods and Detrended Fluctuation Analyses (DFA) are better analyses for non-stationary time series. Moving average methods also help. These are not being described elsewhere. Below, are some analyses and methods used for time series analysis in general and for data from neuroscience experiments.

(A) Power Spectrum: We lose some crucial information when we study a dynamical system in time domain, so frequency scale is used for looking into patterns and behaviour of time

series, e.g. correlations in noise. Here, it is to be noted that noise is not a signal composed of events rather the finer fluctuations which appear to be useless but contain important information about the dynamics of the system. Power spectrum is the most common plot used to show spectral density of the signal and its fluctuations. This spectral density could be power spectral density (PSD) or amplitude spectral density (ASD). For drawing a power spectrum the time scale is converted to frequency scale through fast fourier transform (FFT). A power spectrum is based on the Fourier transform, which expresses the relationship between time domain and frequency domain descriptions of any physical process. The Fourier transform of a function of time, $h(t)$, is written

$$H(f) = \int_{-\infty}^{\infty} h(t) \cdot e^{-2\pi i f t} dt,$$

Where $H(f)$ is a function of frequency, f , measured in *Hertz (Hz)*. The square of the Fourier Transform, $H(f)^2$, is called the “power spectral density”, and expresses the amount of temporal fluctuation that can be described by a combination of sine and cosine waves at a particular frequency f . The power spectrum of a function of time is a plot of the squared Fourier transform versus frequency, usually in log-log coordinates for convenience (*i.e.* $\log H(f)^2$ versus $\log f$). The power spectrum of real, discretely sampled time series is usually estimated by a method called “fast fourier transform” (FFT), which gives the power spectral density in each of several small bands of frequencies into which the relevant frequency range is divided, usually referred to by indicating the centre frequency of the band. This description of FFT and spectral density is borrowed from a book, “Dynamical Cognitive Science”, by Lawrence M. Ward. Slope of PSD is used to characterize the type of noise exhibited by the system, e.g. if the slope is ‘ α ’, then $\alpha=1$ is called pink noise (correlated), $\alpha=0$ is called white noise (uncorrelated) and $\alpha=2$ is called

Brownian noise. ‘1/f’ noise is ubiquitous and has been reported in neuronal systems also. A detailed explanation of 1/f noise with examples is provided in chapter 3. It may be mentioned here that Bak et al. (1984) explained 1/f noise through their popular model known as ‘Self-Organized criticality’.

(B) Probability Distributions: Second most commonly used plots are Probability Density Functions (PDFs). In probability theory, a probability density function (abbreviated as pdf, or just density) of a continuous random variable is a function that describes the relative likelihood for this random variable to occur at a given point in the observation space. The probability of a random variable falling within a given set is given by the integral of its density over the set. Usually people consider the two terms ‘Probability Density Function’ and ‘Probability Distribution Function’ equivalent but they are mathematically different. Physicists prefer calling it Probability Density Function and denote by ‘PDF’. Here, the distribution of probabilities of different class intervals of data is plotted and regressions help to characterize the distribution.

A probability density function is most commonly associated with continuous univariate distributions. A random variable X has density f , where f is a non-negative Lebesgue-integrable function, if:

$$P[a \leq X \leq b] = \int_a^b f(x) dx.$$

Hence, if F is the cumulative distribution function of X , then:

$$F(x) = \int_{-\infty}^x f(u) du,$$

and

$$f(x) = \frac{d}{dx}F(x).$$

Intuitively, one can think of $f(x) dx$ as being the probability of X falling within the infinitesimal interval $[x, x + dx]$.

The existence of power laws in avalanche size and recurrence time for large events indicates a ‘scale free’ or ‘scale independent’ dynamics in the complex system. Scale invariance is a feature of objects or laws that do not change if length scales (or energy scales) are multiplied by a common factor. The power law distributions exhibit scale invariance, where the PDF is defined by its exponent (common factor for all scales), called ‘power law exponent’ (Zinn-Justin, Jean). Extensive discussion of scale invariance in quantum and statistical field theories, applications to critical phenomena and the epsilon expansion and related topics. Different power laws are described in the next chapter. Existence of power laws could be studied through statistical methods like estimation of power spectral density and plotting probability density functions followed by appropriate regression.

Various parameters provide diverse data sets in complex systems’ dynamics which are plotted in different scales, e.g. linear, semi-log or log-log which provide information about the behaviour of data set up on suitable regression. Plotting and regression are essential parts of time series analysis in general or in neuroscience in specific. Usually log-log plots are used to illustrate a power law distribution of PDF and semi log scale to illustrate exponential distributions for PDF.

1.7 Concept of Self-Organized Criticality (SOC):

Self-organized criticality is one of a number of important concepts made in statistical physics and related fields over the latter half of the 20th century, concepts which relate particularly to the study of complexity in nature. Self-organized criticality (SOC) usually refers to a mechanism of slow energy accumulation and fast energy redistribution driving a system towards a critical state without requiring any tunable parameter (Bak et al. 1988). SOC has been invoked to explain variety of natural phenomena like earthquakes (Bak & Tang 1989; Sornette & Sornette 1989), solar flares (Lu & Hamilton 1991), evolution of biological systems (Bak & Sneppen 1993), fluctuations in confined plasma (Politzer 2000), snow avalanches (Faillettaz et al. 2004), and rainfall (Peters et al. 2002). The events in these systems are typically called “avalanches”. The size and duration of avalanches in SOC have been observed to obey power laws. In addition, these systems exhibit self-induced temporal and spatial correlations that follow power-law dependence of signals on frequency. For example, the interval distribution between consecutive large events in earthquakes and solar flares have been observed to obey power law distribution (Corral 2004; Corral 2005; Boffetta et al. 1999), which is attributed to the absence of any time scale in the system (Verma et al. 2006). A critical state is supposed to facilitate information processing in neural networks (Beggs and Plenz, 2003; Kinouchi and Copelli, 2006; Legenstein and Maass, 2007). Diverse evidences of SOC indicate that it is a kind of universal phenomenon. In nonlinear systems, self-organized criticality (SOC) is a property of (classes of) dynamical systems which have a critical point as an attractor. Their macroscopic behaviour thus displays the spatial and/or temporal scale-invariance characteristic of the critical point of a phase transition, but without the need to tune

control parameters to precise values. The present work revolves around the concept of ‘Self-Organized criticality (SOC)’. The detailed discussion with appropriate examples about SOC is provided in the next chapters.

1.8 Universal Laws of Scale invariance and SOC in Brain:

Usually power laws in avalanche size, duration and recurrence time of large events are valid up to certain scale in the time or space or the dynamics of system itself, but in case of emergent systems they do not follow any scale. If a characteristic scale is absent the power laws are called ‘Scale invariant’. For example, the interval distribution between consecutive large events in earthquakes and solar flares have been observed to obey power law distribution (Corral 2004; Corral 2005; Boffetta et al. 1999), which is attributed to the absence of any time scale in the system (Verma et al. 2006). This scale invariance is ubiquitous and hence called ‘universal’. Physiological evidences indicate that animal brain exhibit phenomena like ‘critical phenomenon’ which are scale independent. Universality is illustrated through collapse of the data as shown by Corral (2004). Reports from reduced (lower) systems for studying brain suggest that brain dynamics is scale invariant, e.g. recently de Arcangelis et al. (2006) constructed SOC based model of neuronal networks and observed an avalanche-like activity with its power spectral density proportional to $f^{-0.8}$, which is in agreement with the experimental observations of Novikov et al. (1997). Also, intact brain systems exhibit scale invariant phenomena, e.g. research groups of Beggs and Chialvo has shown scale invariant phenomena in local field potentials in brain slices and spontaneous electrical activity in the neurons of rhesus monkey brain respectively. These can be categorized as ‘systems following universal laws of scale invariance’.

1.9 SOC as a phenomenon in Brain and Behaviour:

As per discussions above, it is understood that SOC is a phenomenon with scale invariance and is found often in nature, especially in intact and reduced brain. Evidences show that SOC is found in complex animal behaviours. For example, existence of SOC could be a possible reason for scale invariance in motor activity of laboratory rat (Anteneodo et al. 2009) and mice (Nakamura et al. 2008) reported recently. Considering the facts that SOC is the happening phenomenon both in brain functioning and behaviour, in the present work we look for the possible evidences of various power laws, i.e. temporal power laws in dynamics of rat exploratory behaviour and we interpret there as power laws as phenomenon of ‘Self-Organized Criticality (SOC)’. Similar results are found for neural correlates in brain through local field potentials recorded from the related region of brain, i.e. CA1 region of hippocampus. Finally we interpret that SOC is a universal phenomenon operating in brain in various states and extending its validity up to resultant behaviour.

1.10 The aim of the dissertation:

Animal behaviour as well as its neural correlates is very complex dynamical systems. Though they represent different behavioural organizations, a common phenomenology is postulated. Inspired by reports from other groups (please refer citations above) we wanted to look for evidences of universal phenomenon in these nonlinear systems. The existence of temporal power laws is interpreted as a ‘critical phenomenon’. The concept of ‘Self-Organized Criticality’ is used to explain the spatial information processing during active exploration by rats, which is used to establish a home base. The overall aim

of the work lies in finding a connection between the dynamics of behaviour and neuronal avalanches in associated area. Statistical analysis of the behavioural and electrophysiological data is used to illustrate existence of a universal phenomenon in both. Behaviour is considered as a cognitive task and neuronal avalanches in awake-behaving rats is proposed to be a function of the ‘cognition’.

CHAPTER 2

**SELF-ORGANIZED CRITICALITY IN
EXPLORATORY BEHAVIOUR OF RATS**

INTRODUCTION

Open field exploration by animals (rats) has been a good choice to understand various aspects of behavioural psychology. Tchernichovski et al. (1995) studied the open field exploration of rats in which they observed that the rats perceive the provided space as spatial gradients and have their individual preferences. Animals perform various actions during exploration, e.g. ‘looping’ (where there is feeble coupling with the environment) and ‘home base behaviour’ (where there is firm anchorage with the environment). In other words, a location with maximum residence probability during explorations constitutes the ‘‘home base’’ of the rat. A home base is usually a starting point and an end point of an exploration once it is established. After gathering information about the space, a rat returns again and again to its home base that acts as an ‘‘attractor’’. Home base is typically established at a distinctly featured landmark in the provided space (Alyan 1996; Draï et al. 2001; Geyer et al. 1986; Loewen et al. 2005; Tchernichovski et al. 1998). Tchernichovski et al. (1998) established a relation between the location of the rat and its speed by performing a phase-plane analysis, and observed that the speed of the rat is maximum during its return to its home base. Animal shifts from directional to positional progression to acquire spatial information (Reut et al. 2006). Home base establishment is sudden in light conditions. In dark conditions home base is not established suddenly. Various forms of exploratory excursions like ‘looping’, repeated visits to one location etc. ultimately lead to construction of a home base (Reut et al. 2006). It is believed that home base behaviour represents the recruitment of several composite forms of navigation. Reut et al. (2006) suggested that shift from different exploratory behaviours, like looping to home base behaviour, is a part of the process of recruitment of navigation via a transition from sequential to parallel, and ultimately to continuous processing of spatial information. It is in general agreement that a home base exists to

which animal returns with high speed ('running') after careful progressions with relatively lower speeds and in bouts. There are reports suggesting sequential establishment of home base and steps involved in it, but it is not well understood (Tchernichovski et al. 1998). Previous studies suggest that homebase establishment is an important event in rat exploratory behaviour (Tchernichovski et al. 1995; Alyan 1996; Draï et al. 2001; Geyer et al. 1986; Loewen et al. 2005). Locations of a rat over a time scale are related to its speed profile (Tchernichovski et al. 1998). Hence, speed is an important parameter to study rat's exploratory behaviour (navigation) and homebase establishment.

Self-organized criticality (SOC) usually refers to a mechanism of slow energy accumulation and fast energy redistribution driving a system towards a critical state without requiring any tunable parameter (Bak et al. 1988). SOC has been invoked to explain variety of natural phenomena like earthquakes (Bak & Tang 1989; Sornette & Sornette 1989), solar flares (Lu & Hamilton 1991), evolution of biological systems (Bak & Sneppen 1993), fluctuations in confined plasma (Politzer 2000), snow avalanches (Faillettaz et al. 2004), and rainfall (Peters et al. 2002). The events in these systems are typically called "avalanches". The size and duration of avalanches in SOC have been observed to obey power laws. In addition, these systems exhibit self-induced temporal and spatial correlations that are power-laws. For example, the interval distribution between consecutive large events in earthquakes and solar flares have been observed to obey power law distribution (Corral 2004; Corral 2005; Boffetta et al. 1999), which is attributed to the absence of any time scale in the system (Verma et al. 2006). In the present work we have studied exploratory behaviour of rats in the light of self-organized criticality (SOC). The motivating factor was that probing existence of SOC in speeds of rats would help us to understand the phenomenon of spatial learning and homing behaviour better.

