Behavior:

Evolution, &

Emergence

– a dynamic perspective

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BEE2026: BEHAVIOR, EVOLUTION, EMERGENCE

The workshop is to introduce recent developments in the use of quantitative methods for understanding the collective dynamics of biological & social complex systems and their evolution.

Topics

- The Mathematics of Conflict & Cooperation
- Evolutionary Games and Adaptive Dynamics
- Statistical Physics of Collective Phenomena
- Crowds in Motion: Herding, Flocking, Swarmi
- Complex Networks: Theory & Algorithms
- Nonlinearity and Pattern Formation
- Group Behaviour in Living Systems

“TO BEE OR NOT TO BEE”

Behavior: range of actions, reactions, and conduct of individuals, organisms, or systems in response to internal or external stimuli. It acts as the interface between an entity and its environment. Human/Animal behavior, Management, Organizational, Health, Social, ……..

In Mathematics, Physics, Engineering, **dynamic behavior** refers to how a dynamical system, material, or process changes, responds, or deforms over time in reaction to external forces, varying conditions, or environmental shifts. It highlights the difference between a static (steady) state and an active state involving transient conditions, fluctuations, and memory of past inputs.
Involves studies on stability, long term behavior, dependence on parameters, existence of periodic, stochastic or chaotic behavior to predict the spatial or temporal evolution of the system.

In biology **Evolution** is the process by which the heritable traits of populations change over successive generations. It is driven by natural selection, genetic drift, and mutation, and explains the diversity and adaptation of life on Earth.

Evolution in dynamical systems refers to the change in the state of a system over time according to a deterministic rule. It provides a mathematical framework to analyze and predict temporal transformation of complex phenomena.

The evolution rule is expressed mathematically with Differential equations or Discrete Maps (for Continuous and Discrete time events)

Emergence

Emergence is the process of something coming into existence, becoming visible, or developing. It is most prominently known as a fundamental concept in systems theory and philosophy, where it describes how complex entities or behaviors arise from the interactions of simpler, individual parts.

Emergent behavior occurs when a complex, large-scale pattern or property arises from the simple, individual interactions of components within a system. The whole becomes greater than the sum of its parts, often happening spontaneously without a central director or specific prior design. Traffic jam, Mexican wave in stadium, Starling murmuration.

“Systems almost always have the peculiarity that the characteristics of the whole cannot (not even in theory) be deduced from the most complete knowledge of' the components, taken separately or in other partial combinations. This appearance of new characteristics in wholes has been designated as emergence.
“The Growth of Biological Thought: Diversity, Evolution, and Inheritance” Ernst Mayr, (Harvard University Press, 1982)

Deborah M. Gordon (1995): “The Development of Organization in an Ant Colony”, American Scientist 83 50-57.

https://www.theguardian.com/artanddesign/2022/jun/05/a-fragment-of-eternity-the-mesmerising-murmurations-of-europes-starlings

No Single Leader: Despite their fluid, wave-like movements, these massive flocks operate without a leader. It is found that each starling responds almost instantly to the movements of its six or seven closest neighbours

Individual and Collective
Emergent Collective Behavior

Giant Honeybees form shimmering waves, the behavior is likely in order to deter bee predators (such as hornets) - Thailand

Fairy Circles

Namibia

Ecosystem Engineers

TERMITES

Regular patterns of plant growth & termite/ant mounds that blanket arid landscapes

Understand how multiple pattern mechanisms could interact at multiple scales.

Territorial aggression (long range) & Scale-dependent feedback (animal-plant)

The relation between local changes and global effects.

Spatial Pattern Enhances Ecosystem Functioning in an African Savanna. Robert M. Pringle et al. *PLOS Biology*, 8, No. 5, Article e1000377; 2010.

Termite Mounds Can Increase the Robustness of Dryland Ecosystems to Climatic Change Juan A. Bonachela et al. *Science*, 347, 651; 2015

A Theoretical Foundation for Multi-Scale Regular Vegetation Patterns. Corina E. Tarnita et al. *Nature*, 541, 398–401; 2017

- **Collective behavior operates without central control to regulate activity and growth.**
- **Systems that operate in this way are ubiquitous in nature.**
- **Decipher how local interactions produce collective global outcomes**
- **How environment shapes collective behaviour.**

The fit between the particular pattern of interaction that regulates activity, and the environment in which it functions.

"To understand the action of any part, we need to look at what is going on around it."

- **The Ecology of Collective Behavior.** Gordon DM. PLoS Biol (2014)
- **Architecture, constraints, and behavior.** Doyle, Csete. *PNAS USA (2011)*
- **Contextualizing context for synthetic biology** – identifying causes of failure of synthetic biological systems**.** Cardinale, Arkin*. Biotech. J. (2012)*

COLLECTIVE BEHAVIOUR OF CELLS

Collective behaviour in multi-cell systems is primarily synchronised

It may not always be the same as the constituent single cell dynamics.

The collective dynamics is generally robust even if the single cell behaviour is not.

Such a property confers functional advantage to the coupled multi-cell system in natural noisy environment.

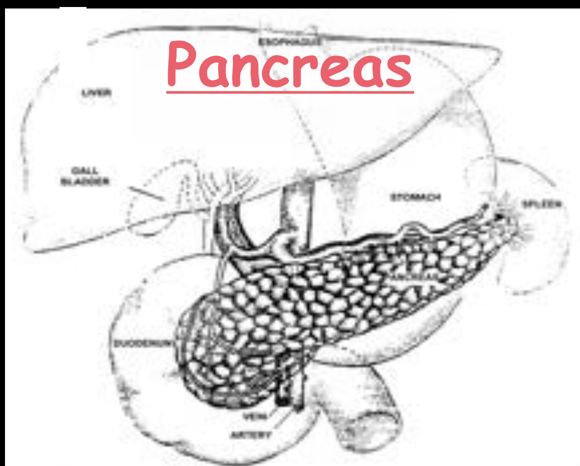
Theoretical study provides clues that increase the general understanding of how nature may engineer collective robustness in the face of local complexity.

COLLECTIVE BEHAVIOUR OF CELLS

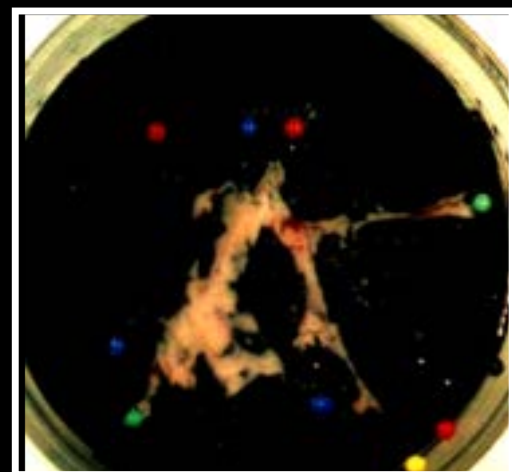
The case of beta cells in pancreatic islets

Beta cells in the Islets of Langerhans secrete insulin into the blood vessels in response to elevated levels of glucose

In the abdominal cavity just below the *liver* and under the *stomach*.

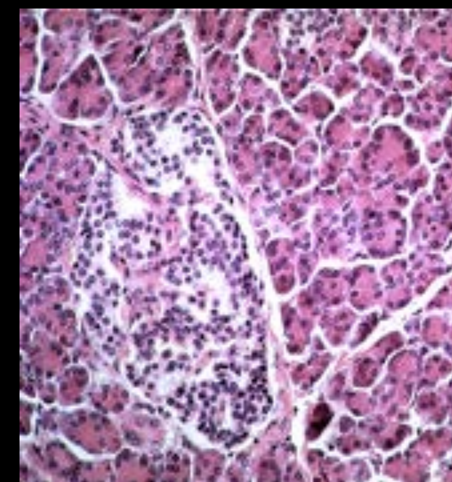


Islets of Langerhans



Islets

Diameter: 0.2-0.5mm
Each contains a few thousand cells



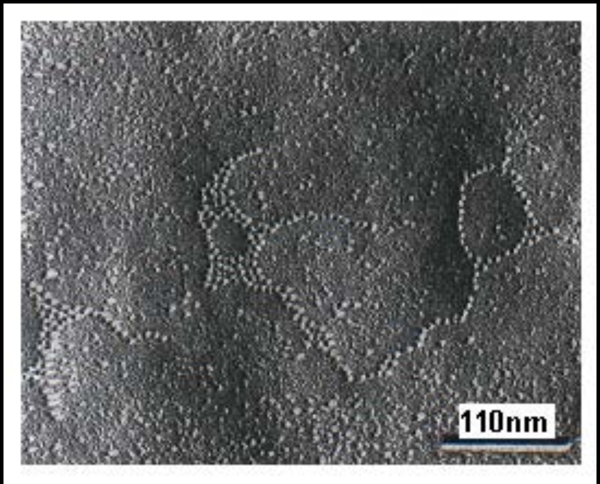
Non random distribution of cells

Beta cells in the Islet of Langerhans is an electrical system are coupled to each other through gap junctions

