EPSRC Symposium Workshop Dendrites, Neurones and Networks

University of Warwick, June 7-10, 2010

Abstracts

Alla Borisyuk	Brent Doiron	Vincent Hakim	Arnd Roth
Paul Bressloff	Gaute Einevoll	David Hansel	Walter Senn
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Role of dendrites in noise-induced synchronization

Alla Borisyuk (University of Utah, USA)

Many types of epilepsy have been traced to mutations in somatic and dendritic ion channels. At the same time, seizures have long been associated with synchronization in networks of cells. In this project we are investigating how changes in the dendrite affect tendency of the cells towards synchronization. We focus on synchronization of uncoupled neurons driven to synchrony by a common noisy input; as may occur when neighboring tissue is recruited by the seizure focus. We use Lyapunov exponents (introduced in this context by Teramae and Tanaka) as a measure for noise-induced synchronization. We extend the theory to include dendrites via two different approaches: first, treating the soma and the dendrite as a single oscillator described by the dendrite. We demonstrate that either approach can be used in the case of passive dendrites and some of the active currents, including non-uniform spatial channel distribution. We find that some of the epilepsy-implicated currents can have either synchronizing or de-synchronizing effect and that distal dendrites can have a stronger synchronizing effect than proximal ones if "synaptic democracy" is included.

Cable theory of protein receptor trafficking in a dendritic tree Paul Bressloff (University of Oxford, UK)

We develop an application of linear cable theory to protein receptor trafficking in the surface membrane of a neuron's dendritic tree. We assume that receptors diffuse freely in the dendritic membrane but exhibit periods of confined motion through interactions with small mushroom-like protrusions known as dendritic spines. We use cable theory to determine how receptor trafficking depends on the geometry of the dendritic tree and various important biophysical parameters such as membrane diffusivity, the density of spines, the strength of diffusive coupling between dendrites and spines, and the rates of constitutive recycling of receptors between the surface of spines and intracellular pools. We also use homogenization theory to determine corrections to cable theory arising from the discrete nature of spines. Finally, we discuss extensions of the theory to active transport in dendrites driven by molecular motors.

Spike-timing and firing-rate dependent plasticity as calcium-induced transitions in a bistable synaptic model

Nicolas Brunel (Université Paris Descartes, France)

Synapses can change their strength in an activity-dependent manner. Multiple stimulation protocols have been found to be effective in changing synaptic efficacy, and parts of the molecular machinery involved in plasticity induction have been identified. However, the underlying mechanisms linking specific activity patterns to observed synaptic changes remain elusive. To better understand these mechanisms, we develop a simplified bistable synaptic model that has two stable states at resting calcium concentration. Transitions between the two stable states can be induced by calcium transients, provided these transients reach a depressing or a potentiating threshold. These thresholds implement in a simplified fashion biochemical dephosphorylation/phosphorylation processes that have been shown to be involved in synaptic plasticity. The model is studied analytically and numerically and is shown to account for a large body of experimental data on how spike timing and/or firing rate of pre- and postsynaptic neurons affect plasticity.

Effective activity equations for spiking neural networks

Carson Chow (NIH, USA)

Neural network rate or activity equations such as the Wilson-Cowan equations have been used for decades to successfully describe a wide range of neural phenomena. However, these equations do not consider correlations between spikes as would occur in synchronous neural firing or fluctuations due to the finite size of the network. These effects are generally studied using networks of spiking neurons, which are difficult to analyze. Here, I will describe an approach to derive effective activity equations systematically from an underlying network of spiking neurons that includes these effects. The equations reduce to conventional activity equations in the large network asynchronous limit. The method is based on perturbing around a formal expression for the probability density functional of phase or voltage histories of all the neurons in the network. The method is applicable to fully deterministic or stochastic spiking neurons. I will show examples of the use of probability density functionals to derive various quantities for networks of Kuramoto oscillators, probabilistically firing neurons, and quadratic integrate-and-fire (theta) neurons.