Spatial learning includes acquisition, storage and retrieval of spatial information. This information is used by rats to take decisions during exploration, especially about the homebase. Recently discovered similarities between the power law exponents in earthquakes and solar flares indicate deeper connections between diverse non-equilibrium systems (Baiesi et al. 2006; de Arcangelis et al. 2006). Self-organized criticality has also been applied successfully to explain some complex biological and animal behaviours. Bak & Sneppen (1993) studied biological evolution using simple models of interacting species. They observed critical steady states with intermediate evolutionary avalanches of all sizes mimicking “punctuated equilibrium” behaviour. Adami (1995) also analysed evolution using models that yield self-organized critical states in which the waiting time distribution of epochs are distributed according to $f^{-\alpha}$ power law. SOC and $1/f$ power spectrum have also been observed in single ion-channel currents of voltage dependent anion channels (VDAC) (Verma et al. 2006; Bezrukov & Winterhalter 2000; Banerjee et al. 2006). Time series of electroencephalogram (EEG) data, which is useful to neurologists for discerning sleep phases, diagnosing epilepsy and other seizure disorders, brain damage etc., have been analysed widely (Gevins et al. 1995; Buzsaki & Draguhn 2004). Analysis by Buzsaki & Draguhn (2004) shows neuronal oscillations in cortical networks with $1/f$ power spectrum in some regimes. Recently de Arcangelis et al. (2006) constructed SOC based model of neuronal networks and observed an avalanche-like activity with its power spectral density proportional to $f^{-0.8}$, which is in agreement with the experimental observations of Novikov et al. (1997). Segev & Benveniste (2003) have reported self organization in clusterized neural networks. Very recently Levina et al. (2009) described a transition scenario to self-organized criticality (SOC) in a network of pulse-coupled neurons. Ketzopoulous et al. (1997) reported $1/f$ power spectrum in rat movements during open field explorations. All these indicate that existence of $1/f$ pattern is

the hallmark of SOC. However some reports suggest that $1/f$ pattern may not follow a power law in waiting time distribution, which is considered to be the result of SOC (Bedard et al. 2006). This prompted us to look into the possibilities of SOC phenomenon in exploratory behaviour of rat.

Materials and Methods:

(A) Animals:

Major factors that modulate rat exploratory behaviour are sex, strain, species, lighting conditions, environment etc. For our experiment we took five 25-30 days old female rats (wistar). The rationale behind using the female rats is that they perform larger excursions and move with relatively faster speed than the male rats. Our experiments were performed under dark conditions since rats move more rapidly in dark environment than in bright light (Alstott & Timberlake 2009). The five rats were housed in cages in animal house facility. Animals were exposed to 12 hours of light and 12 hours of dark cycles. Prior approval for conducting experiments on rats was obtained from concerned competent authorities, i.e. CPCSEA (Committee for the Purpose of Control and Supervision of Experiments on Animals, Animal Welfare Board of India through IAEC (Institutional Animal Ethics Committee, University of Hyderabad, Hyderabad, India).

(B) Experiments:

Behavioural experiments: The experiments were conducted in a behavioural test box made up of wood with a lid made up of glass with wooden frames. The floor of the box was of the size 35.8 cm.x 35.8 cm x 30.5 cm that served as an arena for the exploration by a rat. The glass lid was kept open during an experiment to facilitate video recording. The floor was painted black fully and the surface was uniform, hence the floor of the cage could be qualified as unbiased. The rats

were gently transferred to the behavioural apparatus. The rats were allowed to explore the arena for 30 minutes after an acclimatization period of 5 minutes. The exploratory behaviour was video recorded using a web camera of 3 mega pixels resolution through a computer interface. All the video recordings were performed in the night between 11: 00 P.M. to 12:30 A.M. (local time) in a diffused light that does not affect the animal behaviour but facilitates the video recording. Rats' behaviour in the above lighting conditions is expected to be similar to that in the desired dark condition.

(C) Computational Analysis:

The videos were encoded in MatLab compatible format ('indeo' compression). The capture rate was 30 frames per second, hence the resolution time is $\Delta t = 1/30 = 0.033$ second. A time series containing spatio-temporal locations of the rat in x, y coordinates was computed from the video recording using a MatLab script which has been developed in our laboratory. The instant speed at the i-th instant, V_i , was calculated using the coordinates of the rats:

$$V_i = \Delta r_i / \Delta t, \text{ where } \Delta r_i = [(x_i - x_{i-1})^2 + (y_i - y_{i-1})^2]^{1/2}.$$

Time series of V_i was plotted to identify durations for which rat was physically active. The probability distribution function (PDF) of the speed was computed to know pattern of distribution. The power spectral density of instantaneous speed signal was obtained using the time series data. The PDF of the interval between the large events was also computed (explanation follows). We adopt the same strategy as Corral (2004, 2005) & Banerjee et al. (2006) regarding time series analysis. Large speeds are characterized using two different thresholds: (a) twice the mean speed, (b) thrice the mean speed. The mean speeds are computed

by averaging the instantaneous speeds from the time series. We have computed PDF $[P(\tau)]$ of the interval (τ) between two consecutive large speed instants.

Results and Discussions:

The time series for rat movements was generated as described in Materials and Methods. We illustrate the time series of the instantaneous speed of Rat 1 in Fig. 1. The probability distribution function (PDF) of the speed, plotted in Fig. 2, is a power law ($P(v) \sim v^{-2.07 \pm 0.07}$). The time series as well as the PDF of the speed of all the five rats are similar (Table 2). The power law distribution of the speed indicates non-equilibrium nature of the system. We have computed the power spectrum of the instantaneous speed signal using the time series data. It is observed that the spectral density follows an approximate power law for the low frequency regime, $P(f) \sim f^{-\alpha}$, with α close to 1. The power spectrum is flat (white noise) in the high frequency regime. Fig. 3 illustrates the low frequency power spectrum of the instantaneous speed of Rat 2. The spectral exponent ' α ' of the (five) rats lie in the range of 0.66 to 0.88 as listed in Table 1. Hence we conclude that the speeds of the rats during an exploration have a $1/f$ power spectrum. These results are in general agreement with the earlier results reported by Kafetzopoulos et al. (1997). Further we have also computed the probability distribution function of the interval between the rapid movements (large speed events) of the rat. In Fig. 4 we plot $P(\tau)$ versus τ for Rat 2. We observe that $P(\tau)$ fits reasonably well with a power law, i.e., $P(\tau) \sim \tau^{-\beta}$. The exponent ' β ' for various rats are listed in Table 1, and it lies between 1.56 and 2.30. The above-mentioned exponent of the interval PDF is related to the spectral index for the systems exhibiting SOC (Verma et al. 2006; Schuster & Just 2005). The above mentioned discussion indicates existence

of SOC in the rat exploratory behaviour. Many systems that exhibit SOC have $1/f$ power spectrum (Maslov et al. 1994, Hwa & Karder 1992), which is linked to the power-law temporal correlations between the large events in the system (Corral 2004; Corral 2005; Verma et al. 2006). Schuster (2005) has shown that $\alpha = \beta - 1$ under the condition that all the large events have the same amplitude. To the best of our knowledge a similar relationship between the exponents for general conditions (where events have variable amplitudes) has not been derived. It is interesting to note that our exponents for the rat movement are $\alpha \approx 1$, and $\beta \approx 2$, hence $\alpha \approx \beta - 1$ is satisfied approximately. This behaviour resembles earthquakes, solar flares, ion-channel currents in VDAC, and some other SOC systems. The exponents reported by us are in the same range as that for the ion-channel currents of VDAC (Bezrukov & Winterhalter 2000; Banerjee et al. 2006). Thus the exploratory behaviour of rats and ion-channel currents appear to belong to the same class of SOC systems. It may be mentioned here that earthquakes and solar flares too show power law behaviour, but their exponents, α and β , differ from those described above.

We wanted to show absence of a time scale in the dynamics and universality through collapse of the data as Corral (2004) did, but unfortunately, the collapse was not satisfactory due to limited data available to us. In our experiment, a rat typically moves for 15 min (900 sec.) and $P(\tau)$ vs τ shows power law correlations for $1s < \tau < 10s$. Also the scatter of α and β is quite large. Hence our data is rather limited due to various constraints of the system. As a result data collapse similar to Corral is not possible in our system. Note that the earthquake time series of Corral goes from 2 min to 20 years (157680000×2 min), and his power law regime for $R\tau$ covers around 4 decades. This is due to extremely long-range temporal correlations observed in earthquakes.

We expect a somewhat better fit if we perform the experiment in a larger box that will allow the rate to explore the box for a longer time hence yielding a longer range of power law regime. However experiments on larger box have their own limitations that will be described below. We believe the results presented in the paper are by themselves quite interesting and they shed important light on the temporal correlations of rat's movements. We plan to explore other issues like box size etc. in future.

The power spectrum of these systems exhibit $1/f$ behaviour. $1/f$ noise has been observed in many systems. SOC is only one of the mechanisms to explain $1/f$ noise. Bak et al. (Phys. Rev. Lett., 1987; Phys. Rev. E, 1988) derived $1/f$ power spectrum for SOC systems by a superposition of many uncorrelated avalanches with Poisson inter-avalanche distribution. However systems like earthquakes and solar flares have strong temporal correlations between events (see Corral Phys. Rev. Lett., 2004; 2005; Boffetta et al, Phys. Rev. Lett., 1999), and another mathematical derivation is invoked to relate temporal correlations with $1/f$ noise. Banerjee et al. (EPL, 2006) showed that events of equal amplitudes but with power law recurrence time statistics ($P(\tau) \sim \tau^{-\beta}$) exhibit $f^{-(\beta-1)}$ energy spectrum energy spectrum. However the distribution of recurrence time for some of them follows a Poisson distribution, and some others follow power law distribution. Bak's original model (BTW) belongs to the former category, while earthquakes, solar flares, turbulence etc. belong to the latter category. see Verma et al. (EPL, 2006), ``In the original BTW model, the pdf of recurrence time (τ) of large events is $\exp[-\tau/\tau_c]/\tau_c$, which indicates that the triggering of large events in this system is uncorrelated and memory less (Boffetta et al., Phys. Rev. Lett., 1999; Sanchez et al., Phys. Rev. Lett. 2002). This is a generic feature of Poisson process. It was however soon realized that the events are correlated in many nonequilibrium systems. In fact Sanchez et al. (Phys. Rev. Lett., 2002) and Paczuski et al. (Phys.

Rev. Lett. 2005) constructed variants of BTW model with different thresholds and larger input rate of sand; these features induce temporal correlations in the system, and produce power law behaviour for the probability distribution of recurrence-time in contrast to BTW model. Also note the comments of Sanchez et al. (Phys. Rev. Lett., 2002), “It is argued that a system governed by self-organized-criticality (SOC) dynamics can lack Poisson waiting-time statistics not only when the experimental resolution lies within the self-similar scale range but also if the system is slowly driven in a correlated way. This result thus suggests that waiting time statistics cannot be used as a necessary test for SOC behaviour in real physical systems”. That is, the recurrence time distribution for an SOC system could be either a Poissonian or a power law.

There were serious debates around 10 years back whether system exhibiting powerlaw distribution for the interval distribution should be called a SOC system or not. Sanchez et al. (Phys. Rev. Lett., 2002), Corral (Phys. Rev. Lett., 2004; 2005), Paczuski et al. (Phys. Rev. Lett. 2005), and deArcangelis (Phys. Rev. Lett., 2006) showed that the power distribution for the interval distribution exhibit temporal correlation of the system, and these systems too should be called SOC. Note that Sanchez et al. (Phys. Rev. Lett., 2002) obtained Poission and power law distribution in a same sandpile system by varying the input rate.

SOC appears to be a unifying theme to study animal behaviour. We use evidences of SOC to explain the possible mechanism of exploration, gathering spatial information and finally a home base establishment. The spatial information gathered in slow and careful excursions in bouts is self-organized and this slow accumulation of information is used to construct a home base. The high speed return to the home base (running) does not take place all of a sudden but is a decisive behaviour made on the basis of the acquired spatial information. During exploration rats acquire information about the provided space. It learns about the locations and remembers various

landmarks. Sequential moves from one position to other are related to the speed of the movement (Tchernichovski et al. 1998). As mentioned earlier various parameters like lighting condition, shape and size of arena, sex of animal etc., can modulate the duration of ‘looping’ or ‘home base’ behaviour. We understand that the spatial information acquired by the rats during exploration is consolidated in an organized manner. Home base establishment is one of the outcomes of the structure of this organization. This understanding provokes us to think that speed profile may reflect structural organization of spatial information in rat brain. $1/f$ power spectrum, power law in PDF of the recurrence interval and the event size are generally used to claim self-organized criticality (SOC). Therefore, we have computed the $1/f$ power spectrum and PDF of the instantaneous speed to probe SOC in our system. Recurrence time interval PDF for big events (rapid moves) also follows a power law, which strengthens the argument. Big events are important to maintain organization of spatial information as a rat returns to home base again and again. We think that it does so to maintain accuracy of reference frame or the home base during exploration. Hence big events play a major role during exploration of a novel space. As mentioned earlier we observed power law behaviour in event size distribution as well as recurrence time distribution of large events. These findings indicate the existence of Self-Organized Criticality (SOC) in organizing spatial information. Power-law distribution of crucial parameters have been used to study behavioural organization, which is reported to be related to the mental health of the animals and extending its relevance up to humans (Nakamura et al. 2008). Any psychological tuning and environmental anchorage with the animal behaviour are important in the analysis of the exploration. The above findings provide evidence for the existence of a universal phenomenon known as ‘Self Organized Criticality (SOC)’. Existence of SOC could be a possible reason for scale invariance in motor activity of laboratory rat

(Anteneodo et al. 2009) and mice (Nakamura et al. 2008) reported recently. Universality of SOC (specially its existence at different levels of organization in brain) invokes logical thinking to relate its existence with the cognitive processes like spatial learning.