Beta cells form the core
Dark cells on the periphery are non-beta cells

Beta cells: coupled to each other through gap junctions

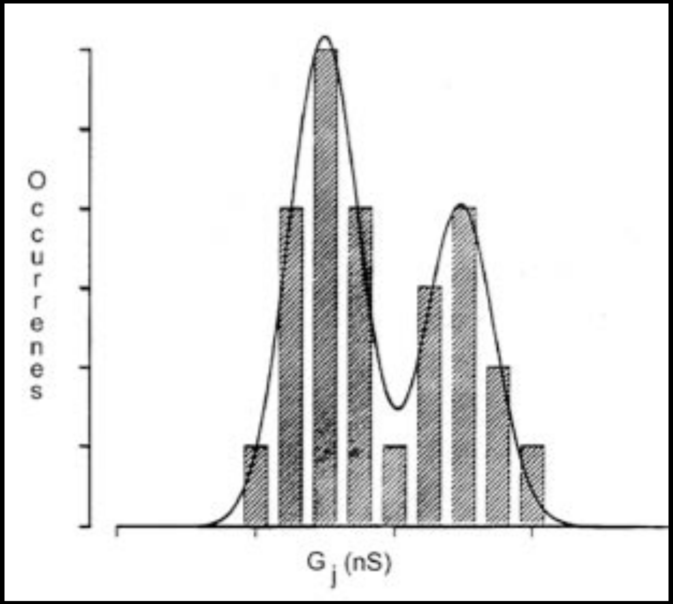
Freeze-fracture electron microscopy reveals clusters of gap junctions in membranes of beta cells in islets
(Meda et al, Exp.Cell.Res. 1991)



Major gap junction protein is Connexin-36

(Meda *et al*, Diabetes, 2000; J. Clin. Invest. 2000)

Spatial Distribution of Conductance



26 in-situ cell pair experiments

2.49 nS (SD 0.25 nS)

3.47 nS (SD 0.25 nS)

Range 4.11 - 2.1

Bimodal distribution of coupling conductance

Non-random distribution of gap junctions in beta cells

FACTS

Release of insulin from beta-cells is **pulsatile**

Correlated with **oscillations in membrane potential**

- **Synchronised electrical activity precedes insulin secretion**
- **Malfunction of electrical activity leads to failure in insulin secretion**

Within an islet

β-cells are electrically coupled via gap junctions

Heterogeneity in beta cell properties

Non-random distribution of gap junctions

Modulation of gap junction distribution by glucose

DATA

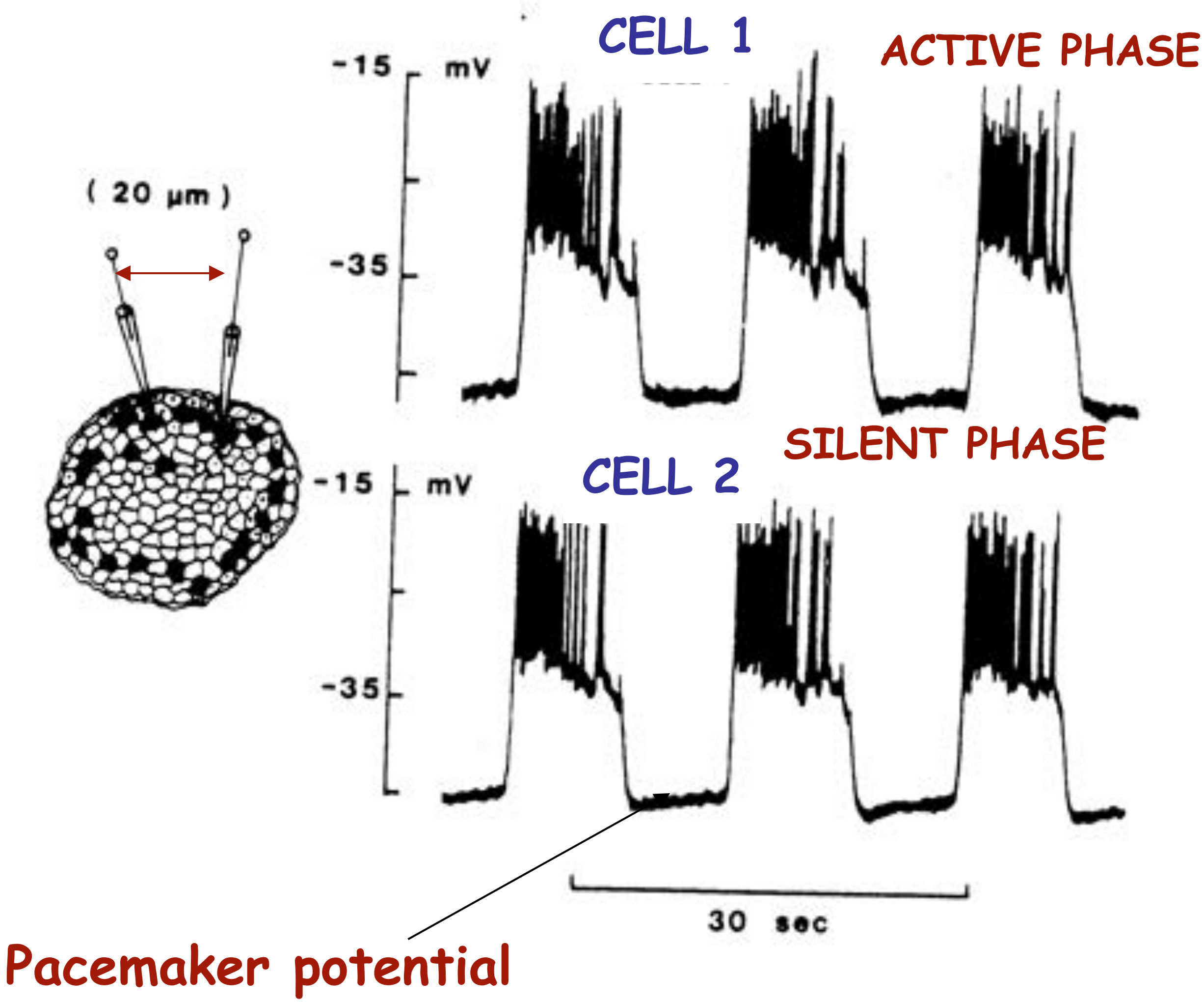
Experimental results
on
bursting patterns
in
beta cells