Neuronal spike-train responses in the presence of threshold noise: First passage times, stochastic mode-locking, and coding

Stephen Coombes (University of Nottingham, UK)

The variability of neuronal firing has been an intense topic of study for many years. From a modelling perspective it has often been studied in conductance based spiking models with the use of additive or multiplicative noise terms to represent channel fluctuations or the stochastic nature of neurotransmitter release. However, another important source of neuronal noise occurs at the axon hillock, which may be more appropriately considered as modulating excitability. Motivated by this we investigate the consequences of a noisy threshold in a simple leaky integrate-and-fire model. From a functional perspective such threshold noise can also provide a phenomenological model of a wide variety of stochastic neural processes, as well as being more convenient for analysis. Initially, we develop a mathematical treatment of the neuronal response to periodic forcing using tools from linear response theory and use

this to highlight how a noisy threshold can enhance downstream signal reconstruction. We further develop a more general framework for understanding the responses to large amplitude forcing based on a calculation of first passage times. This is ideally suited to understanding stochastic mode-locking, for which we numerically determine the Arnol'd tongue structure. To quantify how the shape of the stationary threshold distribution affects neuronal responses we focus on a zero-mean Gaussian and track the evolution of the tongue structure (parameter windows for the existence of stochastic mode-locked behaviours) as we increase the variance. Interestingly, this predicts a certain pattern of tongue erosion as the noise level is systematically increased. An examination of data from regularly firing stellate neurons within the ventral cochlear nucleus (VCN), responding to sinusoidally amplitude modulated pure tones, shows tongue structures consistent with these predictions and highlights that stochastic, as opposed to deterministic, mode-locking is utilised at the level of the single stellate cell to encode periodic stimuli. The range of the observed regularity of stellate cell responses leads us to a tentative proposal for the role of VCN stellate cells in stimulus encoding: a sub-population of regularly firing cells ('onset' units and 'sustained choppers') may extract specific information about the stimulus envelope (such as the periodicity) in the mode-locked timing of their spikes, whilst a sub-population of less regular neurons ('transient choppers') should more faithfully replicate the exact shape of the stimulus envelope.

Toward a minimal model of a large spiking cell

Steven Cox (Rice University, USA)

Experimentalists will soon be able to ascertain the highly nonuniform morphology and channel distributions of the large, pyramidal cells that populate the mammalian cortex. This advance is captured and quantified via tens of thousands of coupled nonlinear ordinary differential equations, per cell. The circuit modeler then asks, "How many of these equations must I keep in order to guarantee a fixed level of accuracy in the input-output map?" We argue that the combined application of Principal Orthogonal Decomposition and the Discrete Empirical Interpolation Method to the strongly excitable portion of the cell, and Balanced Truncation to the weakly excitable portion, permit one to reduce the system size by more than one order of magnitude and decrease simulation time by a factor of 5 without sacrificing synaptic specificity in space or time.

Correlation shaping in the nervous system

Brent Doiron (University of Pittsburgh, USA)

Correlated spiking activity between pairs of neurons is widespread across the brain, well documented in sensory, cognitive, and motor areas. Recently, it has been shown that the correlation between neurons can be shaped by both stimuli and the cognitive state of a subject, and a variety of correlation shifts have been reported. While in simplified systems the functional impact of such a shaping is clear, the underlying mechanisms responsible remain poorly understood. I will present a basic framework from which to address how the shaping of neural correlation occurs and relates to shifts in overall neural activity. Using a non-equilibrium statistical mechanics approach I will motivate and discuss an emerging concept of correlation susceptibility, which extends the more common input-output single neuron model to encompass pairwise neural statistics. Theoretical results will match experimental findings from cortical slices, and in vivo recordings from somatosensory cortex as well as brainstem areas in weakly electric fish.

What can we learn from multielectrode recordings of extracellular potentials in the brain? Gaute Einevoll (Norwegian University of Life Sciences)

Mathematical modelling relies on experimental data to make progress, both to constrain and to test

the models. A common experimental method has been in vivo single-unit extracellular recordings: when a sharp electrode is placed sufficiently close to the soma of a particular neuron, the recorded potential reliably measures the firing of individual action potentials in this neuron. This information is contained in the high-frequency part of the recorded potentials. The low-frequency part, that is, the local field potentials (LFP), has proved much more difficult to interpret and has typically been discarded.

Other experimental methods, particularly methods that measure population-level activity in vivo, are needed to facilitate development of biologically relevant neural network models. Large-scale electrical recordings using various types of multielectrodes, i.e., electrodes with many contacts, are one such option. As techniques for such recordings are rapidly improving, there is a need for new methods for extraction of relevant information from such data. Here we present results from projects in our group aimed at elucidating the link between recorded extracellular potentials and the underlying neural activity.