In conclusion we may state that any mode of rat exploratory behaviour is related to spatial information acquisition and its organization. Instantaneous speed and location of the rat during an excursion depends on the information gathered in previously performed excursions. The above mentioned process, we demonstrate, follows Self-Organized Criticality.

TABLE 1: WAITING TIME STATISTICS AND POWER SPECTRUM

Cut-off and step size	RAT1	RAT2	RAT3	RAT4	RAT5
Twice the Mean 0.5 Sec.	2.13 ± 0.24	2.5 ± 0.28	1.62 ± 0.15	1.46 ± 0.12	1.7 ± 0.14
Twice the Mean 0.4 Sec.	1.96 ± 0.12	2.33 ± 0.25	1.47 ± 0.18	1.44 ± 0.15	1.74 ± 0.12
Twice the Mean 0.7 Sec.	2.12 ± 0.31	2.49 ± 0.24	1.82 ± 0.20	1.52 ± 0.16	1.77 ± 0.16
Twice the Mean 0.8 Sec.	2.20 ± 0.25	2.4 ± 0.32	1.78 ± 0.24	1.70 ± 0.26	1.82 ± 0.16
Thrice the Mean 1 Sec.	1.52 ± 0.22	2.09 ± 0.19	1.67 ± 0.33	1.61 ± 0.27	1.64 ± 0.09
Thrice the Mean 0.8 Sec.	1.65 ± 0.2	2.19 ± 0.18	2.06 ± 0.24	1.60 ± 0.17	1.67 ± 0.11
Thrice the Mean 1.2 Sec.	1.59 ± 0.28	2.12 ± 0.33	1.52 ± 0.27	1.59 ± 0.18	1.67 ± 0.12
Average values of exponent ' β '	1.88 ± 0.11	2.30 ± 0.06	1.71 ± 0.08	1.56 ± 0.03	1.72 ± 0.02
Values of exponent ' α '	0.69 ± 0.08	0.88 ± 0.05	0.83 ± 0.05	0.66 ± 0.06	0.76 ± 0.05

TABLE 2: Event Size distribution PDF

Step size	RAT1	RAT2	RAT3	RAT4	RAT5
5 Pixels/Sec.	2.09 ± 0.04	2.11 ± 0.07	2.13 ± 0.06	2.24 ± 0.06	2.12 ± 0.05
8Pixels/Sec.	2.18 ± 0.02	2.33 ± 0.07	2.19 ± 0.05	2.37 ± 0.07	2.10 ± 0.05
10 Pixels/Sec.	2.23 ± 0.03	2.51 ± 0.11	2.21 ± 0.07	2.29 ± 0.09	2.07 ± 0.07
Average value of	2.17 ± 0.04	2.32 ± 0.12	2.18 ± 0.02	2.30 ± 0.04	2.10 ± 0.01

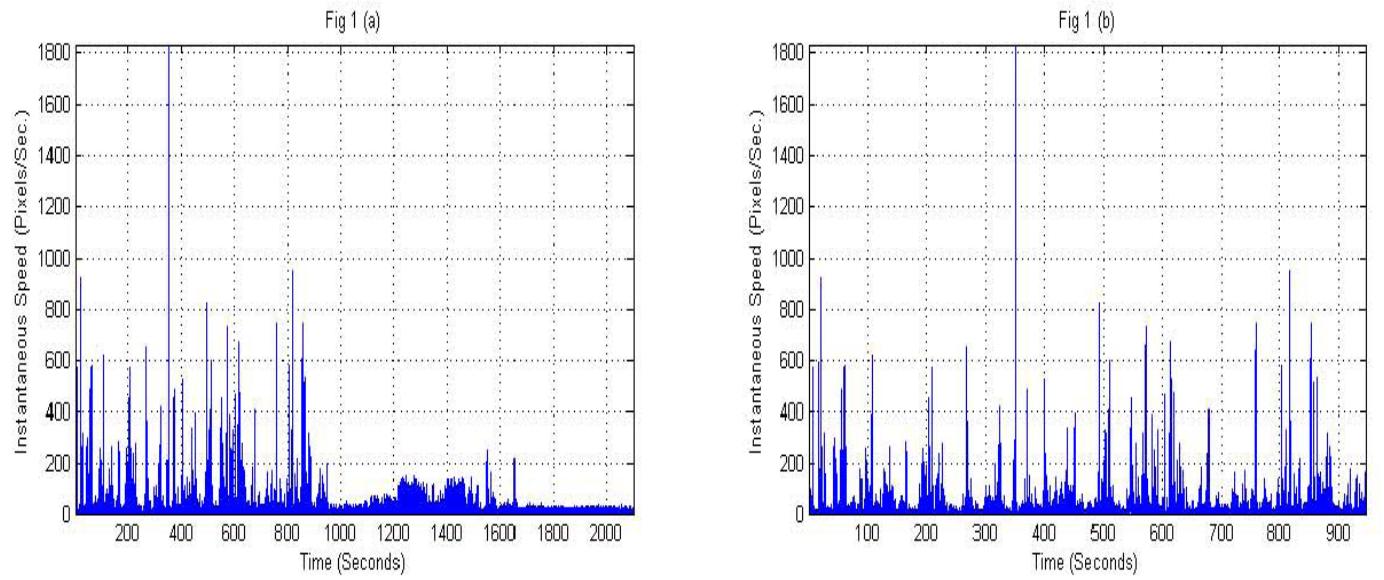


Fig. 1

Fig 1: A representative time series used for analysis (Selected part of the instantaneous speed of Rat 1). A time series of total duration of 2097.9 seconds for the same rat is visible in figure 1(a), whereas selected portion of time trace used for computational analysis is illustrated as figure 1(b).

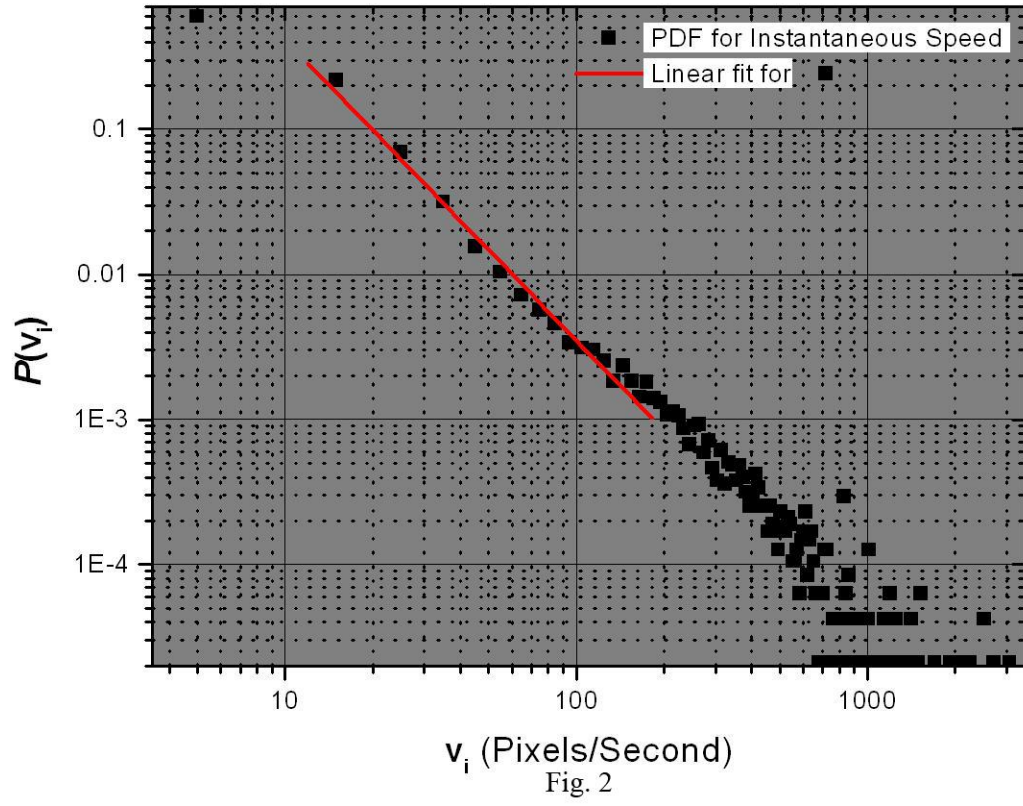


Fig 2: A representative PDF plot for the instantaneous speed of Rat 5 in log-log scale. The power law exponent = 2.07 ± 0.07 . step size:10 pixels/sec.; data size: 47800.

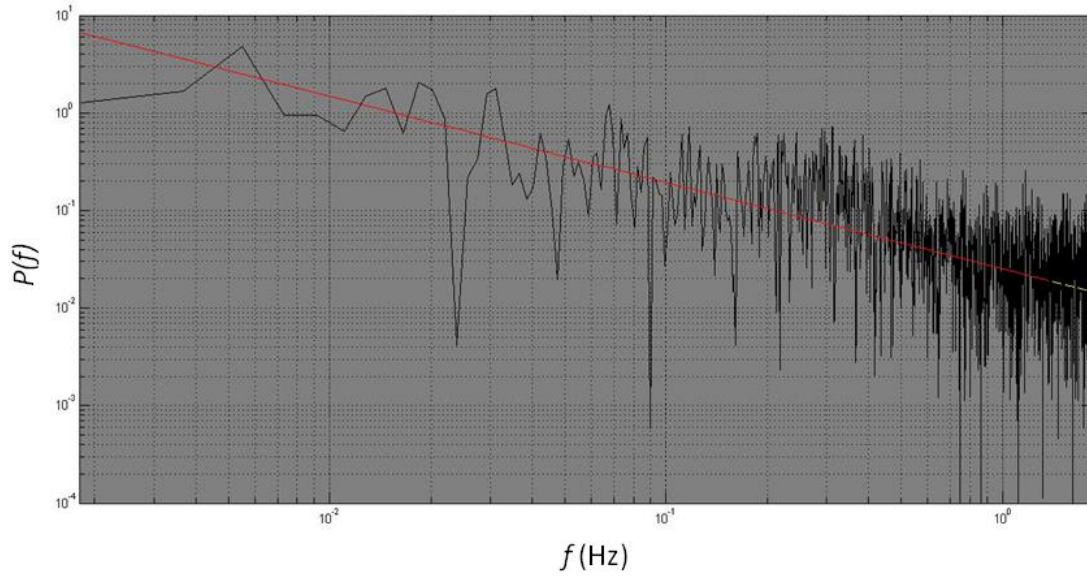


Fig. 3

Fig 3: The low-frequency power spectrum $P(f)$ of the instantaneous speed of Rat 2 in log-log scale. A power law $f^{-\alpha}$ with $\alpha = 0.88 \pm 0.05$ fits the experimental data reasonably well.