Electrical Coupling in Islet Cells

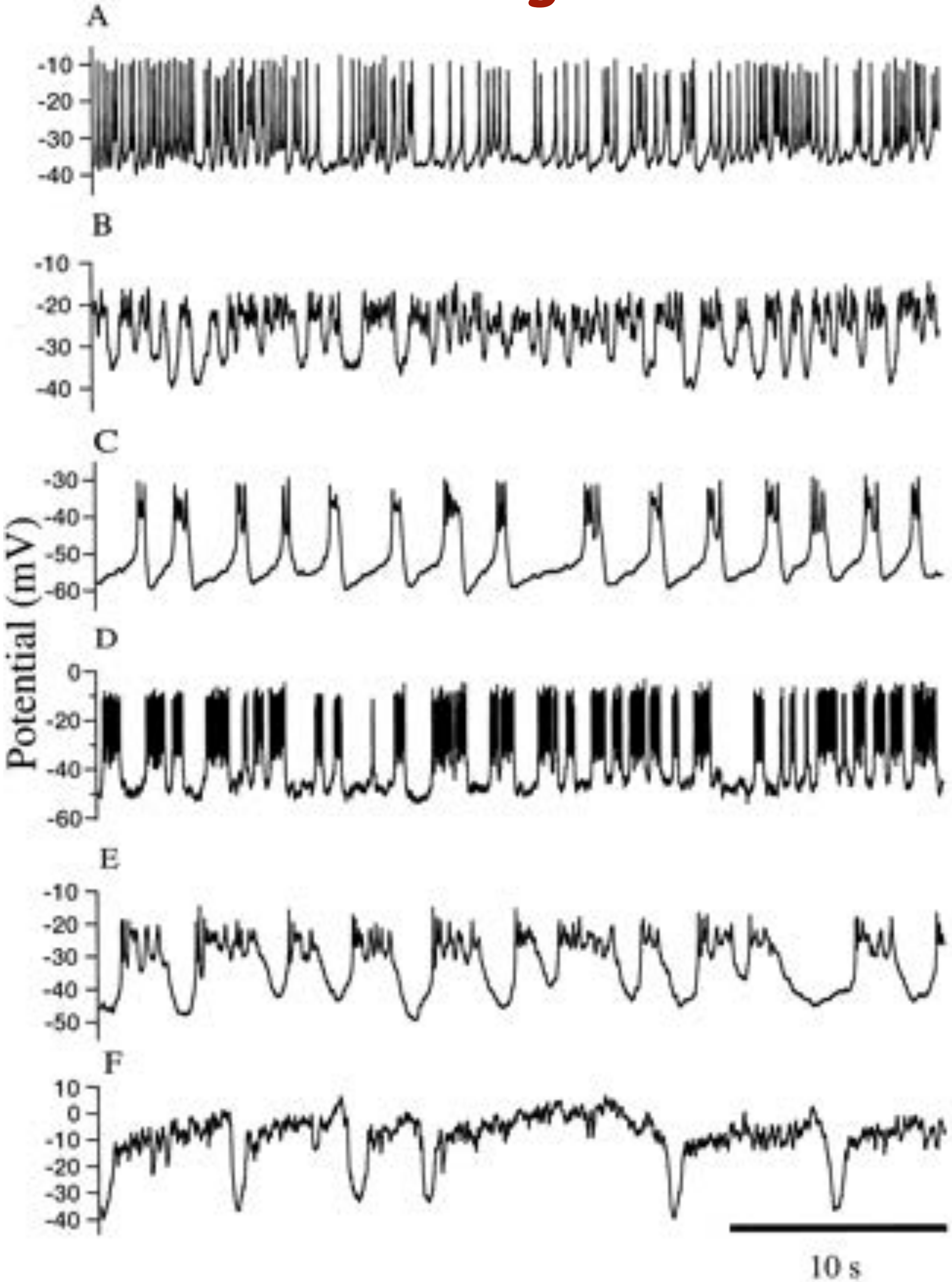
Simultaneous recording using intracellular microelectrode in voltage clamped state at 11.1 mM Glucose

Rhythmic slow plateau waves depolarise the cells from -45 to -30mV for 10s

Riding on the slow plateaus are rapid Ca^{+2} dependent voltage spikes that further depolarise to -15mV



Single Beta Cell Firing Patterns



(A) Class I - repetitive fast spikes

(B-E) Class II -
Fast spikes superposed on brief (<5s) periodic depolarizations

- **One-third are spikers**
- **Half are fast bursters**
  - **Period: < 5 sec**
- **The rest are plateau cells**

(F) Class III - Slow bursts with long active phase

(Kinard et al., Biophys J, 1999)

FACTS

- Single beta cells burst over wide time scale
- Coupled beta cells, within an islet, burst synchronously with medium frequency
- Beta cells in the islet have different gap junctional coupling
- The collective interaction of beta cells is critical for their normal functioning in insulin secretion.

How does a collection of beta cells, having a wide variety of bursting frequencies, exhibit emergent synchronised bursts of medium frequency (~25 sec) in the islet?

Model

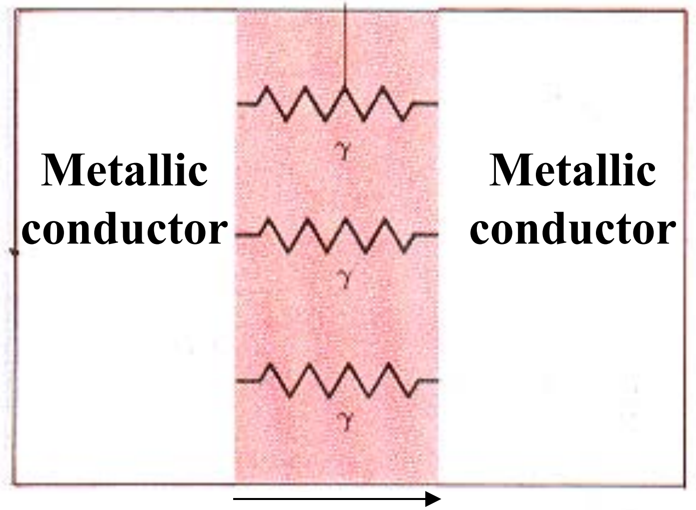
Beta cell
&
Islet

Modelling Electrical Activity in Cells

The plasma membrane maintains an unequal concentration of ions on either side resulting in membrane potential.

Component	Intracellular conc. (mM)	Extratracellular conc. (mM)
Na^+	**5-15**	**145**
K^+	**140**	**5**
Mg^+	**30**	**1-2**
Ca^+	**1-2** (10^{-7} is free)	**2.5-5**
H^+	**4×10^{-5}** (pH 7.4)	**4×10^{-5}**
Cl^-	**4**	**110**

Resistors embedded in insulating medium



Current = I
Voltage drop = V

γ = conductance of single resistor

Eqlbn potentials:

V_{Na} = +50mV to +65mV

V_K = -70mV to –100mV

Through parallel resistors:

Total current - $I = (\gamma+\gamma+\gamma)\ V = gV$

g = total conductance

Model for the single beta cell

Bursting electrical activity in the cell is due to the interplay of ionic mechanisms- *Hodgkin & Huxley (1952)*

The channels that are most important to beta cell activity are -

Membrane capacitance

$$C_m \frac{dV}{dt} = -I_{Ca} - I_K - I_{s1} - I_{s2} - I_l$$

Kirchoff's law

$$I_{Ca} = g_{Ca} \; m_\infty(V) \; (V - V_{Ca})$$ **Fast Ca^{2+} current**

$$I_K = g_K \; n \; (V - V_K)$$ **Fast K current**

$$I_{s1} = g_{s1} \; s_1 \; (V - V_K)$$ **Slowly inactivating K current**

$$I_{s2} = g_{s2} \; s_2 \; (V - V_K)$$ **Very slow inhibitory K current**

$$I_l = g_l \; (V - V_L)$$ **Leakage current**

(Bertram, et al, Biophys. J. 2000; Zimliki, et al, Biophys. J. 2004)

$$\frac{dn}{dt} = \frac{n_\infty(V) - n}{\tau_n(V)}$$
$$\frac{ds_1}{dt} = \frac{s_{1\infty}(V) - s_1}{\tau_{s1}}$$
$$\frac{ds_2}{dt} = \frac{s_{2\infty}(V) - s_2}{\tau_{s2}}$$

$$m_\infty = \frac{1}{1 + exp\left[\frac{(-22-V)}{7.5}\right]}$$
$$n_\infty = \frac{1}{1 + exp\left[\frac{(-9-V)}{10}\right]}$$
$$s_{1\infty} = \frac{1}{1 + exp\left[\frac{(-40-V)}{0.5}\right]}$$
$$s_{2\infty} = \frac{1}{1 + exp\left[\frac{(V_{s2}-V)}{0.4}\right]}$$

Candidates for

s_1 -- K-Ca activation, $I_{K(Ca)}$ inactivation

s_2 -- Ca^{2+} in ER store, ADP ($I_{K(ATP)}$)

n -- gating variable

$$\tau_n = \frac{9.09}{1 + exp\left[\frac{(V+9)}{10}\right]}$$

$$\tau_{s1} = 1\text{–}5\ sec$$

marginally slow

$$\tau_{s2} = 60\text{–}120\ sec$$

very slow

PARAMETERS

$$g_{s1} = 3\text{–}33\ ps$$
$$g_{s2} = 32\ ps$$
$$V_{Ca} = 100\ mV$$
$$V_K = -80\ mV$$
$$V_L = -40\ mV$$
$$V_{s2} = -42\ mV$$

