Neural code and integrate & fire models of neuron

COSC422 – lecture 12

How is the information coded in the brain?

Simplified models of neurons

Brain functions

- generation of electrical oscillatory activity
- transmission of electro-chemical signals
- monitoring and control of bodily functions

- **sensory percepcion**
- **learning new information**
- **performing memory functions**
- **forming thoughts**
- **making decisions**
- **awareness & consciousness**

Cognitive functions

Methods of studying brain functions

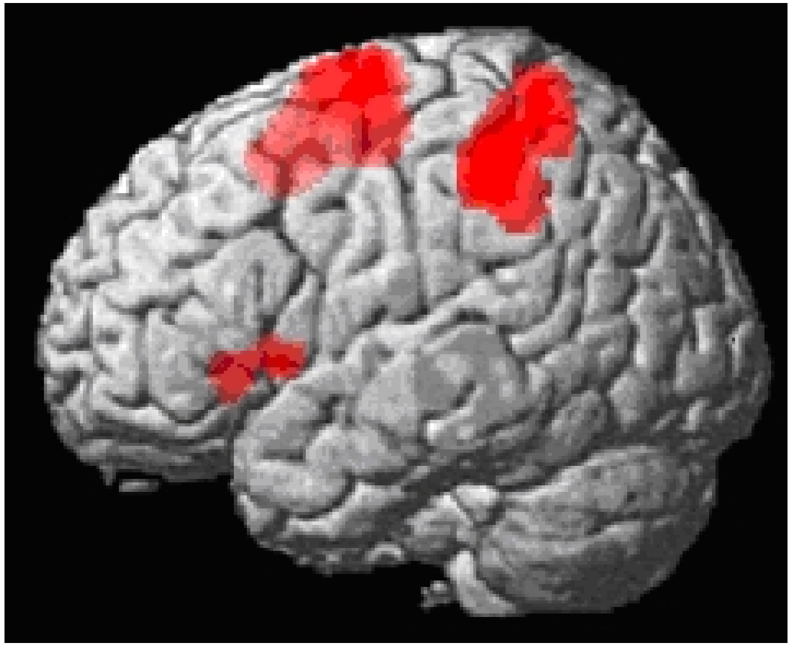
- As a result of various **lesions** (head injury accident, stroke, disease) different brain functions are affected, thus we can infer, which areas of the brain play role in the affected function.

- **Invasive methods**: electrodes inserted into the brain tissue and recording activity of single multiple neurons.

- **Noninvasive methods** (based various physical principles)
  - **EEG** – electroencephalography (recording brain electric activity)
  - **MEG** – magnetoencephalography (recording magnetic activity)
  - **PET** – positron emission tomography
  - **fMRI** – functional magnetic resonance imaging (measures micro-blood flow, which reflects the underlying neural activity)