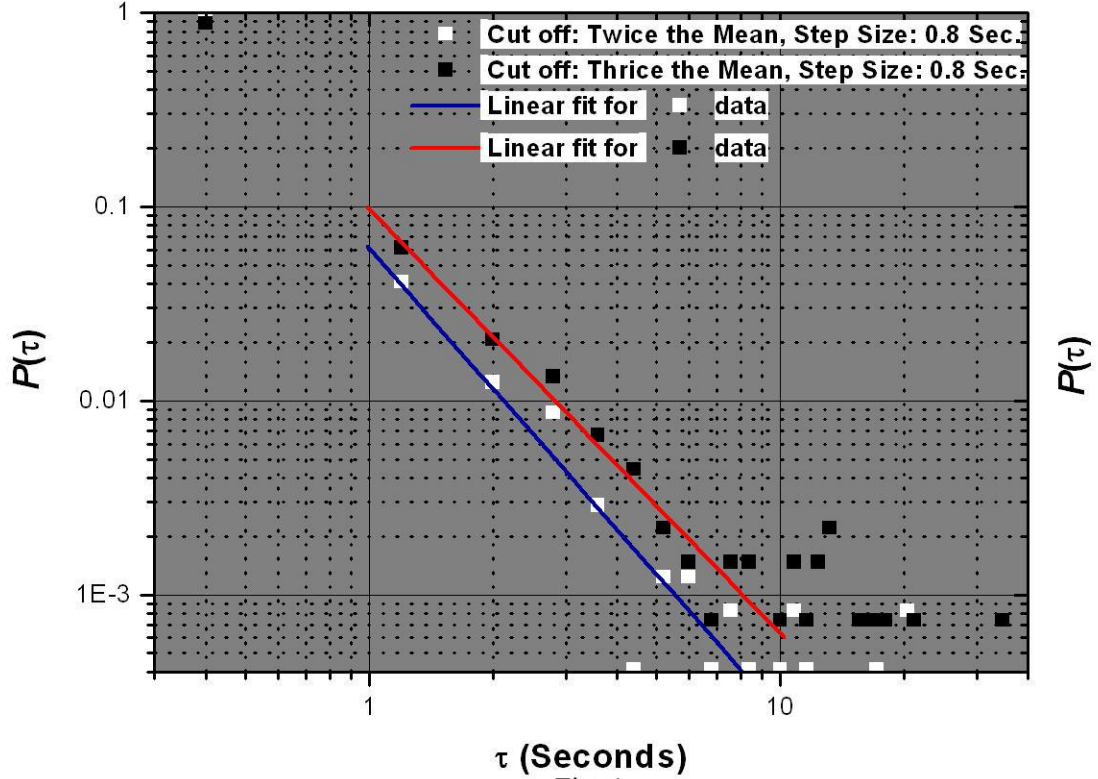


Fig 4: The recurrence time distribution $P(\tau)$ of the large speed for Rat2 in log-log scale. The function $P(\tau) \sim \tau^{-\beta}$ is a good fit for the data. For the fluctuations greater than thrice the mean with the step size = 0.8 Sec. and data size = 1362, $\beta = 2.19 \pm 0.18$. For the fluctuations greater than twice the mean with step size = 0.8 Sec. and data size = 2447, $\beta = 2.4 \pm 0.32$. The value of the slope does not change appreciably with the variation of the threshold values.

CHAPTER 3

Neuronal Avalanches Dynamics in Rat Brain

Hippocampus (CA1)

Section 1: Awake-Behaving Rat

INTRODUCTION

What are local field potentials (LFPs)?

A local field potential (LFP) is a particular class of electrophysiological signals, which is related to the sum of all dendritic synaptic activity within a volume of tissue. A signal is recorded using a low impedance extracellular microelectrode, placed sufficiently far from individual local neurons to prevent any particular cell from dominating the electrophysiological signal. This signal is then low-pass filtered, cut off at ~300 Hz, to obtain the local field potential (LFP). The low impedance and positioning of the electrode allows the activity of a large number of neurons to contribute to the signal. The unfiltered signal reflects the sum of action potentials from cells within approximately 50-350 μm from the tip of the electrode (Legatt, 1980; Gray, 1995) and slower ionic events from within 0.5-3 mm from the tip of the electrode (Juergens 1999). The low-pass filter removes the spike component of the signal and passes the lower frequency signal, the LFP.

About the CA1 cells in Hippocampus:

The hippocampus is composed of multiple subfields. Though terminology varies among authors, the terms most frequently used are dentate gyrus and the cornu ammonis (literally "Amun's horns", abbreviated CA). The dentate gyrus contains the fascia dentata and the hilus, while CA is differentiated into fields CA1, CA2, and CA3. In rodents, the hippocampus is positioned so that, roughly, one end is near the top of the head (the dorsal or septal end) and one end near the bottom of the head (the ventral or temporal end). As shown in the figure, the structure itself is curved and subfields or regions are defined along the curve, from CA4 through CA1 (only CA3

and CA1 are labeled). The CA regions are also structured depth wise in clearly defined strata (or layers).

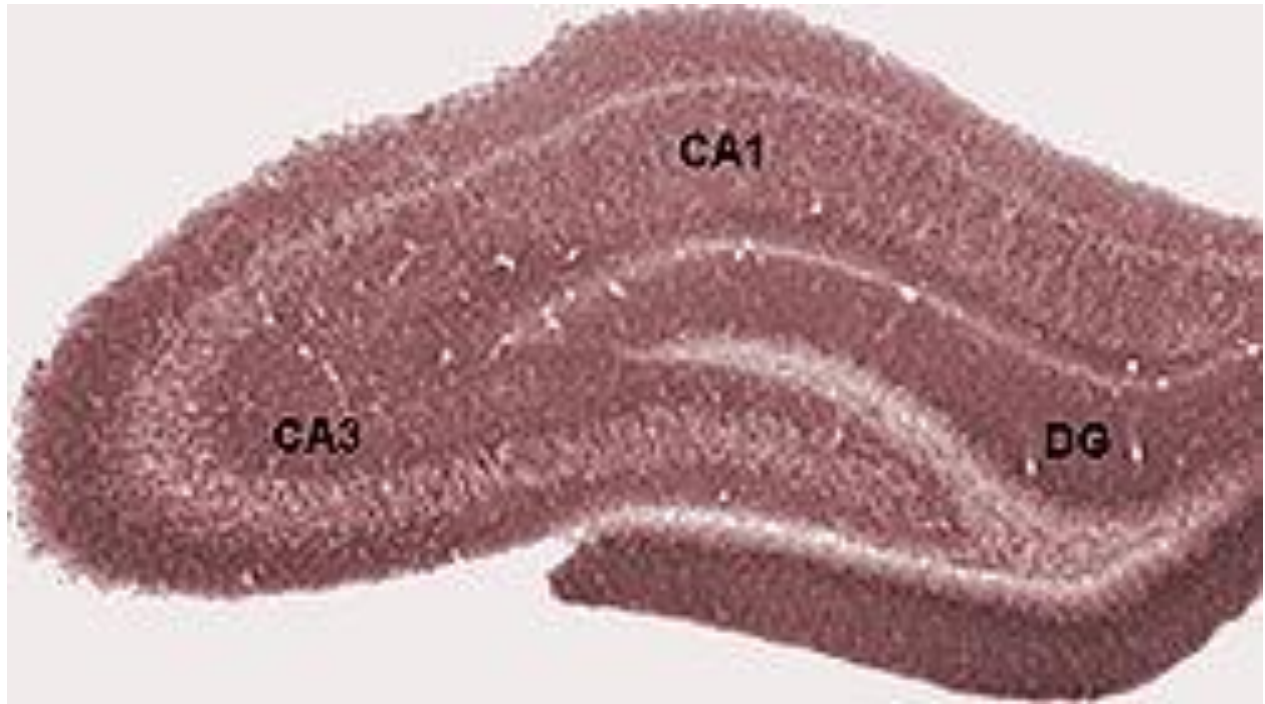


Diagram of hippocampal regions in a rat brain.

Dentate Gyrus (DG)

Image is for public use, (downloaded from: http://en.wikipedia.org/wiki/Hippocampus_anatomy)

Hippocampus is an important and integral part of the brain. Physiological importance of hippocampus is attributed to its computational capabilities in relation to information processing and storage. Dense neuron to neuron connections facilitate complexity in neuronal dynamics through various excitatory and inhibitory inputs-outputs. Local field potentials (LFPs) have been studied in recent years in light of ‘Critical Dynamics’ (Touboul and Destexhe, 2010; Petermann

et al., 2009; Plenz and Chialvo, 2010). Negative deflections of LFPs (nLFPs) are of particular interest due to their well established relation with neuronal spiking. Spontaneous cortical activity in slice cultures, acute slices, anesthetized rat and awake rhesus monkeys (Petermann et al., 2009) has a scale-invariant dynamics called ‘neuronal avalanches’ (Beggs and Plenz 2003; Plenz and Thiagarajan 2007; Gireesh and Plenz 2008). Petermann et al. (2009) studied spontaneous cortical activity in awake rhesus monkeys composed of neuronal avalanches during ‘ongoing’ or ‘resting state’ which persists in absence of sensory stimuli or motor outputs. However, neuronal dynamics during active behavioural states is not fully understood. In present work, neuronal dynamics of hippocampus (CA1 region) is studied in the light of ‘Self-Organized Criticality (SOC)’ phenomenon. Studies include statistical analyses of nLFP data recorded from aforesaid region of rat brain while a rat moves freely. Square and cylindrical shaped arenas were used for behavioural task variations. SOC is illustrated through simple power laws, e.g. $P(s) \sim s^{-\alpha}$ for avalanche size probability density function (PDF). Avalanche size (s) is defined as size of clusters comprised of spontaneous bursts of synchronized activity of neurons. This activity is quantified as number of active sites in an electrode array. Other than avalanche size, avalanche duration and inter-avalanche (event) intervals exhibit respective power laws. Long range correlations in critical dynamics are illustrated through these power laws. Phenomenology of information processing in hippocampus (CA1 region) is studied in the light of SOC.

Self-organized criticality (SOC) usually refers to a mechanism of slow energy accumulation and fast energy redistribution driving a system towards a critical state without requiring any tunable parameter (Bak et al., 1987 and 1988). The “critical state” however refers to power law behaviour (borrowed from equilibrium statistical mechanics description of phase transition). A

more detailed discussion about SOC has been discussed in previous chapter. This ‘criticality’ is supposed to play an important role in information processing in the neural networks.

Rat exploratory behaviour (unpublished data with authors) exhibits temporal power laws indicating towards a SOC like phenomenon. It is illustrated through examples mentioned above that SOC phenomenon is exhibited in micro as well as macro systems in nature. SOC phenomenon in relation to neuroscience has become great focus in recent years. Very recently Levina et al. (2009) described a transition scenario to self-organized criticality (SOC) in a network of pulse-coupled neurons. Previous analysis by Buzsaki & Draguhn (2004) shows neuronal oscillations in cortical networks with $1/f$ power spectrum in some regimes. de Arcangelis et al. (2006) constructed SOC based model of neuronal networks and observed an avalanche-like activity with its power spectral density proportional to $f^{-0.8}$, which is in agreement with the experimental observations of Novikov et al. (1997). Segev and Benveniste (2003) have reported self organization in clusterized neural networks. Various levels of functional organization of brain can be studied using different techniques like EEG, MEG, fMRI etc. Local field Potentials (LFPs) have their merits attributed to precise local information about neuronal dynamics. LFPs have their own limitations in form of number of electrodes in array which limit avalanche size. Though many studies have involved LFPs, no consensus about phenomenology of neuronal dynamics has been reached due to lack of extensive analyses of different brain regions in various behavioural states. We provide a statistical evidence for existence of critical state in performing hippocampus. This critical dynamics is proposed to optimize information processing in CA1 region of hippocampus as suggested by other research groups through their modelling studies.

Methods

Experimental data: Local Field Potentials (LFPs) data recorded from CA1 region of hippocampus of long evans rats were generously provided by Dr. Andre Antonio Fenton, Department of Physiology & Pharmacology, Suny medical centre, New York, USA, also at Centre for Neural Science, New York University, New York, USA. The data used for analyses were recorded from a rats foraging for scattered food within a 1.5x1.4 chamber and a cylinder of 68-cm diameter.

Computational Analyses: Statistical analyses methodology described below is the same for both the cases, i.e. LFP recordings from rats foraging in square as well as cylindrical arena. All the computations were performed using MatLab 7 (a product of mathworks, www.mathworks.com) and Origin 5 (a product of Origin Labs, www.originlabs.com) software. First of all time series of LFP were plotted to have a gross idea of statistical central tendencies (Fig. 1a and 1b). Power Spectral Densities (PSDs) were plotted in log-log scale against respective frequencies after computing Fast Fourier transform (FFT). Linear regression (least square fit) was performed on power spectra to get power law exponents of respective PSD distributions (Fig. 1d and Fig. 1e). Avalanches are clusters of events happening in LFP dynamics. Negative deflections of LFPs (nLFPs) were analyzed in our studies on neuronal dynamics due to their well established link with neuronal spiking. Avalanches were computed from nLFP populations using methods similar to Petermann et al. (2009) and Touboul and Destexhe (2010) with slight modifications. First nLFPs were extracted out of LFPs and their mean and standard deviations were computed. Mean was subtracted from nLFP values to avoid inclination towards a trend. Values obtained were used to compute second derivatives to detect raster of nLFPs. Various thresholds like twice and thrice multiples of standard deviation (2SD

and 3SD) were used to detect large events clustering as avalanches. Different time bins (step sizes) e.g. 4 ms, 8 ms and 16 ms were used to compute clusters in respective avalanches. A typical nLFP raster is illustrated through Fig. 1b as indicated by white arrow. Probability Density Functions (PDFs) for avalanche size and inter-avalanche intervals were computed from avalanches detected with different step sizes and thresholds (two thresholds, i.e. 2SD and 3SD and three step sizes for each threshold, i.e. 4, 8 and 16 ms as illustrated by six different colours in PDF plots in Fig. 1 and 2). PDFs were plotted in log-log scale followed by linear regression. Inter-avalanche (event) intervals (IEIs) play important role in maintaining long-range correlations in critical dynamics as proved in other systems (Corral, 2004, 2005; Verma et al., 2006). IEIs were plotted against event number (Fig. 2a and 2b) and statistical properties were computed. Long range correlations were illustrated through PSDs plotted in log-log scale (Fig. 2c and 2d) of IEIs other than their PDFs (Fig. 2e and 2f). PSDs for increments in respective IEIs were also plotted to rule out any ambiguity. Exponents of power spectra for IEI amplitudes and their increments follow a relation of $\gamma = \Delta - 2$, where Δ is slope of PSD plotted against frequency for increments and γ is for the PSD of signal amplitude. This rules out possibility of long range correlations arising due to artefacts. Standard errors are provided for all statistics and fits.