Extracellular potentials in the brain are in general due to complicated weighted sums of contributions from transmembrane currents in the vicinity of the recording electrode. The transmembrane currents accompanying various types of neural activity can be calculated by means of multicompartment models. Given these transmembrane currents, the extracellular potential can in turn be calculated using a electrostatic forward-modelling formula based on the quasistatic version of Maxwell's equations (Holt & Koch, J Comp Neurosci 6:169, 1999). Several projects where this forward-modelling scheme has been utilized will be briefly presented:

(A) investigation of how neural morphology and electrical parameters affect the shape and size of extracellular action potentials (Pettersen & Einevoll, Biophys J 94:784, 2008)

(B) investigation of how the LFP and its frequency content generated by neurons in a population depend on synaptic activity and neuronal morphologies (Pettersen et al, J Comp Neurosci 24:291,2008; Pettersen et al, J Neurosci Meth 154:116, 2006; Linden et al, J Comp Neurosci, to appear)

(C) introduction of laminar population analysis (LPA) where stimulus-evoked laminar-electrode data from rat barrel cortex are analyzed in a scheme where the MUA and LFP are jointly modelled using physiological constraints (Einevoll et al, J Neurophysiol 97:2174, 2007)

(D) extraction of thalamocortical and intracortical network models based on laminar-electrode data from barrel cortex and simultaneous recording of thalamic firing activity recorded in the homologous barreloid (Blomquist et al, PLoS Comp Biol 5:e1000328, 2009)

(E) generation of model data aimed at facilitating the development and objective testing of spikesorting algorithms for data recorded by multielectrodes

Hippocampal place cell assemblies generate oscillating population activity at theta frequency

Caroline Geisler (Universitaet Tuebingen, Germany)

The firing of hippocampal pyramidal cells is known to correlate with the rat's position during exploration ("place cells" discharge in their "place field"), building an internal representation of the rat's environment. The coordinated firing of these active cells is organized by the prominent "theta"oscillations in the local field potential (LFP): place cells discharge preferably at earlier and earlier theta phases on a cycle-by cycle basis as the rat crosses the respective place field ("phase precession"). The discrepancy between the oscillation frequency of all active neurons and their summed population activity (i.e., the theta LFP and mean output spiking) creates a paradox. How do faster oscillating neurons generate a slower oscillating LFP locally and at their targets? To investigate this issue, we recorded both field and unit activity in the hippocampus of the behaving rat and built a mathematical model based on the experimental findings. We show that the LFP theta frequency can be predicted from the oscillation frequency of single place cells and the their temporal offset, in agreement with the experiments. Our results suggest that the faster-than-theta oscillations of pyramidal cells is inherent and thus phase precession is a result of the coordinated activity of temporally shifted cell assemblies, relative to the population activity, reflected by the LFP.

A model of synaptic plasticity spanning scales from dendrites to networks Wulfram Gerstner (EPFL, Lausanne, Switzerland)

A phenomenological model of synaptic plasticity [1, 2] is able to account for a large body of experimental data on Spike-Timing Dependent Plasticity. The basic ingredient of the model is the correlation of presynaptic spike arrival with postsynaptic voltage. The local membrane voltage is used twice: a first term accounts for the instantaneous voltage and the second one for a low-pass filtered voltage trace. Spike-Timing effects emerge as a special case. We hypothesize that the voltage dependence can explain differential effects of STDP in dendrites, since the amplitude and time course of backpropagating action potentials or dendritic spikes influences the plasticity results in the model. The dendritic effects are simulated by variable choices of voltage time course at the site of the synapse, i.e., without an explicit model of the spatial structure of the neuron. Learning with this model of synaptic plasticity is tested in small networks of connected spiking point neurons. We show that the network structure reflects spatio-temporal characteristics of the input stimuli seen during learning.

[1] Claudia Clopath, Lars Busing, Eleni Vasilaki and Wulfram Gerstner (2010) Connectivity reflects coding: A model of voltage-based spike-timing-dependent-plasticity with homeostasis.

http://www.nature.com/neuro/journal/vaop/ncurrent/full/nn.2479.html

Nature Neuroscience, 13:344 - 352 (2010)

[2] Claudia Clopath and Wulfram Gerstner, Voltage and Spike Timing interact in STDP - a Unified Model, Frontiers in Synaptic Neuroscience, to appear.