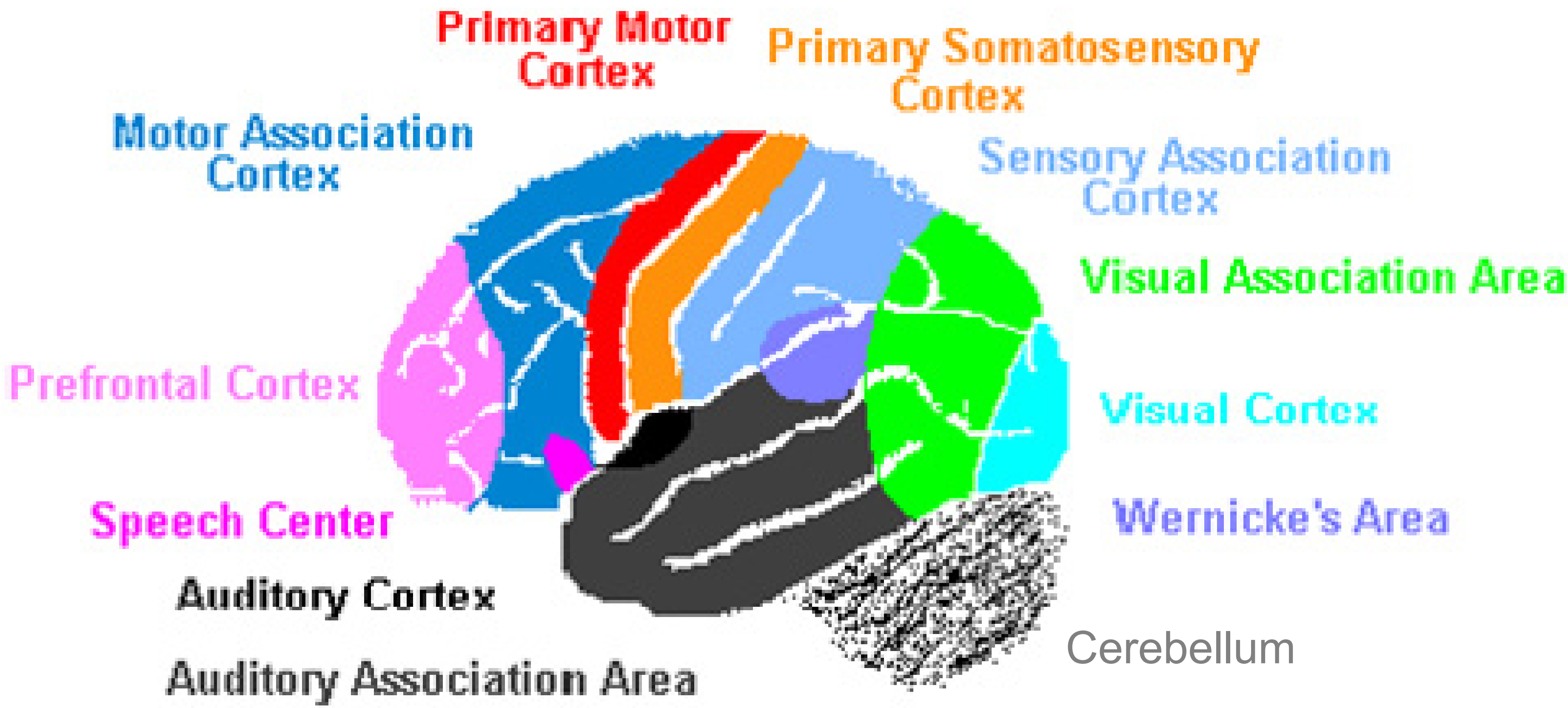
Example: brain activity during motor imagery

- Motor imagery is a mental process during which an individual mentally imagines performing a given action.
- Motor imagery is associated with the specific activation of the neural circuits involved in the planning and execution of actions.
- Motor imagery is now widely used as a technique to enhance motor learning and to improve neurological rehabilitation in patients after stroke.



Picture obtained by functional magnetic resonance imaging or fMRI for short.