RESULTS

First of all the time series for LFPs recorded from freely moving rats in square (Fig. 1a) and cylindrical (Fig. 1b) arena were plotted and central tendencies were computed. Blue and cyan colors are used in figures to illustrate nLFPs. Rasters of nLFPs were detected as described in methods. We show a typical nLFP raster through an enlarged view of both time series superimposed (note that white arrow indicates an nLFP raster) in Fig. 1c. We have computed the power spectra of the LFPs using the time series data for both the cases (Fig. 1d for square and 1e for cylindrical arena). It is observed that the spectral density follows an approximate power law for the low frequency regime, $P(f) \sim f^{-\alpha}$, with α close to 1 in both the cases (0.93 ± 0.04 for square arena and 0.83 ± 0.03 for cylindrical arena). High frequency regime exhibits a slope of more than 2. Hence we conclude that the LFPs from CA1 region of hippocampus recorded during exploration of square as well as cylindrical arena have a $1/f$ power spectrum. These results are in general agreement with previous reports from other groups, e.g. Bedard et al. (2006). Avalanche size PDF for square arena follows a power law of $P(f) \sim f^{-2.55 \pm 0.23}$ on an average (Fig. 1f) irrespective of threshold and step size used for nLFP detection, while it is $P(f) \sim f^{-2.75 \pm 0.14}$ in case of cylindrical arena (Fig. 1g). Fit values are provided for different thresholds and step sizes used for nLFP detection in table 1. The results provide an evidence for ‘critical phenomenon’ operating in the system(s). SOC systems are generally assumed to be robust systems which are resistant to alterations in the basic phenomenon. Here, we observe that avalanche size PDF is not varying much if we compare both the arena. Avalanche duration (life time) PDF (Fig. 1h for square and 1i for cylindrical arena) has the average slope values as 3.29 ± 0.11 for square and 3.86 ± 0.19 for cylindrical arena. This shows that though the life time of avalanches follow definite power laws but the relation is not fully significant in lack of enough

data points for this statistical analysis. It has been proven in other systems that silent or inter-avalanche (event) intervals (IEIs) are responsible for long range correlations in critical dynamics rather than avalanche itself (Anteneodo et al., 2009; Banerjee et al., 2006). This duration which is also known as ‘waiting time’ can be seen as time taken by the system to prepare for next avalanche once previous one ends. Power laws in waiting time have been shown in many systems like motor activity of rats (Anteneodo et al., 2009), single channel opening currents (Banerjee et al., 2006) etc. This indicates existence of similar dynamics but avalanche is defined differently, i.e. as cluster of activities rather single activity called ‘event’. However finding power law in inter-avalanche (event)-intervals suggest maintenance of a system at criticality for long temporal range illustrated through scale free correlations. For statistical analyses of IEIs, first we plotted IEI time series for both the cases and computed their distribution and mean values (Fig. 2a and Fig. 2b). We were interested in long range scale free correlations in IEIs of nFPs as indicated by $1/f$ noise in low frequency regime of LFPs PSD. Sometimes $1/f$ noise arise due to artefacts in spectral density. It is important to make sure that the dynamics is not misinterpreted, so we computed PSD of IEIs and their increments. Power law exponents for PSD of a signal and its increments follow an established relation of $\gamma = \Delta - 2$, where Δ is slope of PSD plotted against frequency for increments and γ is for the PSD of signal amplitude. We illustrate scale free long range correlations in IEIs in case of square arena through Fig. 2c, where $\gamma = 0.35 \pm 0.21$ and $\Delta = 1.71 \pm 0.20$. The results are similar for cylindrical arena with $\gamma = 0.38 \pm 0.1$ and $\Delta = 1.58 \pm 0.09$. In both the cases $\gamma = \Delta - 2$ relation is found to be valid, neglecting artefacts or random noise in the system. Also, we show power law of $P(\tau) \sim \tau^{-\beta}$ for both the systems (with $\beta = 1.51 \pm 0.13$ for square (Fig. 2e) and 1.92 ± 0.02 for cylindrical (Fig. 2f) arena on an average), where ‘ τ ’ is called ‘waiting time’. It is observed in case of square arena that higher threshold

(3SD) used for nLFP raster detection shows correlations in waiting time PDF which is different from if lower (2SD) threshold is used. This indicates that choosing an appropriate threshold for peak detection is important. Higher threshold allows a better detection of avalanches taking place. However, slopes of lower threshold (square arena) and both the thresholds (cylindrical arena) are close enough indicating similar dynamics at lower level. The power laws mentioned above provide a statistical evidence for SOC.

DISCUSSION:

Self-Organized Criticality (SOC) is a universal phenomenon as described through examples in introduction and illustrated through results for our studies. SOC based models for critical dynamics provide examples how the dynamics of a system enable it to evolve into a critical state positioning the system for maximal computational ability. Existence of a critical state has been shown to be advantageous for information processing (Beggs and Plenz, 2003; Kinouchi and Copelli, 2006; Legenstein and Maass, 2007). Neuronal dynamics is composed of avalanches which reflect transient formation of cell assemblies (Plenz and Thiagarajan, 2007). These cell assemblies are called ‘place field cells’ in hippocampus. Neuronal dynamics in CA1 region of hippocampus exhibit a critical dynamics, illustrated by us through statistical analyses of nLFPs recorded from aforesaid region of rat brain while a rat moves freely. We illustrate SOC through power laws in avalanche size, duration and inter-avalanche (event) intervals (IEIs). These analyses are valid for different behavioural states of rat, viz. Exploration of square and cylindrical arena. The critical dynamics explained through SOC phenomenon strengthens our understanding about information processing in hippocampus. Existence of critical dynamics leads to scale free neuronal dynamics with expanded capabilities for information processing.

In conclusion, SOC is proposed to be an underlying phenomenon for information processing in CA1 region of hippocampus. Our results are in agreement with other reports suggesting a critical dynamics in neuronal avalanches (brain). We could show a statistical evidence of temporal power laws in neuronal avalanche dynamics in CA1 region of rat hippocampus (awake and behaving state). These power laws are interpreted as phenomenon of ‘self organized criticality’.

Table: Power law exponents for PDFs of avalanche size, duration and inter-event intervals.

	SQUARE ARENA							CIRCULAR ARENA						
PDF	T=2SD S=4ms.	T=2SD S=8ms.	T=2SD S=16ms.	T=3SD S=4ms.	T=3SD S=8ms.	T=3SD S=16ms.	Mean	T=2SD S=4ms.	T=2SD S=8ms.	T=2SD S=16ms.	T=3SD S=4ms.	T=8SD S=4ms.	T=16SD S=4ms.	Mean
Avalanche Size	3.05 ± 0.14	2.21 ± 0.10	1.78 ± 0.18	3.36 ± 0.30	2.53 ± 0.14	2.39 ± 0.18	2.55± 0.23	3.25 ± 0.08	2.85 ± 0.10	2.52 ± 0.18	3.02 ± 0.11	2.59 ± 0.14	2.30 ± 0.16	2.75± 0.14
Avalanche Duration	3.43 ± 0.11	3.36 ± 0.15	3.67 ± 0.25	3.23 ± 0.15	2.82 ± 0.07	3.23 ± 0.32	3.29 ± 0.11	3.68 ± 0.07	4.04 ± 0.27	4.54 ± 0.32	3.37 ± 0.10	3.38 ± 0.21	4.17 ± 0.37	3.86± 0.19
Inter- Event Intervals	1.83 ± 0.13	1.82 ± 0.17	1.74 ± 0.15	1.22 ± 0.05	1.22 ± 0.05	1.21 ± 0.08	1.51 ± 0.13	1.93 ± 0.11	1.89 ± 0.11	1.87 ± 0.13	1.98 ± 0.10	1.94 ± 0.10	1.90 ± 0.12	1.92± 0.02

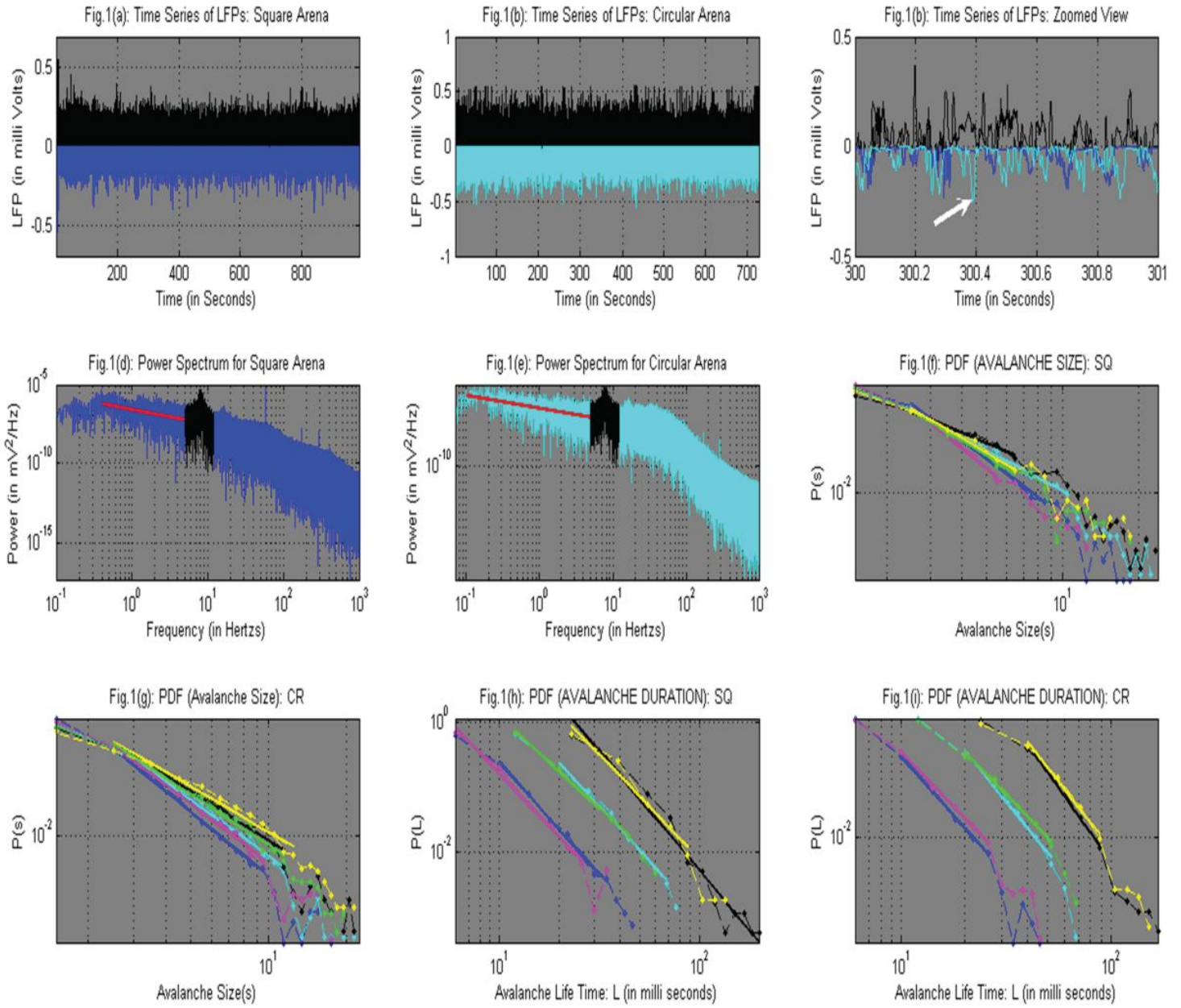


Figure 1

Fig.1 (a) Time series of LFPs recorded from hippocampus (CA1) of rat foraging in square arena. Blue colour is used to illustrate nLFPs. (b) Time series of LFPs recorded from hippocampus (CA1) of rat foraging in cylindrical arena. Cyan colour is used to illustrate nLFPs. (c) Zoomed view of superimposed time series of LFPs for square and cylindrical arena. Positive LFPs (pLFPs) are shown in black for both the cases while nLFPs for square arena are shown in blue and for cylindrical in cyan. (d) Power spectrum (PSD) for square arena in log-log scale (natural logarithm). A red solid line shows least squares fit to PSD corresponding to low frequency regime. Exponent for power law is 0.93 ± 0.04 . Resonant frequencies are shown in black (around 7 Hertz). (e) Power spectrum (PSD) for cylindrical arena in log-log scale (natural logarithm). A red solid line shows least squares fit to PSD corresponding to low frequency regime. Exponent for power law is 0.83 ± 0.03 . Resonant frequencies are shown in black (around 7 Hertz). (f) PDF of avalanche size distribution for square arena in log-log scale. Distributions for Avalanches detected through different thresholds and time bins are illustrated in different colours, i.e. blue: 2SD (4ms), cyan: 2SD (8ms), black: 2SD (16ms), magenta: 3SD (4ms), green: 3SD (8ms), yellow: 3SD (16ms). Solid lines in respective colours show fits. (g) PDF of avalanche size distribution for cylindrical arena in log-log scale. Colour scheme is similar to as used in fig 1(f). (h) PDF of avalanche duration distribution for square arena in log-log scale. Colour scheme is similar to as used in fig 1(f). (i) PDF of avalanche duration distribution for cylindrical arena in log-log scale. Colour scheme is similar to as used in fig 1(f). Slope values for PDFs are provided in Table.