The pyramidal cell as a multi-laminar computational unit

Bruce Graham (University of Stirling, UK)

The pyramidal cell (PC) is the principal excitatory neuron in the neocortex and hippocampus of the mammalian nervous system. Its distinctive morphology (which is reflected in its name) consists of a number of short basal dendrites and a long apical dendrite emerging from a somewhat pyramidalshaped cell body (soma). The apical dendrite consists of one or two main trunks from which sprout short, thin oblique dendrites and a branched distal tuft. Typically a PC receives two main excitatory input streams, one to the apical tuft and the other distributed between the apical oblique and basal dendrites. These streams come from anatomically distinct sources and putatively contain different information that must be suitably combined or integrated in the receiving PC. In addition to these excitatory inputs, a PC also receives inhibitory inputs from anatomically distinct populations of inhibitory interneurons (INs) that make spatially specific synapses onto the PC. These inputs are often in coalignment with the excitatory inputs, with particular populations targeting the apical tuft, the oblique and basal dendrites, the perisonatic region and the axon initial segment. These INs are activated by feedforward excitation from the same pathways driving the PCs and by feedback excitation from the PCs. Though they are much smaller in number than the PCs, their diversity and the specificity and spatial spread of their contacts onto PCs indicate they play a major role in how the PCs respond to their excitatory, information-rich, input streams.

The two excitatory input streams are hypothesized to carry complementary information, variously proposed to be "top-down" and "bottom-up", or "context" and "event". The streams provide both previously learnt knowledge and (preprocessed) current sensory input to a PC. An individual PC may become associated with a given sensory state ("event") in a particular context through the integration of these inputs within the cells dendrites. It is clear from much experimental and computational modelling work that each of these input pathways can be plastic and also instigate cellular output in the form of action potentials. More particularly, they may combine to both affect each others plasticity and ability to influence PC firing. However it is not known how they actually combine during the

different physiological states of a behaving animal, and how local inhibitory network activity controls their interaction.

Results of computer simulations of a hippocampal CA1 network will be presented that begin to explore the interaction between the two excitatory input streams from entorhinal cortex and hippocampal area CA3 onto CA1 PCs, and how this interaction is influenced by diverse temporal and spatiallydistributed inhibitory inputs.

The how, what, and why of the grid cell code for animal location

Ila Fiete (University of Texas at Austin, USA)

Grid cells in the mammalian entorhinal cortex, like place cells in the hippocampus, fire as a function of the animal's location in 2-d space. Unlike typical place cells, a grid cell fires at multiple locations, that fall at regular locations – on every vertex of a regular triangular lattice – and tile the plane. In this talk, I'll describe a neural network model of grid cell response generation, and derive the coding properties of this bizzare multi-modal non-local representation of a local, aperiodic, 2-coordinate variable (location). The grid cell location code is homologous to certain numeral systems and errorcorrecting codes known in computer science, which I will describe.

Neuron spike rate reponses: what are they, what are they useful for and what do they depend on?

Vincent Hakim (ENS, Paris, France)

The spike responses of a neuron describe, at a linear level, how stimuli affect its temporal probability of spike emission. I will recall the role of these functions in determining the characteristics of neural rhythms and in shaping the correlation between spike trains. I will then discuss their dependence on the particular characteristics of a neuron. I will specially focus on recent work that highlights, on the example of cerebellar Purkinje cells, the importance of the electric separation between somatic and dendritic compartments and of the specific targeting of inputs to these different compartments (work performed with S. Ostojic and N Brunel and in collaboration with G Szapiro and B Barbour for the experimental part).

Network mechanisms of visuo-spatial working memory

David Hansel (Université Paris Descartes, France)

Working memory (WM), the ability to temporarily hold, integrate and process information to produce goal-directed behavior, is crucial for higher cognitive functions such as planning, reasoning, decisionmaking and language comprehension. The persistent activity recorded in several cortical areas during WM tasks is thought to be the main neuronal correlate of WM. For example, in an oculomotor-delayed response task, in which a monkey has to remember the location of a transient stimulus for several seconds before making a saccade in its direction, neurons in the prefrontal cortex (PFC) elevate or reduce their activity persistently during the delay period. For a large fraction of these neurons, the delay activity is selective for the direction to be memorized.