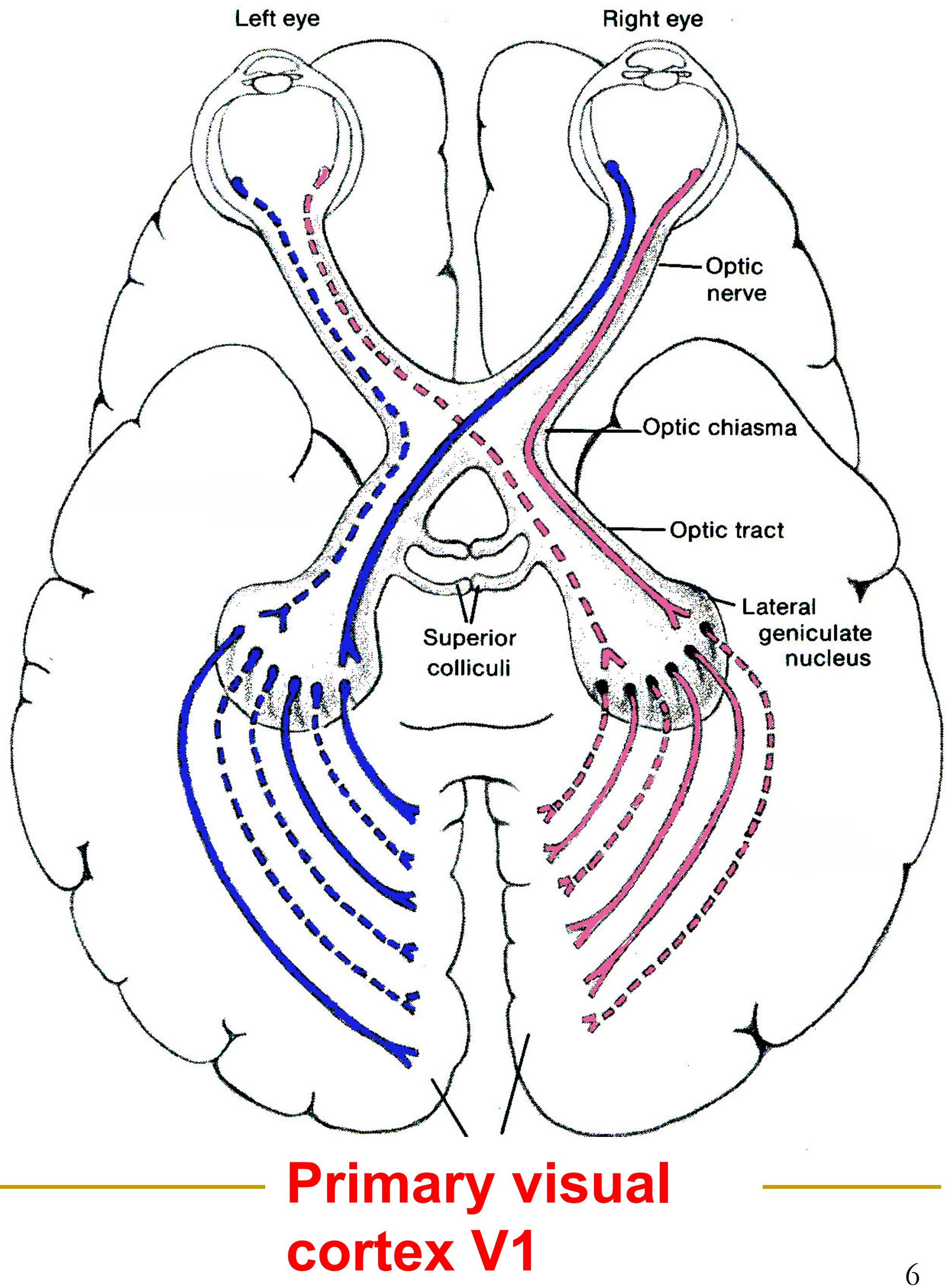
Brain areas and brain functions



Brain areas are specialized. Specialization is genetically determined, but a proper experience must occur early in life to gain full function.