Glucose sensing parameter

$$C_m = 4524\ fF$$
$$g_{Ca} = 280\ ps$$
$$g_K = 1300\ ps$$
$$g_l = 25\ ps$$

DIVERSITY IN SINGLE CELL DYNAMICS

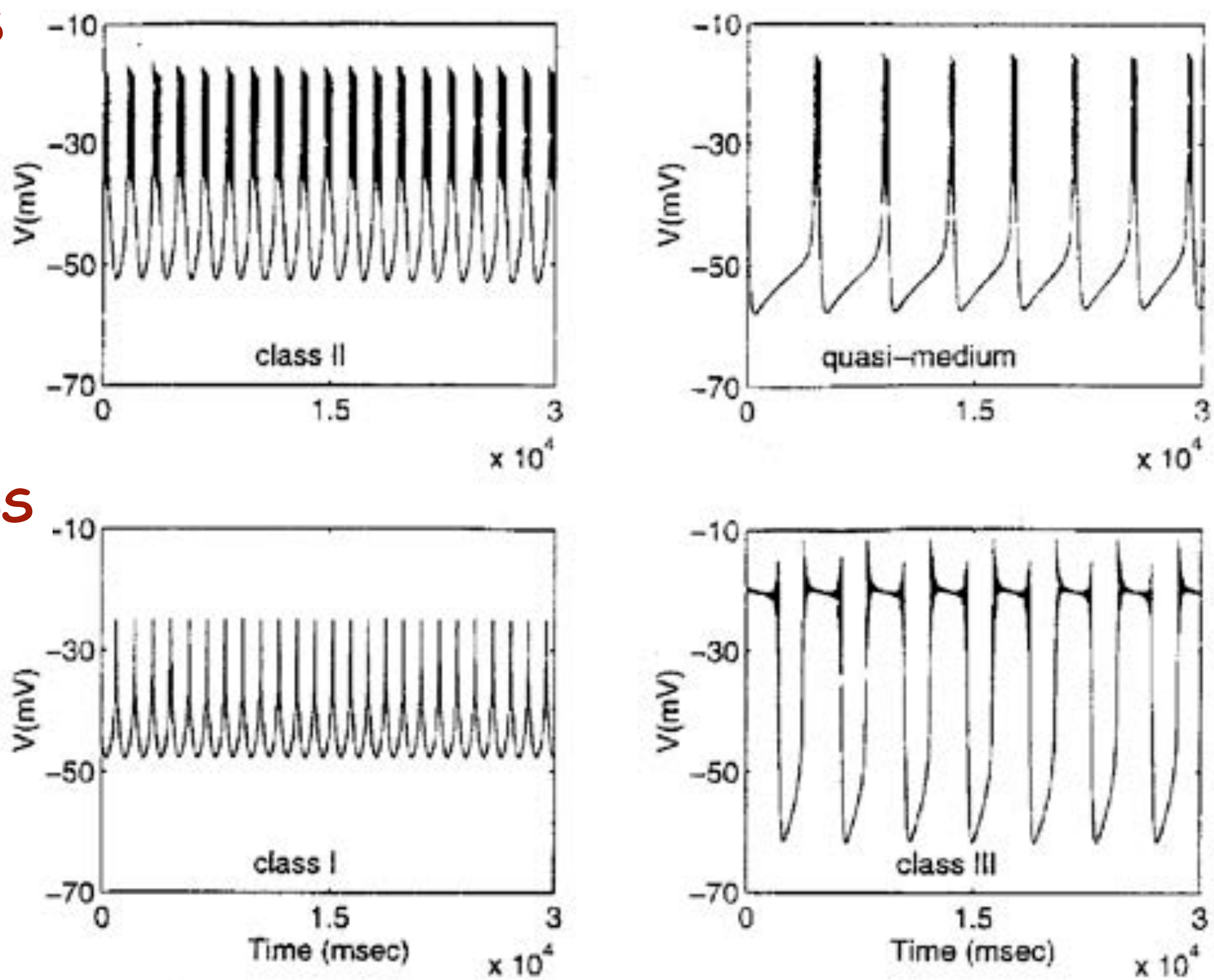
Small heterogeneity in ionic conductances
Different classes of behaviour

gs1 = 33pS

gCa = 300pS
gKATP =15

gK = 1500pS

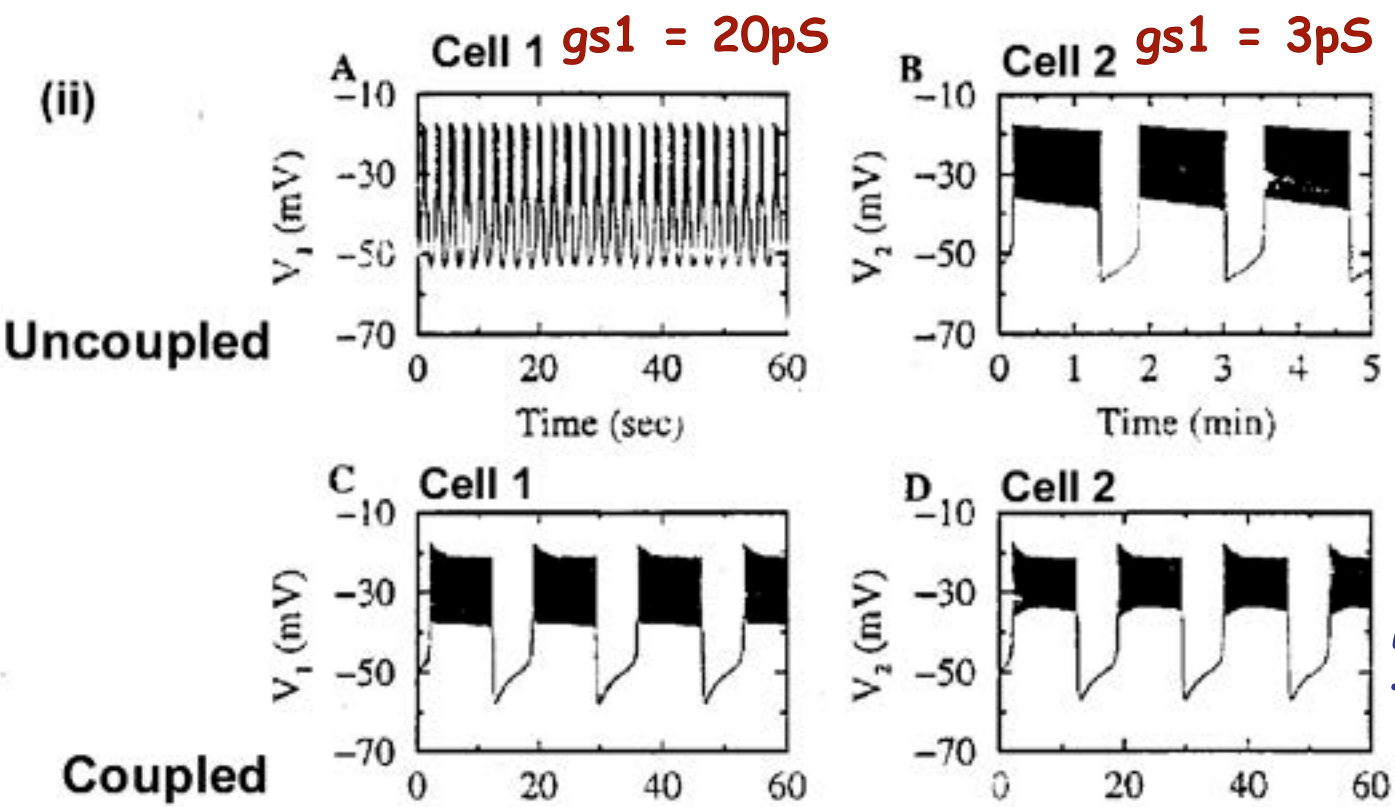
gCa = 325pS



Two cells coupled through gap junction

$$\frac{dV_1}{dt} = -(Iion/Cm) + (gc/Cm)\{V_1-V_2\} \qquad \frac{dV_2}{dt} = -(Iion/Cm) + (gc/Cm)\{V_2-V_1\}$$