The selective persistent delay activity of neurons recorded in such visuo-spatial WM tasks must be created internally since during the delay period the sensory cue disappears. It was hypothesized several years ago that this activity reflects the multistability of the PFC circuits involved. However, the precise mechanism by which this multistability can emerge remains unclear.

In this talk I will show that there are at least three possible network mechanisms involved in selective persistent activity. In the first mechanism, the simplest one, persistence and selectivity originate in a segregated manner from the dynamics of two different recurrent networks embedded in the PFC and coupled in a feedforward manner. In the second mechanism, the two features are generated within the same recurrent network. However, they emerge through two unrelated bifurcations of the dynamics. The third mechanism differs from other two in that both, the selectivity and the persistence, emerge simultaneously via a single bifurcation and are therefore intimately related.

I will analyze how these mechanisms differ in terms of their bifurcation structures, in terms of the roles played by excitation and inhibition, the nature of the nonlinearities that the single neuron input-output transfer function must display, and the dynamics during switch-on and switch-off from persistent selective states. Hence these mechanisms lead to different predictions which make it feasible to test them experimentally.

How do neurons work together? Lessons from auditory cortex

Kenneth Harris (Imperial College, London)

Recordings of single neurons have yielded great insights into how sensory information is represented in the neocortex. However, any one neuron functions as part of a population whose combined activity underlies cortical information processing. Here we review some results obtained by recording simultaneously from auditory cortical populations and individual morphologically identified neurons, in urethane-anesthetized and unanesthetized passively listening rats. Auditory cortical populations produced structured activity patterns both in response to acoustic stimuli, and spontaneously without sensory input. Population spike time patterns were broadly conserved across multiple sensory stimuli and spontaneous events, exhibiting a generally conserved sequential organization lasting for approximately 100ms. Both spontaneous and evoked events exhibited sparse, spatially localized activity in layer 2/3 pyramidal cells, and densely distributed activity in larger layer 5 pyramidal cells and putative interneurons. Laminar propagation differed however, with spontaneous activity spreading upward from deep layers and slowly across columns, but sensory responses initiating in presumptive thalamorecipient layers, spreading rapidly across columns. In both unanesthetized and urethanized rats, global activity fluctuated between "desynchronized" state characterized by low amplitude, high-frequency local field potentials and a "synchronized" state of larger, lower-frequency waves. Computational studies suggested that responses could be modelled by a simple dynamical system model fitted to the spontaneous activity immediately preceding stimulus presentation, reflecting a nonlinear self-exciting system in synchronized states and an approximately linear system in desynchronized states.

Stochastic neural activity

Benjamin Lindner (MPI for Complex Systems, Germany)

In my talk I will first discuss the effect of short-term plasticity on information transfer across a population of synapses. I explain under which conditions the information about a time-dependent signal encoded in the presynaptic spike trains is spectrally low- or highpass-filtered. Secondly, I present a model of a sensory neuron with firing-rate adaptation that shows spiking variability because of different sources of intrinsic channel noise. Analytical results are achieved in the limiting cases of dominating receptor channel noise and dominating adaptation channel noise; these results can be used to draw conclusions from neural spike trains about the dominating source of intrinsic noise.

Coding sensory signals in the whisker thalamus

Rasmus Petersen (University of Manchester, UK)

The early sensory pathways of the brain (visual, tactile, etc) act, in part, as communication channels whose function is to efficiently encode events in the environment and to transmit this information to the decision-making centres of the brain. However, natural patterns of sensory stimulation are complex and it is hard, using experimentation alone, to understand how this communication process operates. Over the past few years, the application of mathematical and computational approaches have led to significant progress.

Two of the key questions are: (1) how is sensory information represented by the activity of neurons? (2) what sensory features are neurons sensitive to? Our model system for addressing these questions is the rat whisker system, which possesses unique anatomical advantages. Our approach is to record the response of neurons to controlled whisker stimuli and to analyse the stimulus-relationship relationship with computational methods. To identify how neurons communicate sensory information, we have applied Shannon's theory of Information. This analysis indicates that the precise timing of action potentials is key to this neural code. To identify the sensory features that neurons encode, we have applied systems identification methods. Finally, we have used predictive modelling to verify that the description is accurate. In this way, we have made some progress towards understanding how neurons communicate sensory information and what sensory information they convey.