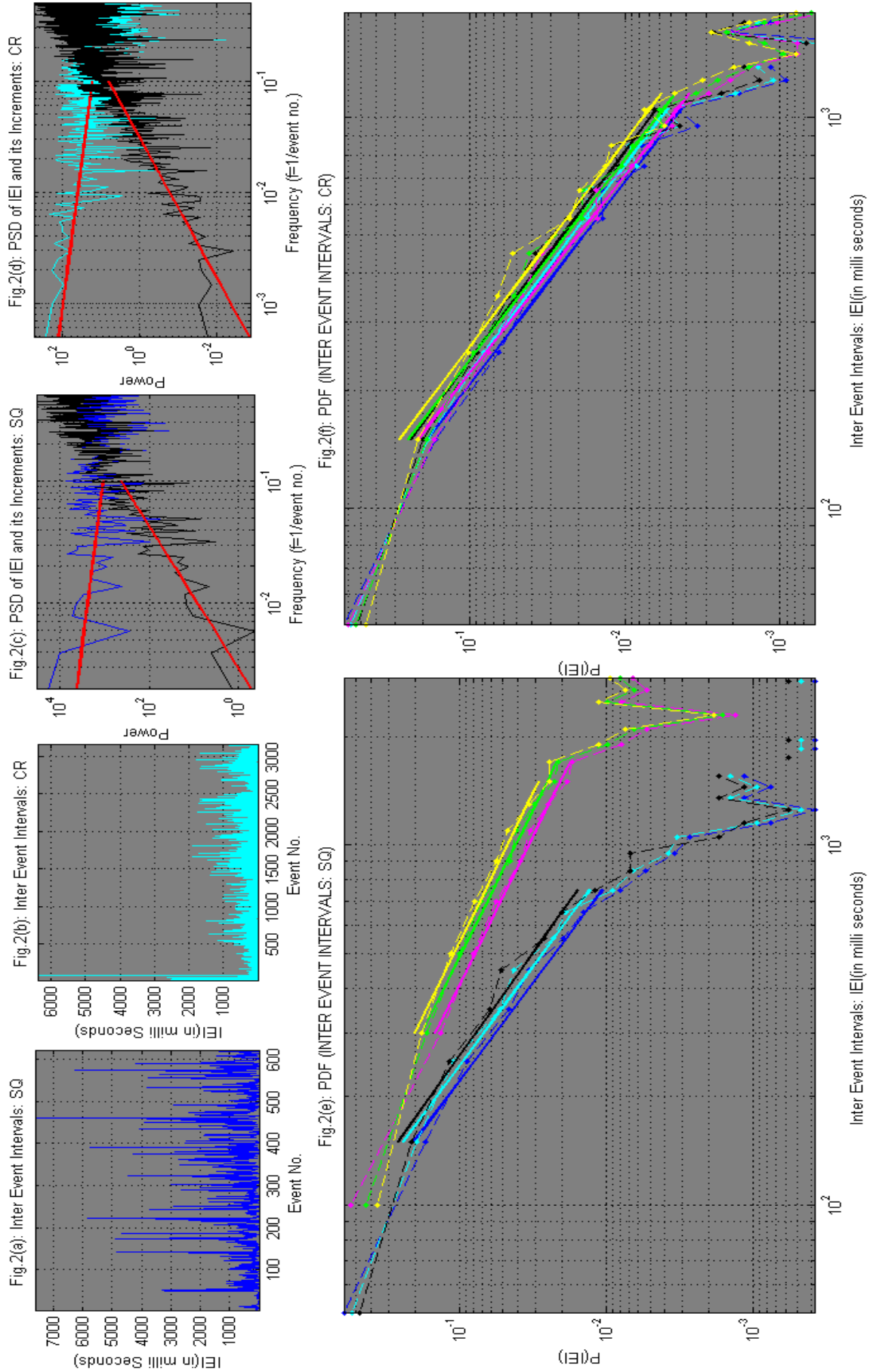


Figure 2

Fig.2 (a) Time series of Inter-Avalanche (Event) intervals (IEIs) for square arena. (b) Time series of Inter-Avalanche (Event) intervals (IEIs) for cylindrical arena. (c) Power spectrum (PSD) of IEIs (blue) and their increments (black) in log-log scale for square arena. Red solid line shows linear regression. (d) Power spectrum (PSD) of IEIs (cyan) and their increments (black) in log-log scale for cylindrical arena. Red solid line shows linear regression. (e) PDF of IEIs distribution for square arena in log-log scale. Colour scheme is similar to as used in fig 1(f). (f) PDF of IEIs distribution for cylindrical arena in log-log scale. Colour scheme is similar to as used in fig 1(f). Slope values for PDFs are provided in Table.

Section 2: Anesthetized Rat

Introduction:

We have reported in the previous chapter that neuronal avalanche dynamics in rat brain hippocampus (CA1) region is a complex system which exhibits a phenomenon called ‘Self-Organized Criticality (SOC)’. The aforesaid dynamics was studied for awake behaving rats (Long Evans strain). This observation provides essential information about the neuronal dynamics happening during behavioural activities of the animal. The LFP data analyzed was recorded while the rats were exploring the variety of arena, i.e. square and cylindrical arena. Now, the question was to look into the generality of the observation, i.e. such dynamics arise due to cognitive function of brain or due to intrinsic activity of the neurons itself ? We proposed a hypothesis:

Hypothesis:

“A universal phenomenon called Self-Organized Criticality operates in hippocampus, which helps in information processing and its organization for further use”.

To test the above mentioned hypothesis we asked a question:

Q: Does SOC have something to do with cognitive functions of hippocampus, or it is independent of cognition but it reflects what neurons in networks do.

To address the above question we required to have a proper control. Anesthetized brain recordings (local field potentials), or spontaneous brain activity recorded during idle state of animal serve as good controls. We took the first one, i.e. LFPs recorded from CA1 region of hippocampus during anesthetized conditions. Essentially the nLFPs from the anesthetized brain

reflect the intrinsic activity of the neurons when the cognitive functioning of brain is minimal or nil.

Data:

Local Field Potentials (LFP) data recorded from CA1 region of rat brain hippocampus (long evans strain, anesthetized conditions) were provided by **Dr. Andre A. Fenton**, Centre for Neural Sciences, New York University, USA & Department of Physiology and Pharmacology, Suny Medical Centre, Brooklyn, New York, USA.

Methods and Data Analyses:

Methods used for avalanche detection and data analyses were similar to as mentioned in the previous chapter. First of all we looked for data traces which are stationary and could be used for time series analyses. Power Spectral Density (PSD) for the anesthetized rat brain hippocampus (CA1) was computed through computation of ‘Fast Fourier Transform (FFT)’ of the signal. This methodology was similar to the PSD plots in preceding chapters.

Probability Density Function (PDF) distribution plots were plotted for ‘Avalanche Size’, ‘Avalanche Duration’ and ‘Inter-Avalanche-Intervals’. Also, Power Spectral Density (PSD) plots for inter-avalanche-intervals (IEIs) and their increments (Incr.IEIs) were plotted to look the existence of possible power laws in the distributions of the same.

Results and Discussions:

Firstly, the time series was plotted to get an idea of the same (Figure 1). The slope of ‘power versus frequency’ plot (PSD plot) in log-log scale was fitted linearly and the slope was estimated (Figure 2). The low frequency regime, which is studied for characterizing noise type in emerging

systems, exhibited $\sim 1/f^0$ noise with slope value close to zero, i.e. 0.3. This type of noise is known as ‘white noise’. White noise is a type of “random noise”. This randomness is in terms of the signal itself and the increments in the signal causing de-correlation of the signal components. White noise is a random signal (or process) with a flat power spectral density. In other words, the signal contains equal power within a fixed bandwidth at any center frequency. This result indicates that the neuronal avalanche dynamics in anesthetized rat brain hippocampus (CA1) is not correlated, rather it is uncorrelated. Thus we conclude that hippocampus exhibits a critical phenomenon which is a function of cognition (spatial information processing) but not a result of intrinsic activity of neurons in a neural network. We infer that the neuronal dynamics in rat brain hippocampus (CA1) does not exhibit any emergent phenomenon like ‘Self-Organized Criticality’ which helps in information processing in brain, but during cognitive processing of the information the system is driven towards a critical phenomenon. This ‘critical state’ is supposed to extend the capabilities of system to process the information in various manners. Phenomenological basis of cognitive functions of brain has not been understood well yet, hence this is the first report which provides statistical evidence of a universal phenomenon, self-organized criticality in awake behaving rat brain hippocampus. For this we rejected the possibility that criticality and self-organization in neuronal avalanche dynamics are results of intrinsic activity (electro-physiology) of neurons itself but not the cognitive processes.

Probability Density function (PDF) plot for Avalanche size (Figure 3) illustrates that there is no power law in the distribution. This neglects the possibility of a critical phenomenon in the dynamics of the neuronal avalanche dynamics. Also, PDFs of avalanche duration (Figure 4) and Inter-Avalanche-Intervals’ (Figure 5) failed to exhibit any power law. We illustrate through Figure 6 that there are no long range correlations in the inter-avalanche interval time series. The

PSD plot for increments in inter-avalanche intervals were plotted to neglect any ambiguity arising in results due to flukes in the data.

The above mentioned plots and analyses indicate the absence of a critical phenomenon in the neuronal avalanche dynamics in CA1 region of anesthetized rat brain hippocampus. Hence we conclude that an intrinsic activity of a neuronal cell cluster (which is dynamic) in anesthetized condition is not following ‘self-organized criticality’.

This becomes clear that cognitive functioning of brain drives and maintains the system (neuronal avalanche dynamics) at criticality which is essential for information processing in brain. As hippocampus is the region of brain which deals with the spatial learning and spatial information processing, hence ‘Self-Organized criticality’ phenomenon may contribute to mechanism of the spatial information processing, consolidation and retrieval which are part of spatial learning in rats. The concept needs to be reproduced in various animals and species for generalization.