V_1 and V_2 are voltages of Cell 1 and Cell2



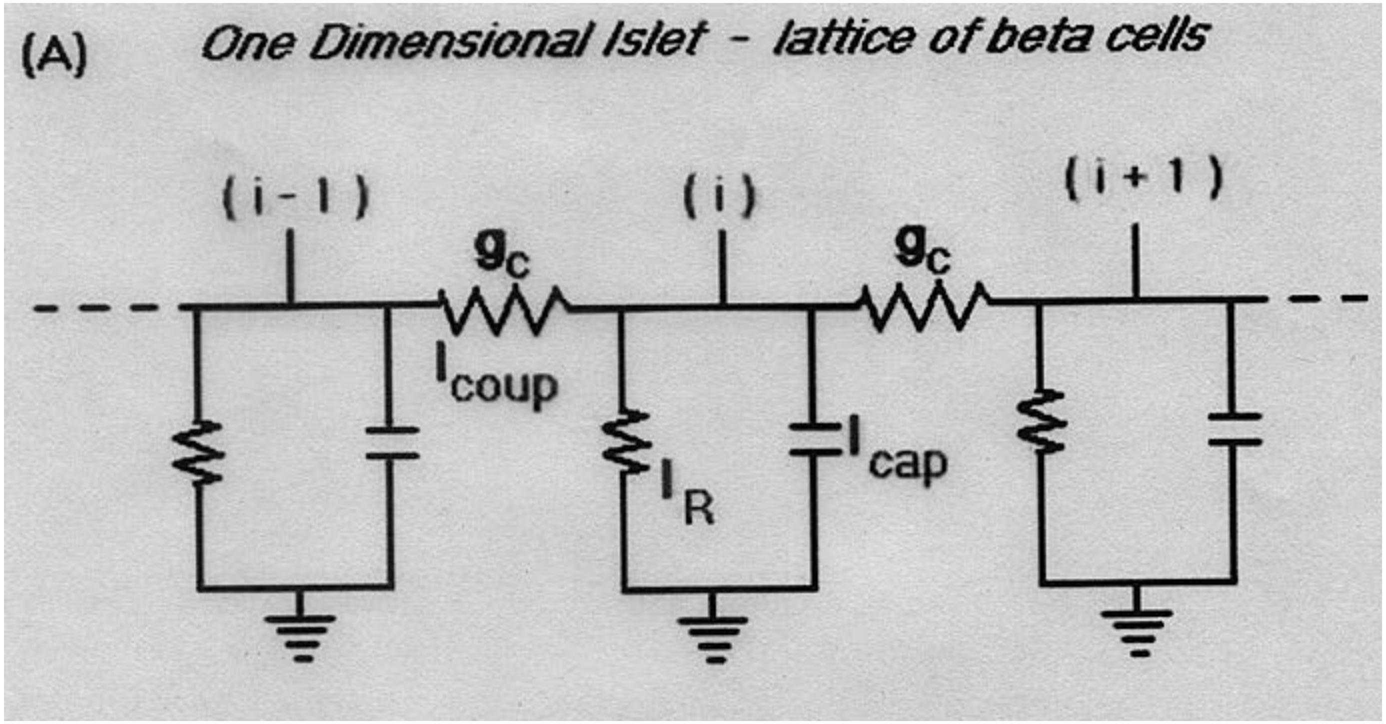
Gap junctional conductance, gc = 130pS

Medium bursting through coupling.

No equivalent time constant involved

MODELLING THE ISLET

One dimensional lattice with each beta Cell coupled to its nearest neighbour through gap junctions



For each cell in the lattice: $$\frac{dV_i}{dt} + gmV_i + gc(V_{i+1} - V_i) + gc(V_{i-1} - V_i) = 0$$

Ionic currents (conductances)

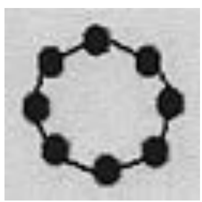
Gap junctional conductance

ASSUMPTIONS OF THE MODEL

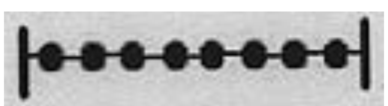
(i) Cellular interaction in the islet is only electrical - through the gap junction !!! (Bertram, et al, Biophys. J. 2004)

(ii) all cells are connected - there is no discontinuity in the lattice

Geometry



Circular
Periodic boundary



Linear
Fixed boundary

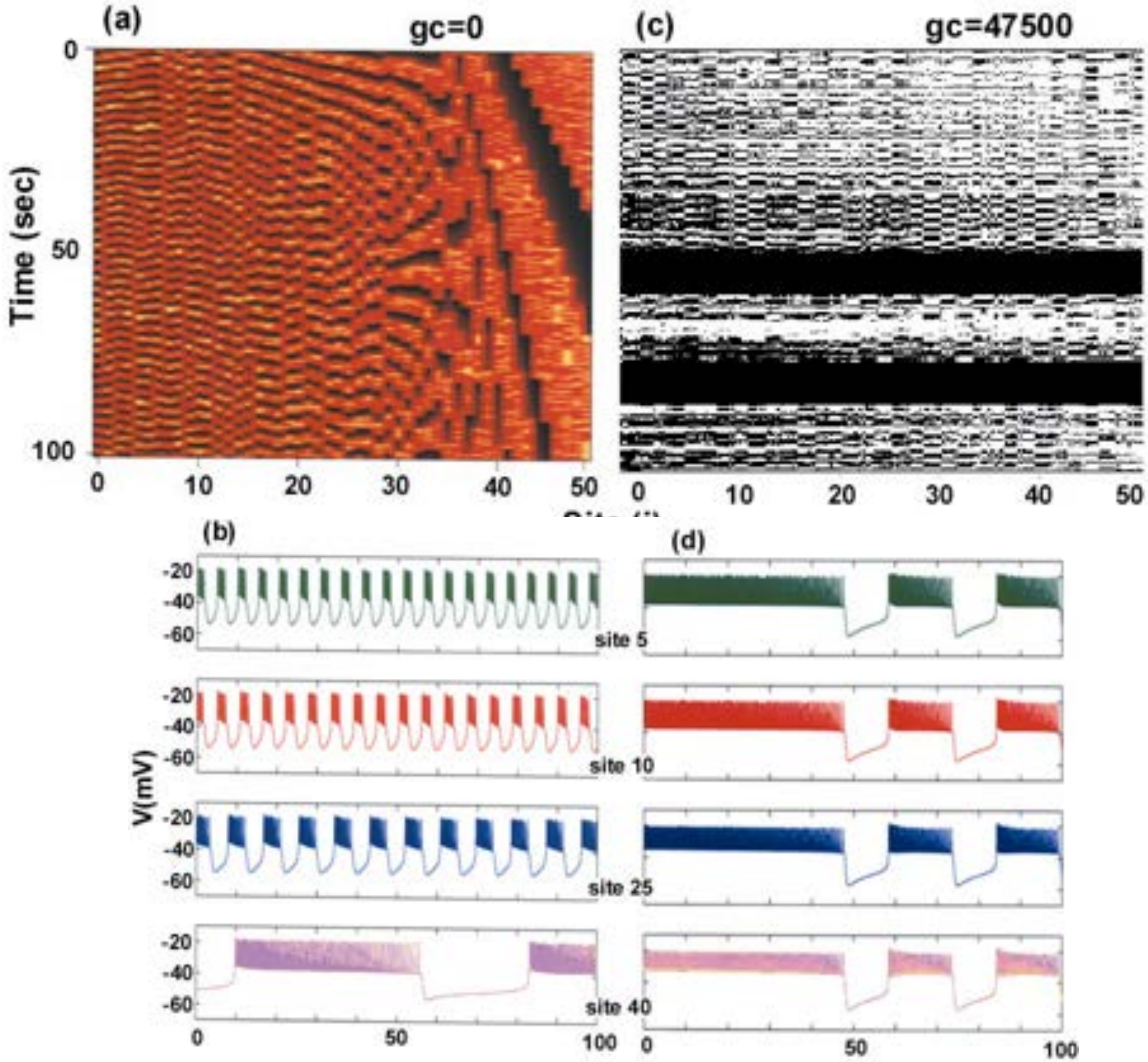
Study lattice dynamics as a function of

coupling strength (gc),

cellular parameters

and their spatial distribution

LINEAR LATTICE - GRADED GS1 (20pS - 2pS)



Beautiful synchronised bursts with medium frequency

(~25s time period) Very high gc !!