Mammalian visual system: top view

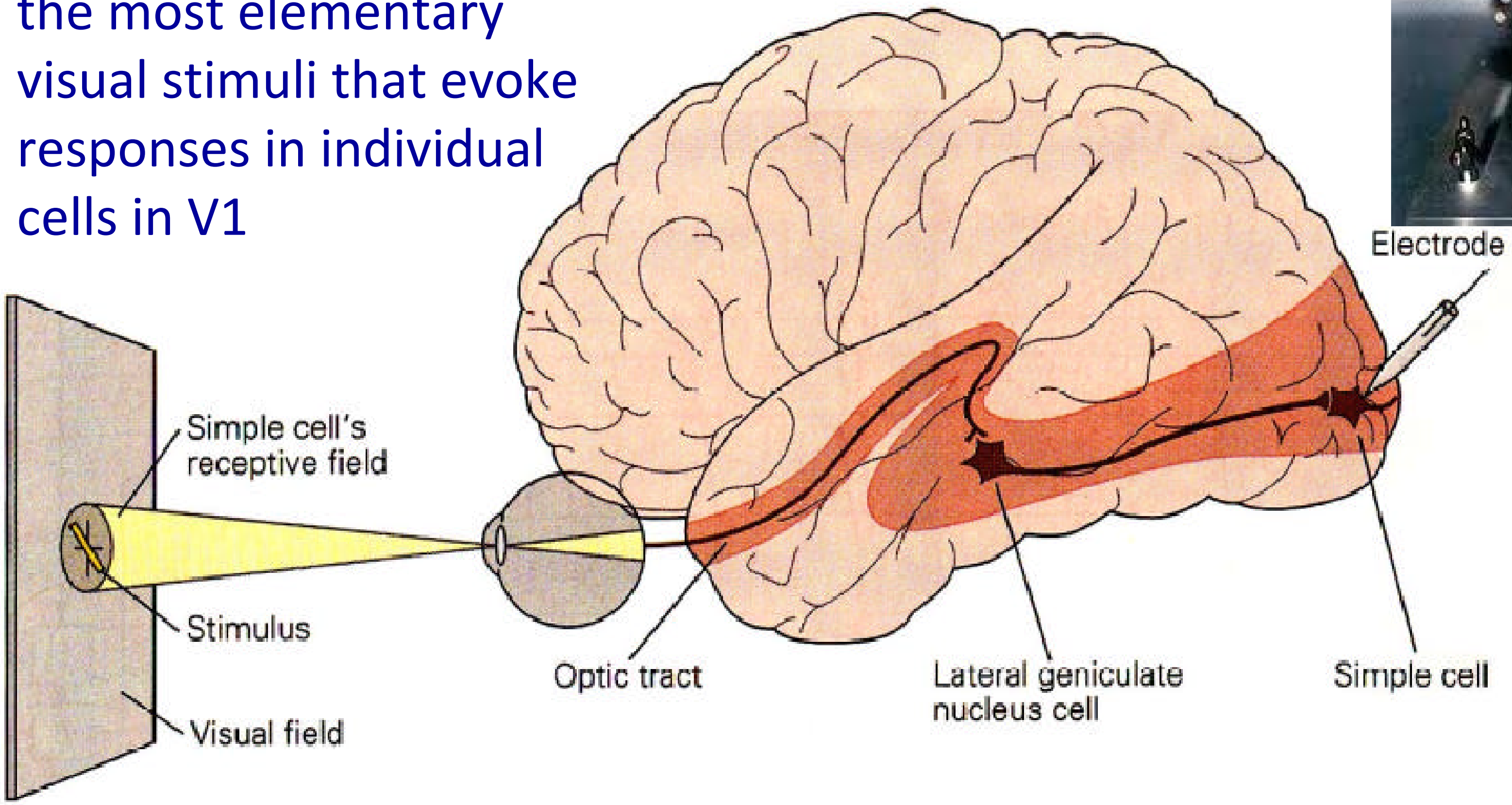
- Visual signals travel from eye to LGN and from there to primary visual cortex V1.
- Information from the left halves of eye retinas goes to the left hemisphere and
- Information from the right halves of eye retinas goes to the right hemisphere.
- There is only one synapse between the eye and cortex in the LGN.



Mammalian visual system: side view

- Free online book by David Hubel: Eye, Brain and Vision.