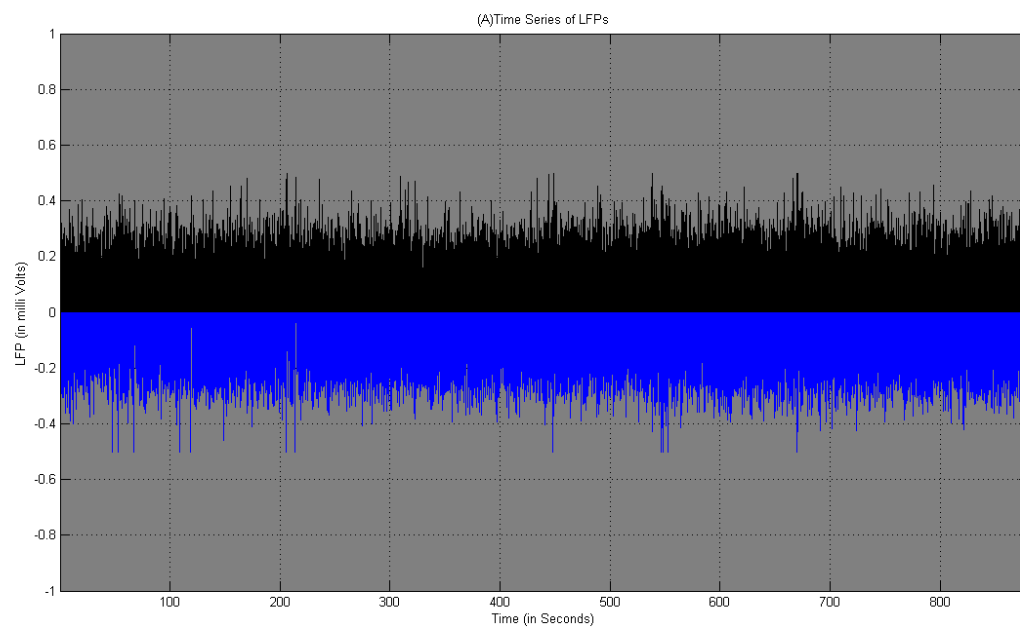


Figure 1 Time series of LFPs from CA1 region of rat brain hippocampus

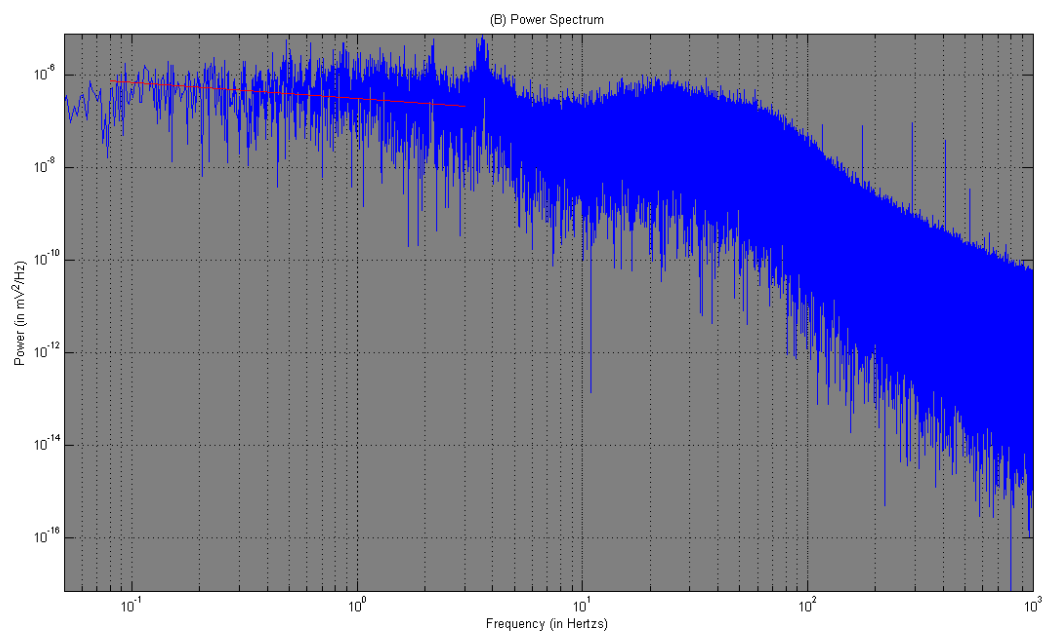


Figure 2 Power Spectrum

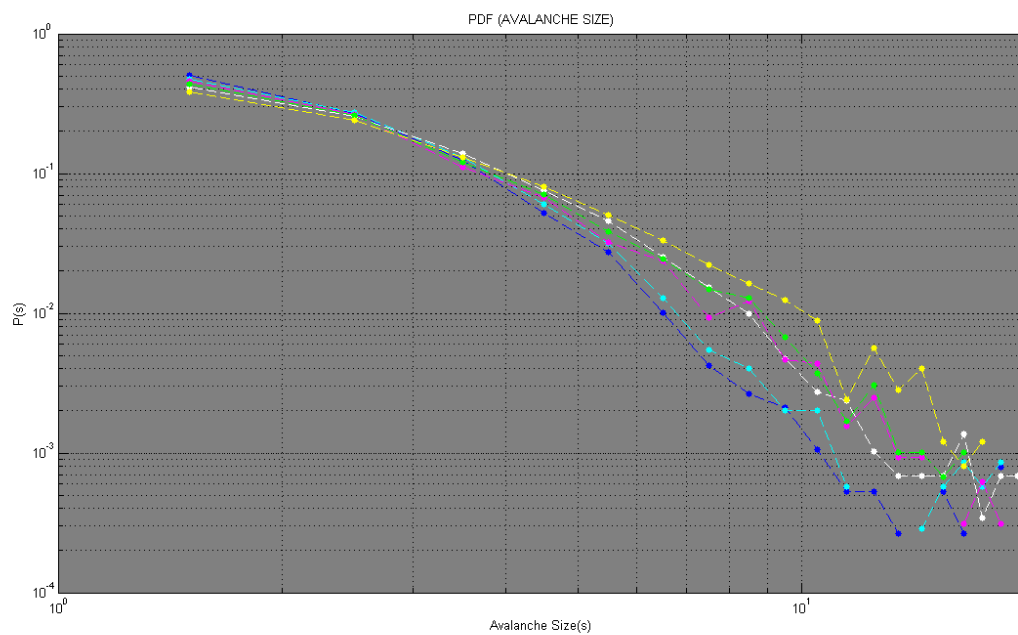


Figure 3: Avalanche Size PDF

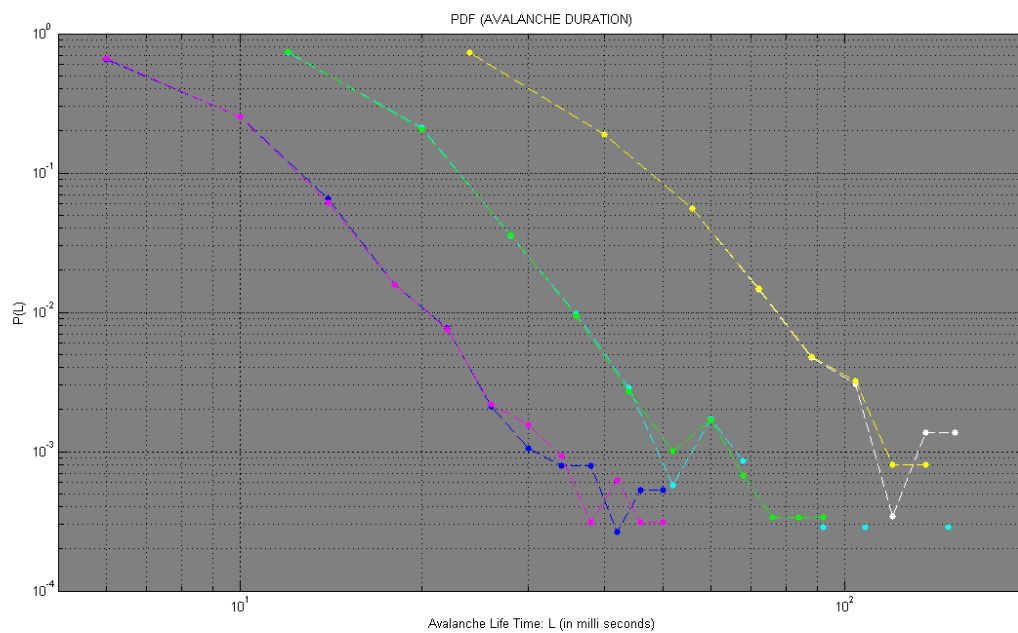


Figure 4: Avalanche Duration PDF

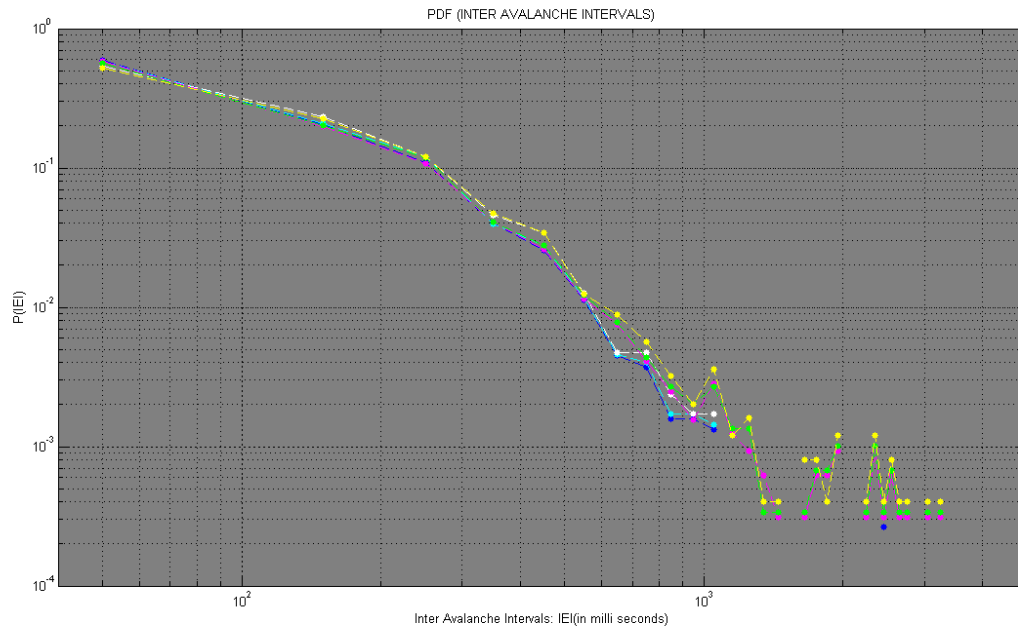


Figure 5: Inter-Avalanche-Intervals PDF

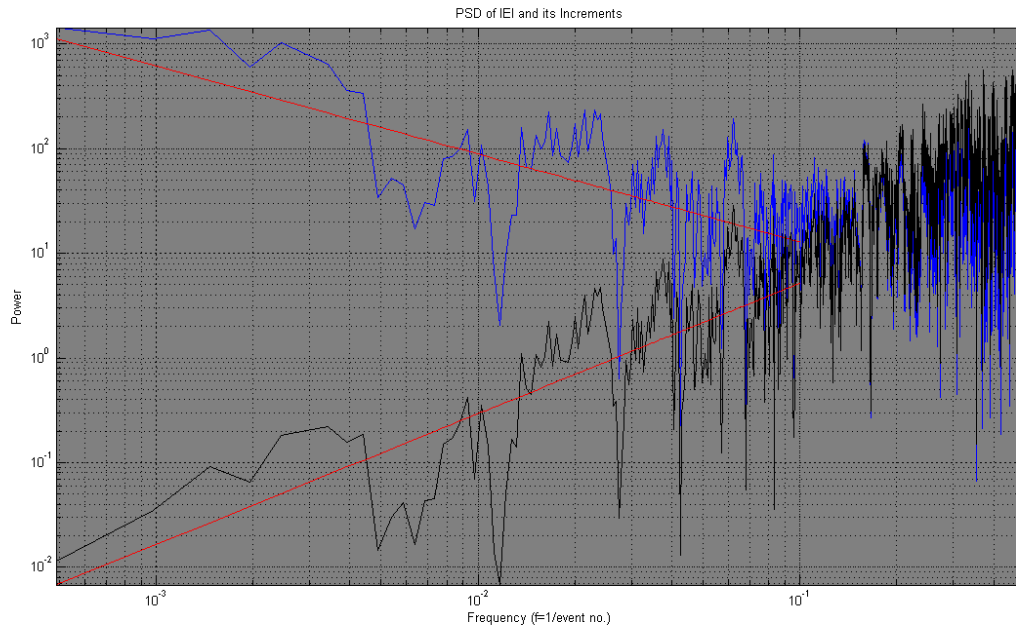


Figure 6: PSD of Inter-Avalanche-Intervals and their increments

CHAPTER 4

GENERAL CONCLUSIONS

In conclusion, rat exploratory behaviour is a complex dynamical system which exhibits ‘Self-Organized Criticality (SOC)’ phenomenon. Various modes of rat exploratory behaviour are related to spatial information acquisition and its organization. Instantaneous speed and location of the rat during an excursion depends on the information gathered in previously performed excursions. The above mentioned process, we demonstrate, follows Self-Organized Criticality. Further, we tested the existence of similar or the same phenomenon in the neural correlates of this behaviour. It is established that ‘Hippocampus’ is the physiological part of brain which deals with spatial information processing required for spatial learning. We adopted methods of statistical mechanics and nonlinear dynamics to look to the possible existence of a ‘self-organized criticality’ phenomenon in the neuronal avalanche dynamics in CA1 region of hippocampus. We were able to illustrate statistical evidences of the aforesaid phenomenon in awake behaving rat hippocampus. SOC is proposed as an underlying phenomenon for information processing in CA1 region of hippocampus. Our results are in agreement with other reports suggesting a critical dynamics in neuronal avalanches (brain).

To interpret the above mentioned findings we proposed hypothesis which assumes that the SOC phenomenon is a property of cognition but not the intrinsic activity of the neurons itself. The local field potentials recorded from CA1 region of rat brain hippocampus in awake behaving and anesthetized conditions were compared to reject the possibility of finding SOC in intrinsic activity of neuronal avalanches and to accept that the SOC is a property of cognition in rat brain hippocampus. This phenomenon maintains the system at a criticality which is responsible for enhanced capabilities of brain to process spatial information gathered during the spatial learning tasks.

Broadly, we connect the results from rat exploratory behaviour, neuronal avalanche dynamics during the exploration and anesthetized conditions to conclude that the spatial information gathered during exploration is a cognitive function performed by neuronal cells of hippocampus. These cells, or cell clusters exhibit complex dynamics similar to several emergent systems. The aforesaid dynamics is maintained at criticality, which enhances the information processing capabilities in the system. We conclude that a universal phenomenon called ‘Self-Organized Criticality’ is exhibited at various levels of spatial learning and cognitive functioning of the brain related to it.

SUMMARY

Animal behaviour is a complex phenomenon. Exploratory behaviour is one of the behaviours which can be observed easily. Though exploration appears to be simple but is a result of complex processing of the spatial information gathered during exploration. This information is used in many ways, one is decision making. In the present work exploratory behaviour of rats is studied. Instantaneous speeds of the movements are taken as behavioural parameter. Home base establishment during exploration is a function of spatial information processing in brain.