Graded gs1 (2-20pS & 20-2 pS), Vs2 (-42 to -52 mV)

Constant coupling (gc)

Slow oscillations

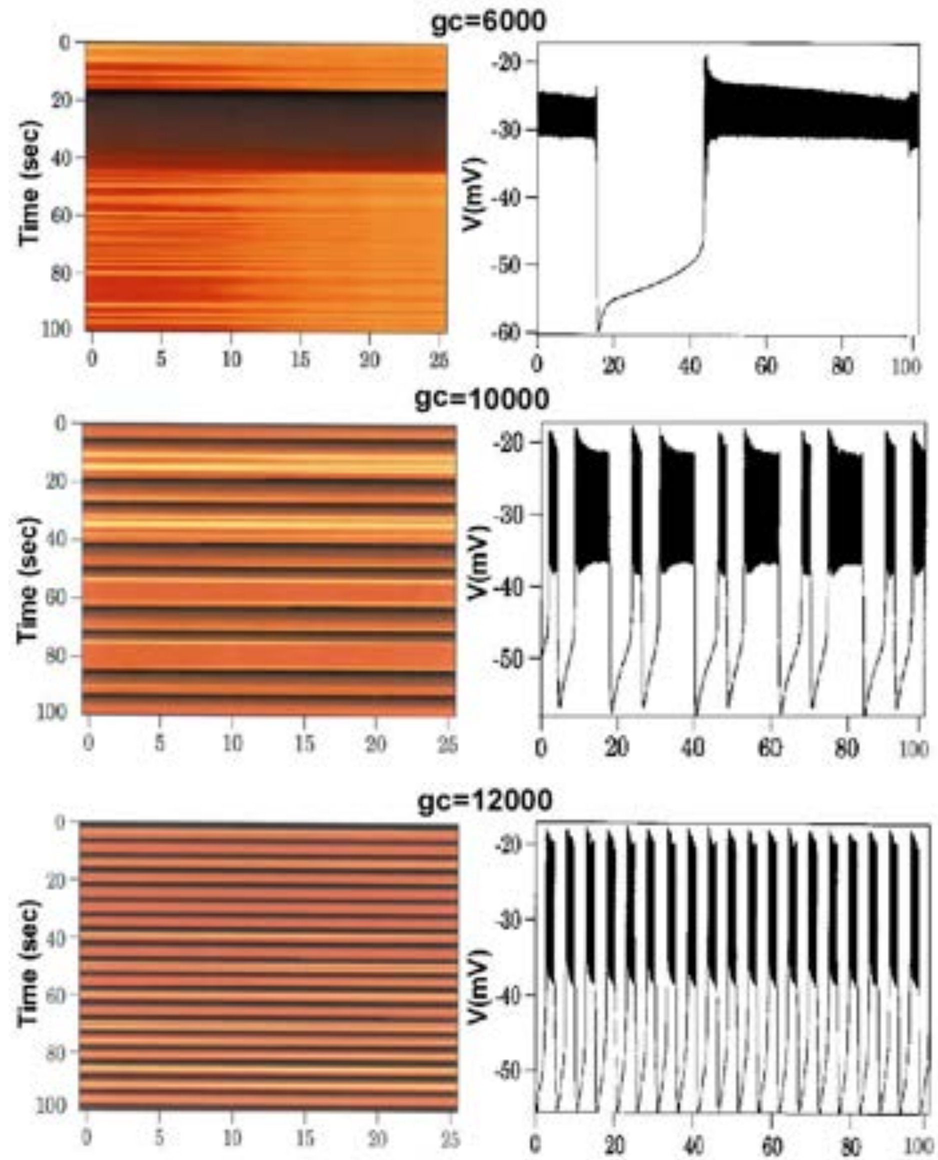
g_c = 4,000

Fast oscillations

g_c = 10,000

Very fast oscillations

g_c = 12,000



Synchronised bursts, but frequency is not realistic

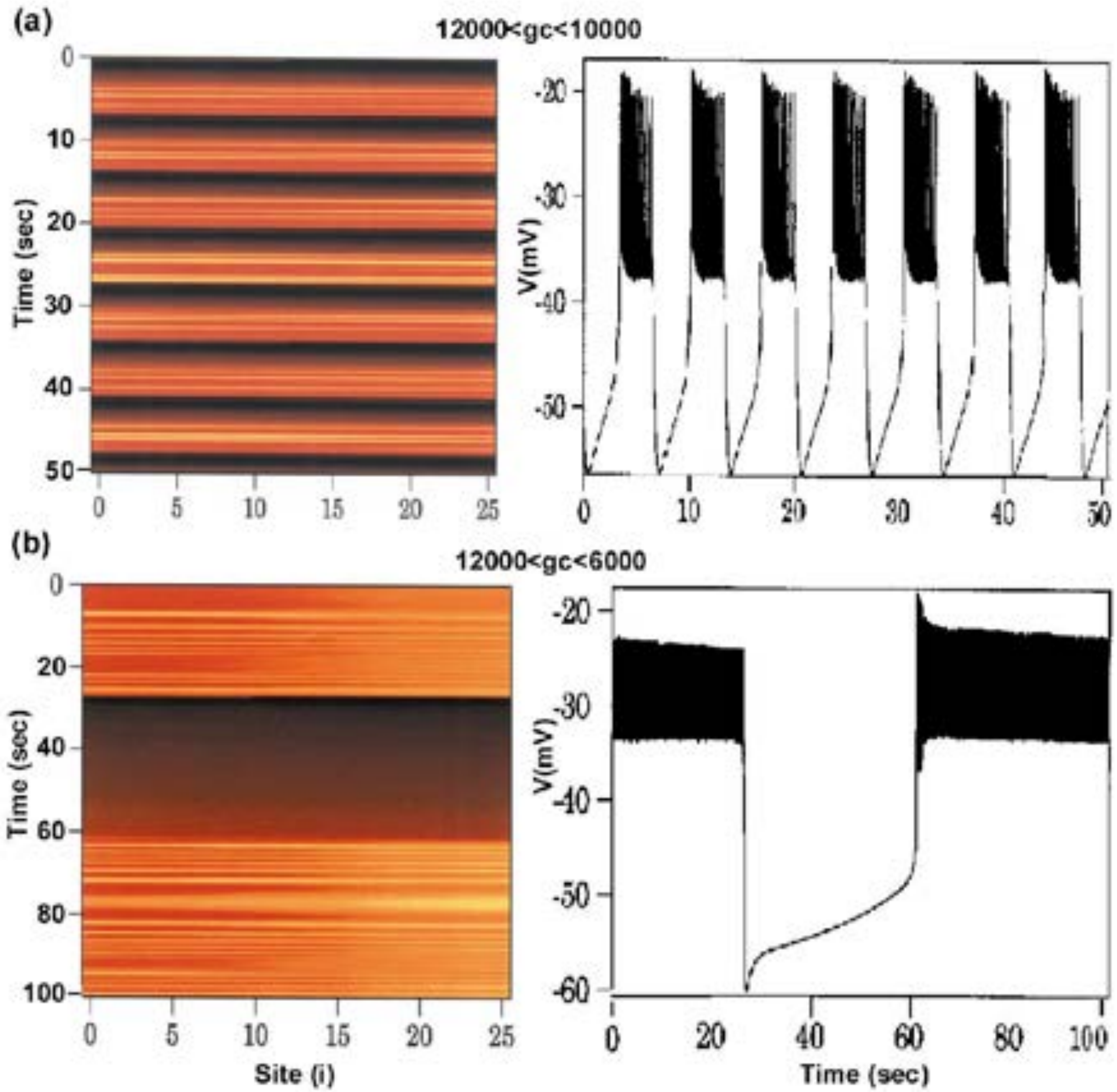
Gradient in gap junctional coupling strength gc & gs1

(20> gs1 >2 pS)

T ~ 7 sec
(12000< gc <10000 pS)

Same dynamics for
(12000> gc >1000 pS)

Very slow
synchronous bursts
(12000< gc <6000 pS)