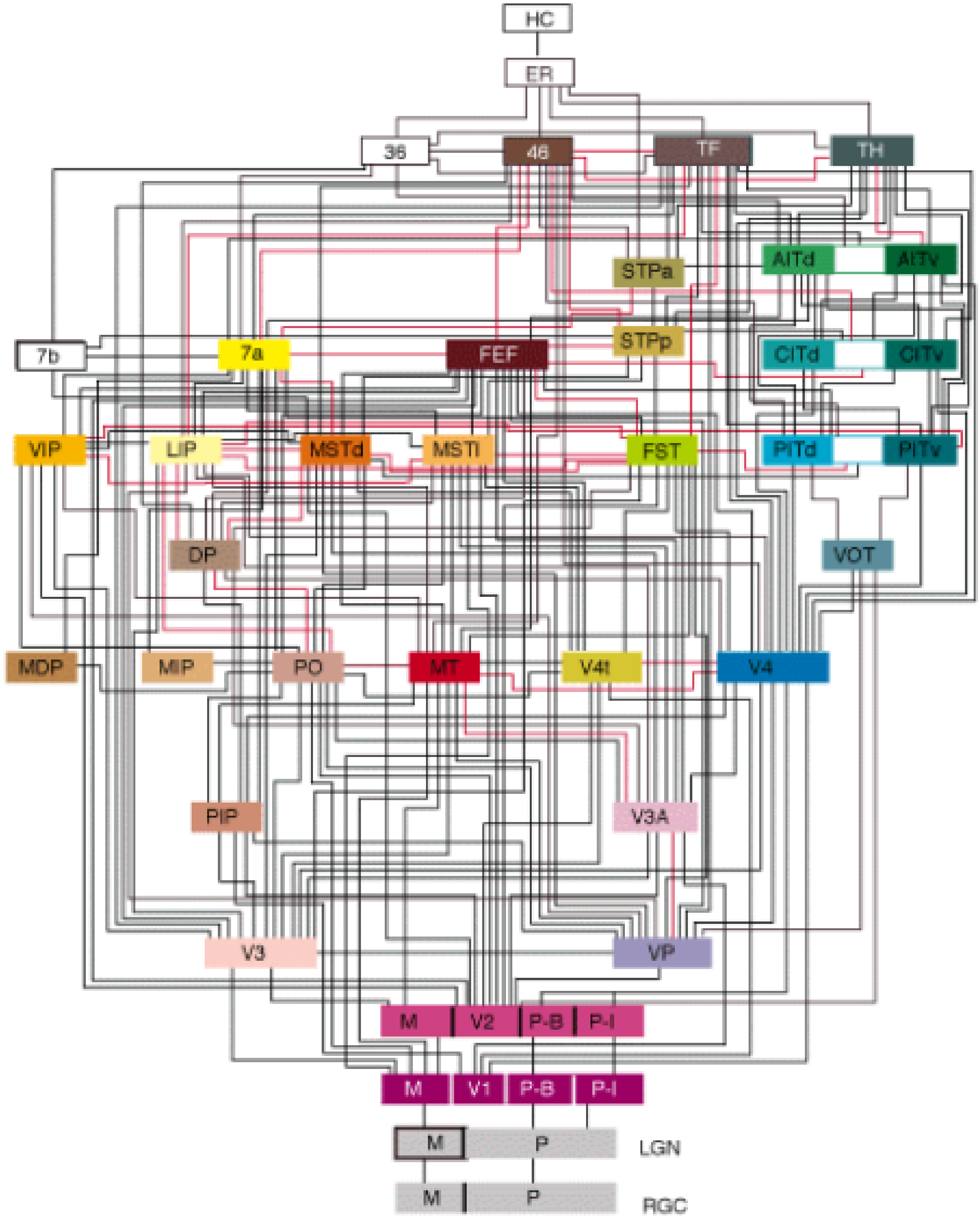
Bar-like visual stimuli are the most elementary visual stimuli that evoke responses in individual cells in V1



- Link: hubel.med.harvard.edu/book/bcontex.htm

Circuit diagram of macaque visual system

- After V1 there are about 30 visual areas that represent/code different features of visual objects (Fellman & Van Essen, 1991).
- These areas are hierachically organised with hundreds of feedforward and feedback pathways between layers.
- It is the same in human brain, i.e. we have as many different cortical areas that process different aspects of visual input.



Ultrafast visual classification of objects

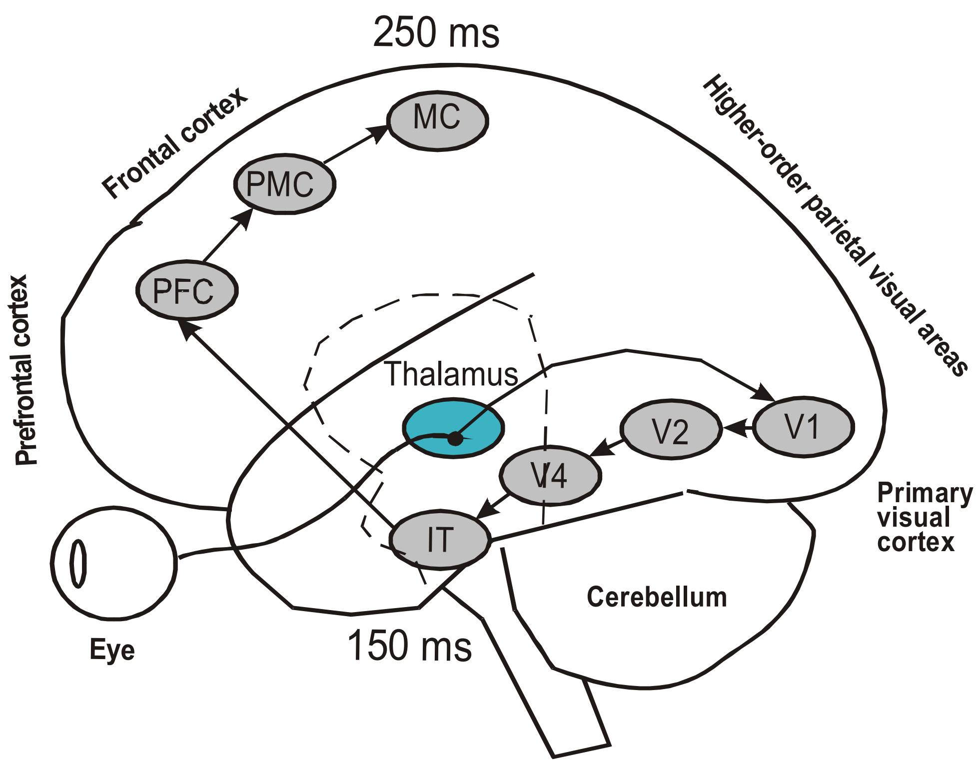
- Simon Thorpe et al. at the University of Toulouse, France, performed an experiment with humans and monkeys, in which subjects were supposed to classify pictures into 2 categories, either an animal category or a non-animal category (Thorpe et al., Science, 1996).