Probability distributions which do not change with length of the time scale are known as ‘scale invariant’. Power law distribution of instantaneous speeds of movements is used to show a ‘critical phenomenon’ in the dynamics of rat exploratory behaviour. Two commonly used ways to illustrate long range correlations are: power spectral analysis and probability density function of the time between large events in the dynamics. The time between these large events is known as recurrence time. The aforesaid dynamics exhibits $1/f$ noise and temporal power laws in “recurrence time statistics”, which illustrates long range correlations in the ‘critical phenomenon’. These correlations and power law distributions are interpreted as a phenomenon called “Self-Organized Criticality (SOC)”. SOC was introduced by Per Bak to explain $1/f$ noise.

“Hippocampus” is the region of brain which is related to spatial learning and spatial information processing. Local field potentials recorded from a brain region provides information about synaptic activity in the same. Local Field Potentials (LFPs) data provides local electrical picture of the precise region of the brain. We have analyzed the LFPs data to look for the possible existence of critical phenomenon in the “neuronal avalanche dynamics”. Hypothesis for possible role of self-organized criticality in neuronal avalanche dynamics is tested. Various temporal

power laws and probability distributions are used to illustrate ‘criticality’ as well as to compare the awake-behaving animal’s LFPs with the anesthetized one. A comparison between awake-behaving rats’ LFPs and anesthetized one is used to look into the role of cognition (spatial leaning through exploration) in such an emergent phenomenon.

Inspired by the above findings we attempt to characterize the rat exploratory behaviour and its neural correlates in category of other nonlinear dynamical systems which exhibit a SOC phenomenon, e.g. earthquakes, solar flares etc. We found the statistical evidence for long range temporal correlations in rat exploratory behaviour and LFPs recorded from rat hippocampus while a rat moves freely. These temporal correlations are illustrated through power laws in avalanche size, duration and their inter-event intervals. We interpret these power laws as self-organized criticality. Finding evidence of a critical phenomenon in behaviour as well as its neural correlate could be interesting, as it provides a phenomenological connection between different levels of brain organization and function. It further raises a number of questions like why the critical phenomenon is happening in awake state but not in anesthetized state and what is its physiological significance in neural networks. Also, existence of such phenomenon in other behaviours and psychological states is a possibility as well as an open question. If it is behaviour or brain state specific then again lot of questions arise, like why a particular brain state and region of brain dealing with a particular behaviour exhibits such dynamics but not others. If it is a general phenomenon in brain and behaviour then what is its mechanistic significance?

BIBLIOGRAPHY

- Adami, C. 1995: Self-Organized criticality in living systems. Phys. Lett. A. 203, 29-32.
- Alstott, J. & Timberlake, W. 2009: Effects of rat sex differences and lighting on locomotor exploration of a circular open field with free- standing central corners and without peripheral walls. Behav. Brain Res. 196, 214-219.
- Alyan, S.H. 1996: Evidence for resetting the directional component of path integration in the house mouse (*Mus musculus*). Ethology. 102, 629-638.
- Anteneodo, C. & Chialvo, D.R. 2009: Unraveling the fluctuations of animal motor activity. Chaos. 19, 033123.
- Bak, P., Tang, C. & Wiesenfeld, K. 1987: Phys. Rev. Lett. 59, 381; 1988: Self-Organized Criticality. Phys. Rev. A. 38, 364-374.
- Bak, P. & Tang C. 1989: Earthquakes as a self-organized critical phenomena. J. Geophys. Res. 94, 15635-15637.
- Bak, P. & Sneppen, K. 1993: Punctuated equilibrium and criticality in a simple model of evolution. Phys. Rev. Lett. 71, 4083-4086.
- Bakchine E, Pham-Delegue MH, Kaiser L, Masson C. 1990. Computer analysis of the exploratory behaviour of insects and mites in an olfactometer. Physiology & Behaviour, 48 (1): 183-187.
- Baiesi, M., Paczuski, M. & Stella, A.L. 2006: Intensity thresholds and the statistics of the temporal occurrence of solar flares. Phys. Rev. Lett. 96, 051103-051106.

- Banerjee, J., Verma, M.K., Manna, S. & Ghosh S. 2006: Self organized criticality and $1/f$ noise in single- channel current of voltage- dependent anion channel. *Europhys. Lett.* 73(3), 457-463.
- Bedard, C., Kroger, H. & Destexhe, A. 2006: Does the $1/f$ Frequency Scaling of Brain Signals Reflect Self-Organized Critical States? *Phys. Rev. Lett.* 97, 118102 (1) -118102 (4).
- Beggs JM, Plenz D. 2003. Neuronal avalanches in neocortical circuits. *J Neurosci* 23: 11167–11177.
- Bezrukov, S. M. & Winterhalter, M. 2000: Examining noise sources at the single-molecule level: $1/f$ Noise of an open Maltoporin channel. *Phys. Rev. Lett.* 85, 202-205.
- Boffetta, G., Carbone, V., Giuliani, P., Veltri, P. & Vulpiani A. 1999: Power laws in solar flares: Self-Organized Criticality or turbulence? *Phys. Rev. Lett.* 83, 4662-4665.
- Buzsaki, G. & Draguhn, A. 2004: Neuronal oscillations in cortical networks. *Science*, 304, 1926-1929.
- Chapman RF, Bernays EA. 1989. Insect behaviour at the leaf surface and learning as aspects of host plant selection. *Experientia*, 45: 217-222.
- Corral, A. 2004: Long-term clustering, Scaling, and universality in the temporal occurrence of earthquakes. *Phys. Rev. Lett.* 92, 108501-108504.
- Corral, A. 2005: Renormalization-group transformations and correlations of seismicity. *Phys. Rev. Lett.* 95, 028501- 028504.

- de Arcangelis, L., Godano, C., Lippiello, E. & Nicodemi, M. 2006: Universality in solar flare and earthquake occurrence. *Phys. Rev. Lett.* 96, 051102 (1) -051102 (4).
- de Arcangelis, L., Perrone-Capano, C. & Herrmann, H.J. 2006: Self-Organized Criticality Model for brain plasticity. *Phys Rev Lett.* 96(2), 028107 (1) -028107 (4).
- Deneubourg JL, Aron S, Goss S, Pasteels JM. 1990. The Self-Organizing Exploratory Pattern of the Argentine Ant. *J. Insect Behaviour*, 3 (2): 159-168.
- Draï, D., Kafkafi, N., Benjamini, Y., Elmer, G. & Golani I. 2001: Rats and mice share common ethologically relevant parameters of exploratory behavior. *Behav. Brain Res.* 125, 133-140.
- Faillettaz, J., Louchet, F. & Grasso, J.R. 2004: Two-threshold model for scaling laws of non interacting snow avalanches. *Phys. Rev. Lett.* 93, 208001 (1) - 208001 (4).
- Gevins, A., Leong, H., Smith, M.E., Le, J., & Du, R. 1995: Mapping cognitive brain function with modern high-resolution electroencephalography. *Trends Neurosci.* 18, 429-436.
- Geyer, M.A., Russo, P.V. & Masten, V.L. 1986: Multivariate assessment of locomotor behavior: Pharmacological and behavioral analyses. *Pharmacol. Biochem. Behav.* 25, 277-288.
- Gireesh ED, Plenz D. 2008. Neuronal avalanches organize as nested theta- and beta/gamma-oscillations during development of cortical layer 2/3. *PNAS* 105: 7576–7581.
- Gray CM, Maldonado PE, Wilson M, McNaughton B. 1995. Tetrodes markedly improve the reliability and yield of multiple single-unit isolation from multi-unit recordings in cat striate cortex. *J. Neurosci. Methods*, 63: 43–54.

- Hwa, T. & Karder, M. 1992: Avalanches, hydrodynamics, and discharge events in models of sandpiles. *Phys. Rev. A*, 45, 7002- 7023.
- Kafetzopoulos, E., Gouskos, S. & Evangelou, S.N. 1997: 1/f Noise and multifractal fluctuations in rat behavior. *Nonlinear Analysis, Theory, Methods and Applications*. 30(4), 2007-2013.
- Kinouchi O, Copelli M. 2006. Optimal dynamical range of excitable networks at criticality. *Nat Phys* 2:348–351.
- Legatt AD, Arezzo J, Vaughan HG. 1980. Averaged multiple unit activity as an estimate of phasic changes in local neuronal activity: effects of volume-conducted potentials. *J. Neurosci. Methods*, 2(2): 203-217.
- Legenstein R, Maass W. 2007. Edge of chaos and prediction of computational performance for neural circuit models. *Neural Netw* 20:323–334.
- Levina, A., Herrmann, J.M. & Geisel, T. 2009: Phase transitions towards criticality in a neural system with adaptive interactions. *Phys. Rev. Lett.* 102, 118110 (1) – 118110 (4).
- Loewen, I., Wallace, D.G. & Whishaw, I.Q. 2005: The development of spatial capacity in piloting and dead reckoning by infant rats: use of the huddle as a home base for spatial navigation. *Dev. Psychobiol.* 46, 350-361.
- Lu, E.T. & Hamilton, R.J. 1991: Avalanches and the distribution of solar flares. *Astrophys. J.* 380, L89.
- Marken, Richard S. 1990. Spreadsheet analysis of a hierarchical control system model of behaviour. *Behaviour Research Methods, Instruments & Computers*, 22 (4): 349-359.

- Maslov, S., Paczuski, M. & Bak, P. 1994: Avalanches and $1/f$ Noise in Evolution and Growth Models. Phys. Rev. Lett. 73, 2162-2165.
- Nakamura, T., Takumi, T., Takano, A., Aoyagi, N., Yoshiuchi, K., Struzik, Z.R. & Yamamoto, Y. 2008: Of mice and men – Universality and breakdown of behavioral organization. PLoS one. 3(4), e2050 (1-8).
- Novikov, E., Novikov, A., Shannahoff-Khalsa, D., Schwartz, B. & Wright, J. 1997: Scale- similar activity in the brain. Phys. Rev. E. 56 (3), R2387- R2389.
- Petermann T, Thiagarajan TC, Lebedev MA, Nicolelis MAL , Chialvo DR, Plenz D. 2009. Spontaneous cortical activity in awake monkeys composed of neuronal avalanches. PNAS 106 (37): 15921-15926.
- Peters, O., Hertlein, C. & Christensen, K. 2002: A complexity view of rainfall. Phys. Rev. Lett. 88, 018701 (1) - 018701(4).
- Plenz D, Thiagarajan TC. 2007. The organizing principles of neuronal avalanches: Cell assemblies in the cortex? Trends Neurosci 30: 101–110.
- Politzer, P.A. 2000: Observation of Avalanche like phenomenon in a magnetically confined plasma. Phys. Rev. Lett. 84, 1192-1195.
- Reut, A., Zadicario, P. & Eilam, D. 2006: Exploration in a dark open field: A shift from directional to positional progression and a proposed model of acquiring spatial information. Behav. Brain Res.171, 313-323.
- Segev, R. & Benveniste, M. 2003: Formation of electrically active clusterized neural networks. Phys. Rev. Lett. 90 (16), 168101 (1) – 168101 (4).

- Schuster, H. G. & Just, W., *Deterministic Chaos: An Introduction* (John Wiley and Sons, New York) 2005.
- Sornette, A. & Sornette, D. 1989: Self-organized criticality and earthquakes. *Europhys. Lett.* 9, 197-202.
- Tchernichovski, O., Benjamini, Y. & Golani, I. 1998: The dynamics of long-term exploration in the rat; Part I. A phase-plane analysis of the relationship between location and velocity. *Biol. Cybern.* 78, 423-432.
- Tchernichovski, O. & Golani, I. 1995: A phase plane representation of rat exploratory behavior. *J. Neurosci. Methods.* 62, 21-27.
- The Nobel Prize in Physiology or Medicine 1973: Karl von Frisch, Konrad Lorenz, Nikolaas Tinbergen official website of the nobel prize: http://nobelprize.org/nobel_prizes/medicine/laureates/1973/index.html
- Tinbergen, Niko 1953 *The Herring Gull's World* - London, Collins.
- Tinbergen, N. 1951 *The Study of Instinct*. Oxford University Press, New York.
- Touboul J, Destexhe A. 2010. Can Power-Law Scaling and Neuronal Avalanches Arise from Stochastic Dynamics? *PLoS ONE* 5(2): e8982.
- Verma, M.K., Manna, S., Banerjee, J. & Ghosh, S. 2006: Universal scaling laws for large events in driven non equilibrium systems. *Europhys. Lett.* 76 (6), 1050-1056.
- Zinn-Justin, Jean ; *Quantum Field Theory and Critical Phenomena*, Oxford University Press (2002). Extensive discussion of scale invariance in quantum and statistical field theories, applications to critical phenomena and the epsilon expansion and related topics.

PUBLICATIONS:

- **Yadav, CK**, Verma, MK, Ghosh S. 2010. Statistical Evidence for Power law Temporal Correlations in Exploratory Behaviour of Rats. **BioSystems** (*accepted for publication*).
- **Yadav, CK**, Fenton AA, Verma MK, Ghosh S. 2010. Neuronal Avalanches Dynamics in Rat Brain Hippocampus (CA1): Statistical Analyses of Local Field Potentials (*to be submitted*).