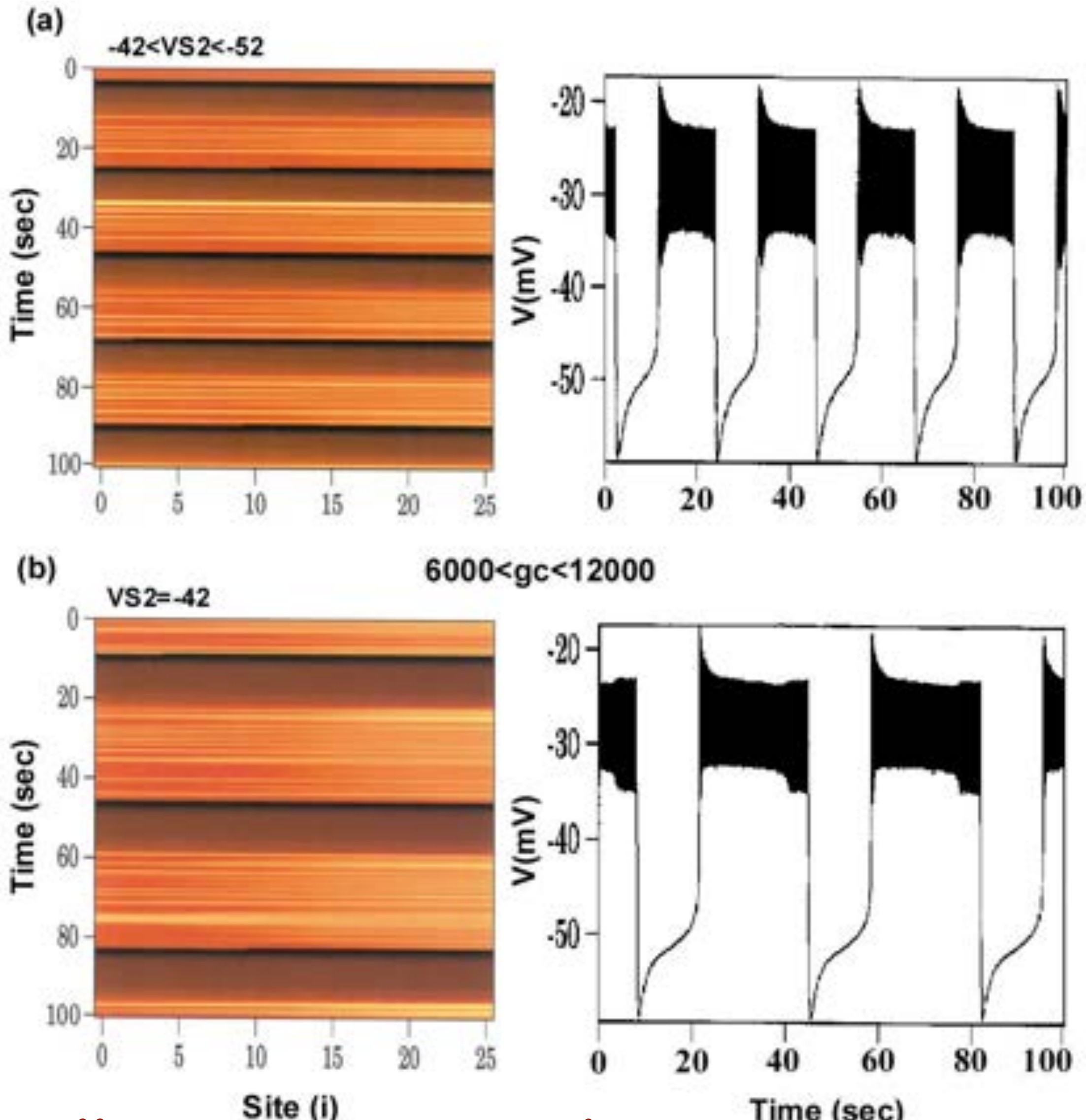
Gradient in gap junctional coupling strength gc & gs1

Loose to tight coupling

(6000< *gc* <12000 pS)
-42< Vs_2 <-52

Well-synchronised bursts of medium Frequency (~25 sec)

(6000< *gc* <12000 pS)



Distribution of cell properties in the tissue controls function

Summary

- Differences in ionic conductances can lead to different burst/oscillation patterns in individual beta cells
- The islet cells may have heterogeneity in cellular properties but coupling can lead to emergent synchronised behaviour
- Islet architecture (specific distribution of cell properties in the islet), which may be developmentally regulated, lead to normal function
- There is a dynamic relation between the cell property distribution and burst frequency that may underlie the variation in burst frequencies with concentration of external signals.

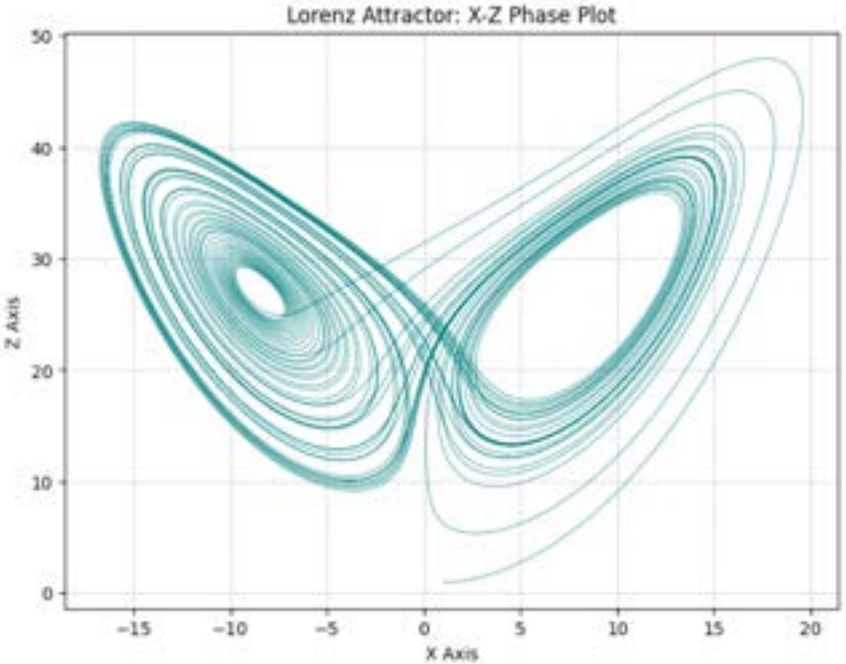
Role of external perturbation on individual and collective dynamics

(Use Lorenz equations as model system)

Meteorologist Edward Lorenz (1963) to model atmospheric convection.

$\sigma = 10$, $b = 8/3$, $r = 28$

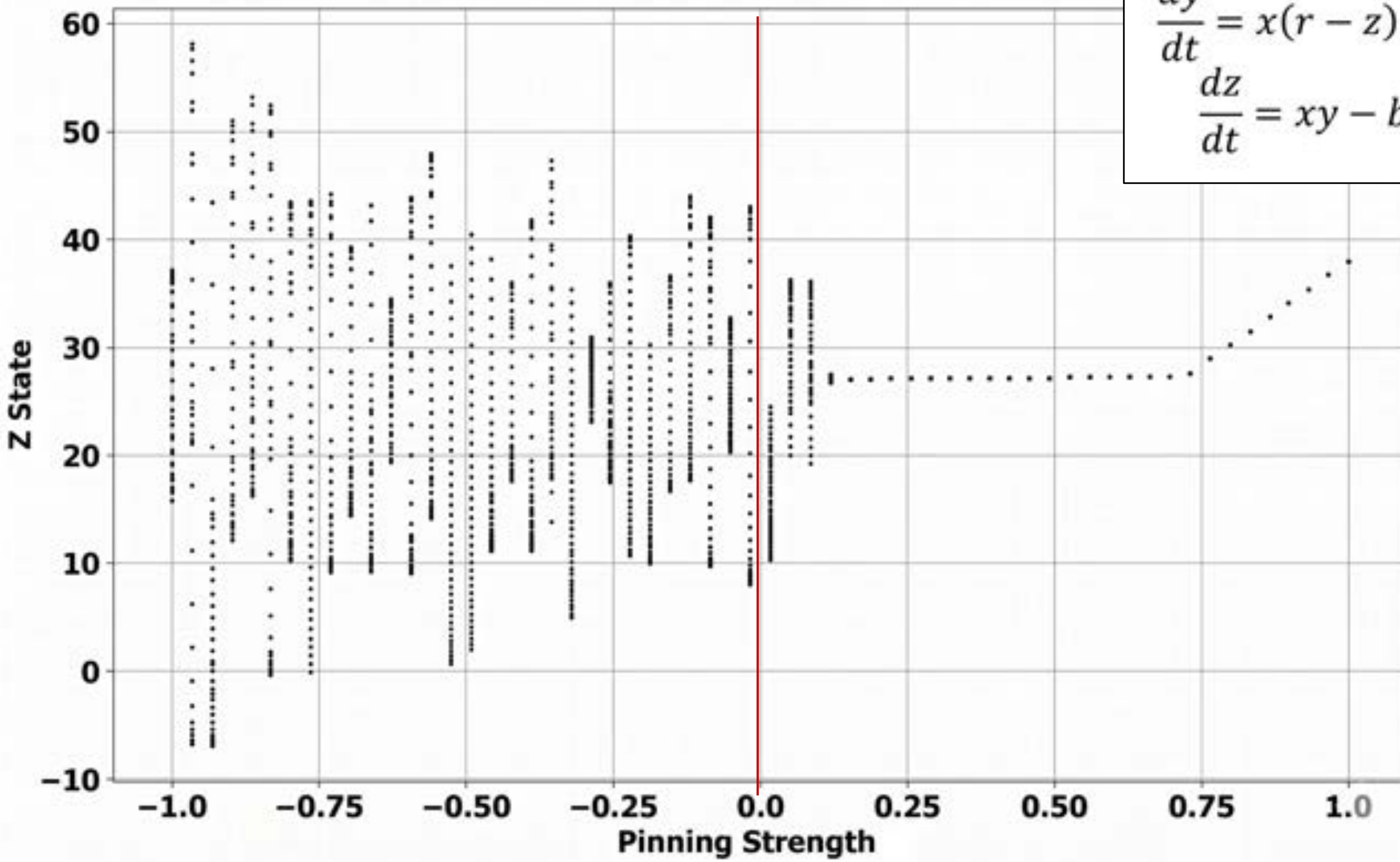
$$\frac{dx}{dt} = \sigma(y - x)$$
$$\frac{dy}{dt} = x(r - z) - y$$
$$\frac{dz}{dt} = xy - bz$$



A completely deterministic system can exhibit unpredictable, aperiodic, and highly sensitive behavior.