- Hundreds of pictures were shown. Pictures were shown just for 20 ms. In spite of that, humans on average correctly classified the pictures in **94%** cases and monkeys in **91%.**

- Ultra-fast classification did not depend on classes of objects, did not depend on colour, and did not depend on attention or eye fixation.

Brain activity during classification

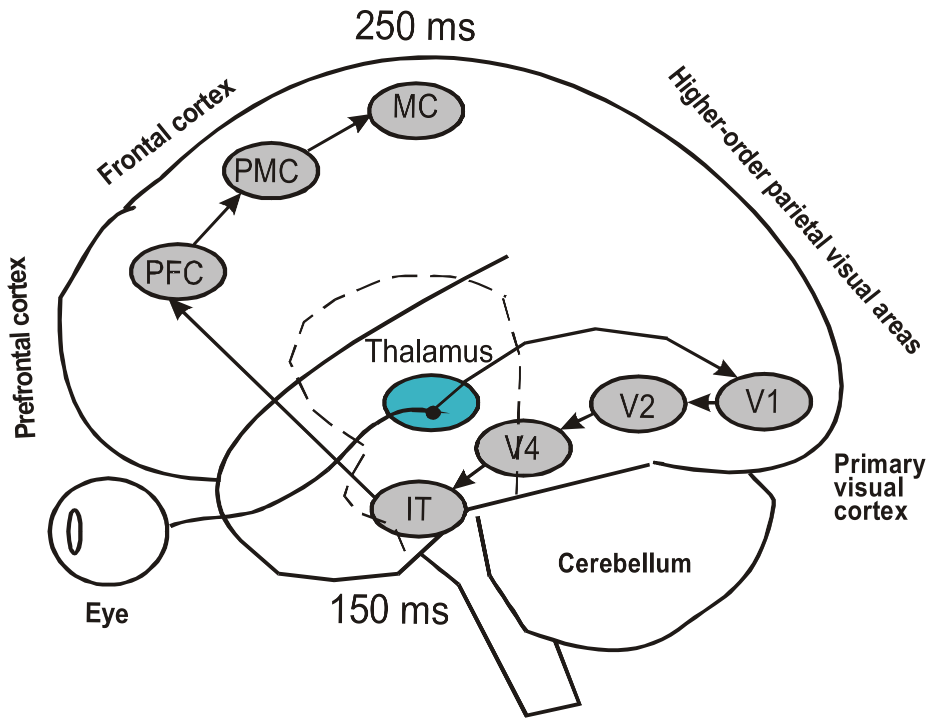
- Reaction time, i.e. time from presentation of picture to pressing the button = 250 ms in humans, on average.
- Activity in the inferotemporal (IT) cortex occurred on average after 150 ms, so the preparation and execution of motor response took on average 100 ms.
- In monkeys, times were shorter by about 80 ms (smaller brains).