Synaptic learning rules: a drunk man's walk to remember

Mark van Rossum (University of Edinburgh, UK)

The strength of the synapses in the brain are presumably continuously subject to increases and decreases as the result of ongoing learning processes. This realization allows one to approximate the synaptic weight evolution as a stochastic process. This has been used to find fundamental limits of storage (Fusi and Abbott 2007).

Recently we introduced a synaptic information capacity measure based on Shannon information (Barrett and van Rossum '08). We use this to find the optimal weight dependent learning rules. We find that soft-bound learning rules are better than hard bound rules, although the improvement is quite small. Furthermore, we show how feedforward inhibition further increases storage.

Energy-efficient propagation of action potentials

Arnd Roth (UCL, UK)

The processing power of any computational device, including the brain, is limited by its energy supply. Thus, the economy of neural signalling mechanisms should be optimized during evolution. Recent experiments in mossy fibres of the rat hippocampus suggest that this is indeed the case for the energy cost of action potential propagation. In these axons a rapid sodium current decay and a matched delay of potassium current onset during action potentials result in a total sodium influx and associated energy demand of only 1.3 times the theoretical minimum, which is given by the sodium charge necessary for pure depolarization of the membrane capacitance. This is in contrast to a sodium influx (and associated energy cost) of four times the theoretical minimum value in the Hodgkin-Huxley model of action potential generation derived from the squid giant axon, which exhibits an inefficient temporal overlap of the sodium and potassium current waveforms during the action potential. If a similarly high efficiency as in the hippocampal mossy fibre is confirmed for other mammalian axons, present calculations of energy budgets of the brain based on the factor of four from squid axon need to be revised, shifting emphasis of activity-dependent energy costs from action potentials to downstream processes elicited by transmitter release. The implications for the interpretation of functional magnetic resonance imaging data will be discussed.

Spatio-temporal credit assignment in population learning Walter Sonn (University of Born, Switzerland)

Walter Senn (University of Bern, Switzerland)

Learning by reinforcement is important in shaping animal behavior, and in particular in behavioral decision making. Such decision making is likely to involve the integration of many synaptic events in space and time. However, using a single reinforcement signal to modulate synaptic plasticity,

as suggested in classical reinforcement learning algorithms, suffers from the spatio-temporal credit assignment: many synapses will have contributed differently to the behavioral decision, and for the same synapse the many releases at different times will have had different effects. We show how we can solve this spatio-temporal credit assignment problem in a population of spiking neurons. The learning rule is spike-time dependent and maximizes the expected reward by following its stochastic gradient. Synaptic plasticity is modulated not only by the reward, but also by a population feedback signal. While this additional signal solves the spatial problem, the population approach can also solve the temporal problem by means of a cascade of synaptic eligibility traces. In contrast to temporal difference (TD) based approaches to reinforcement learning, our rule is explicit with regard to the assumed biophysical mechanisms, and it can also deal with non-Markovian decision processes. We apply the rule to an ongoing sequence of decision makings with delayed reward, and to a stochastic reward scenario with memory, in both of which TD learning fails. Work done together with Johannes Friedrich and Robert Urbanczik.

Interneurons in hippocampus: Modeling their distinct natures

Frances Skinner (University of Toronto, Canada)

The hippocampus is an intensely studied brain structure that is involved in learning and memory. It expresses several population activities that are controlled by a diverse collection of inhibitory cells, or interneurons. These interneurons have distinct characteristics that can contribute to network output such in different ways. For example, some interneuron types have high densities of voltage-gated channels in their dendrites and allow dendritic spike initiation. I will describe our ongoing work involving the development and analysis of models of hippocampal interneurons so as to help understand the contribution of their distinct natures.

Cortical information processing with population spikes

Misha Tsodyks (Weizmann Institute of Science, Israel)

We recently proposed that recurrent cortical networks with short-term synaptic depression can generate brief epochs of near coincident firing across the network that we called Population Spikes (PS). Apart from being an interesting dynamical phenomenon, PSs could constitute a distinctive way for the cortex to respond to external sensory inputs and convey the information further on to higher areas. In this presentation I review the dynamical origin of PSs and their putative functional roles. In particular, PSs could mediate formation of coherent auditory percepts in a complex acoustic environment, and also could be advantageous to overcome the sparseness in the cortical connectivity in transmitting the information between cortical areas.