Fixed external perturbation (pinning, p) in Z-eqn.

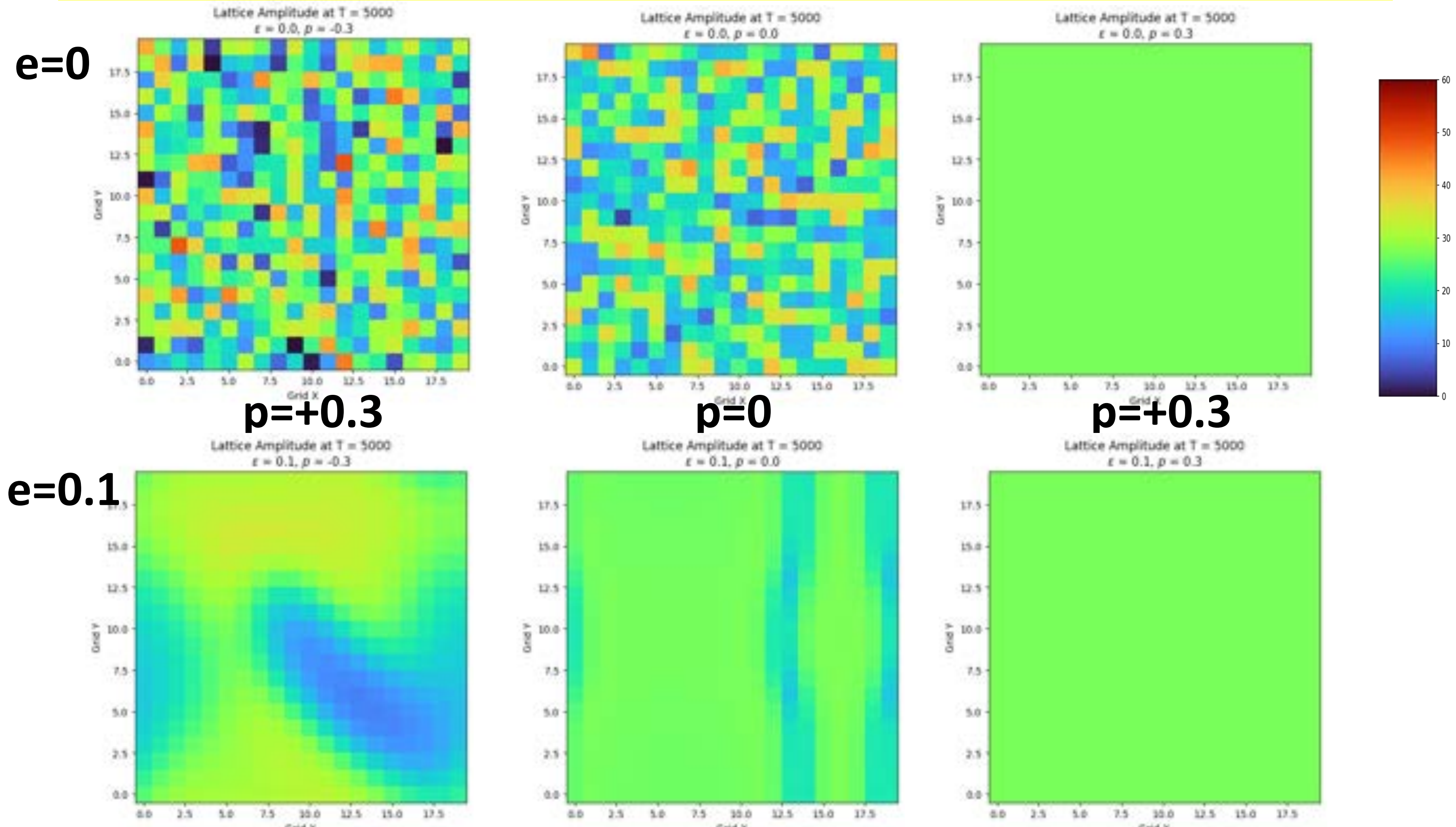
$$\frac{dx}{dt} = \sigma(y - x)$$
$$\frac{dy}{dt} = x(r - z) - y$$
$$\frac{dz}{dt} = xy - bz + p$$



Positive perturbation (+p) suppresses chaotic dynamics but negative perturbation (-p) enhances

Two-dimensional lattice of Lorenz systems

External perturbation on collective dynamics

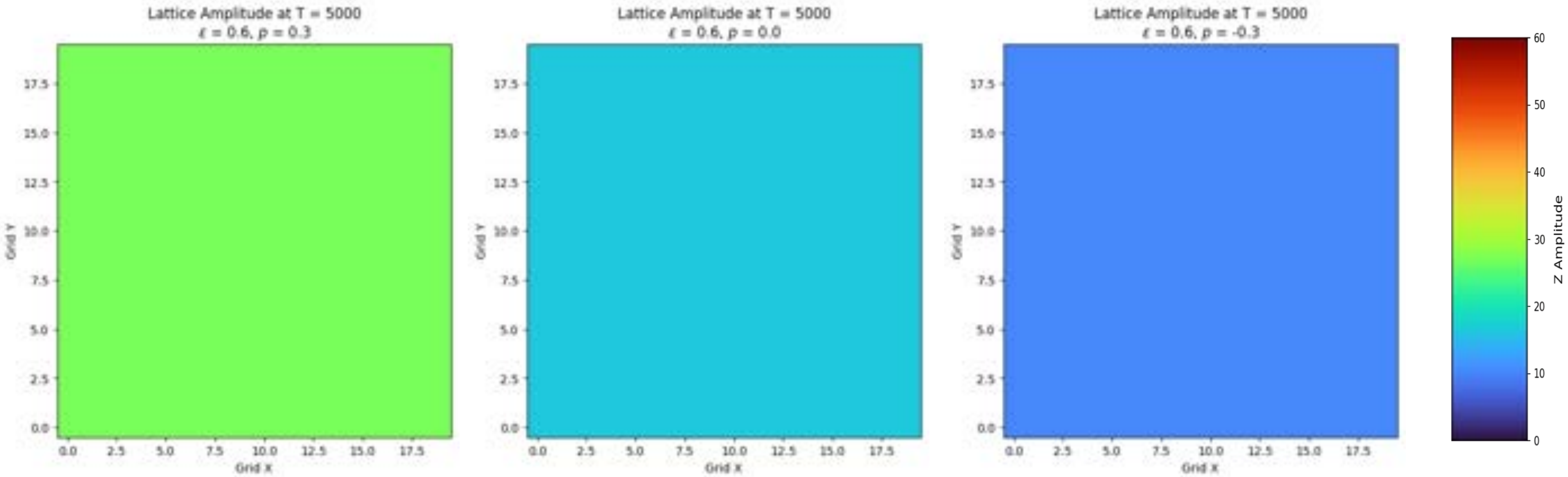


On coupling collective dynamics changes (p=0).

Effect of pinning is also different than pinning individuals

Increased coupling e=0.6

p= - 0.3 **p=0** **p=+0.3**



Increased coupling (e=0.6) induces spatial synchronization in collective dynamics for p=0 and p=- 0.3, but long term dynamics shows bursts of irregular waves for negative p.

Thus highly coupled systems may exhibit regular dynamics for extended period of time but with highly irregular phases.

Behavior, Evolution, Emergence

– a dynamic perspective

- **made some general comments**
- **showed real life examples**
- **described two examples of modelling –**

Biological system

Model physical system

Not discussed –

Individual – single variable/multi-variable.

How does a single variable collective differ from a multi-variable collective - in responding to intrinsic or extrinsic perturbations ?

Thank all my students, co-workers, colleagues, and friends

The Lorenz work is ongoing and being done by Kumar Onker, IISER Mohali MS21 batch

THANK YOU