Neurons use few spikes to communicate

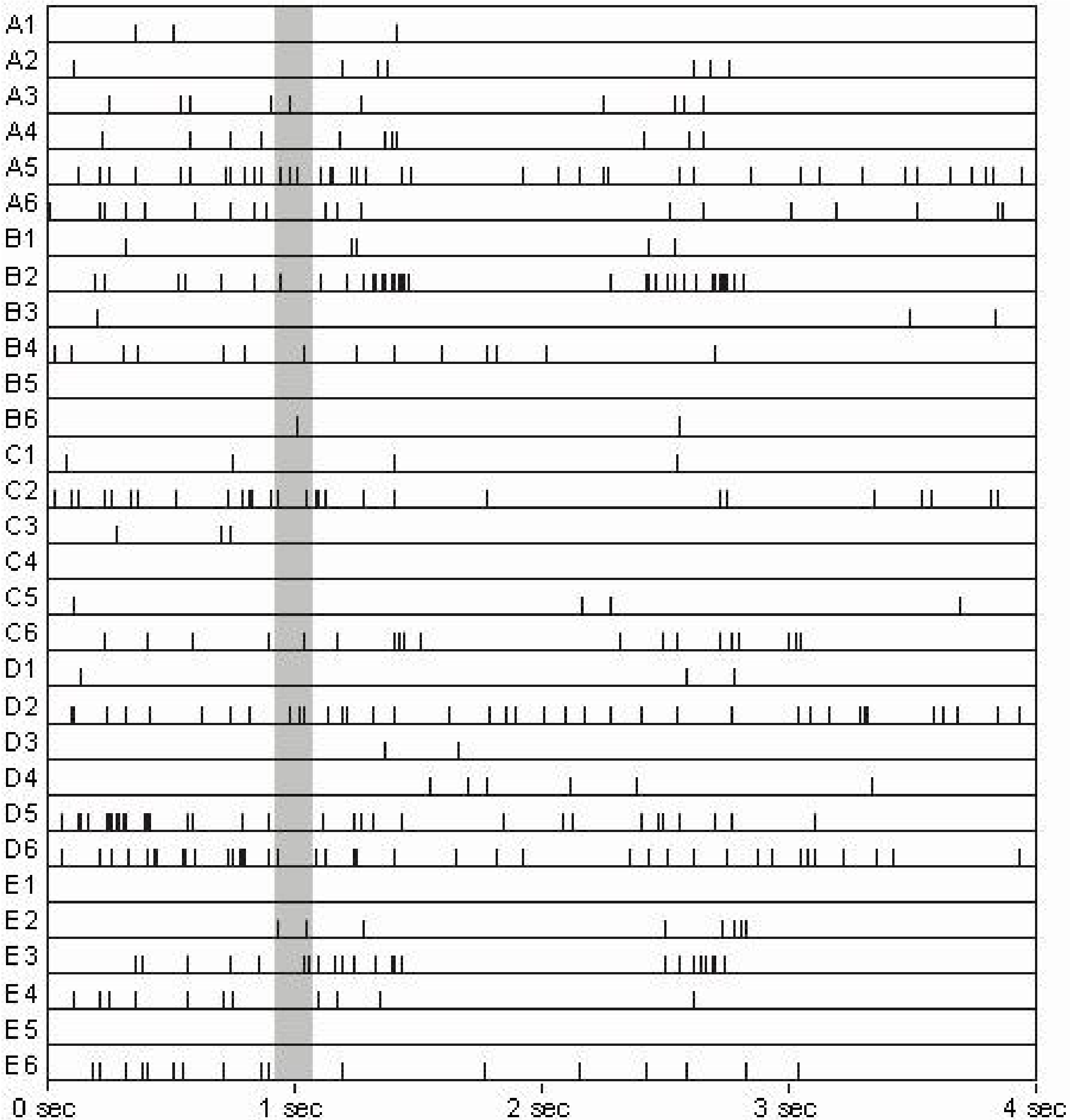
- Projected image stimulates retina for 20 ms. In about 80 ms, thalamus responds. Thalamic neurons activate neurons in the primary visual cortex (V1). Then, activation proceeds to and through higher-order visual areas, V2, V4 and IT, where activity appears after 150 ms.

- Thus (150-80) / 4 areas = 17.5 ms per area. Even if neurons fired with frequency = 100 Hz, this would mean that each one fired 1-2 spikes within this interval…



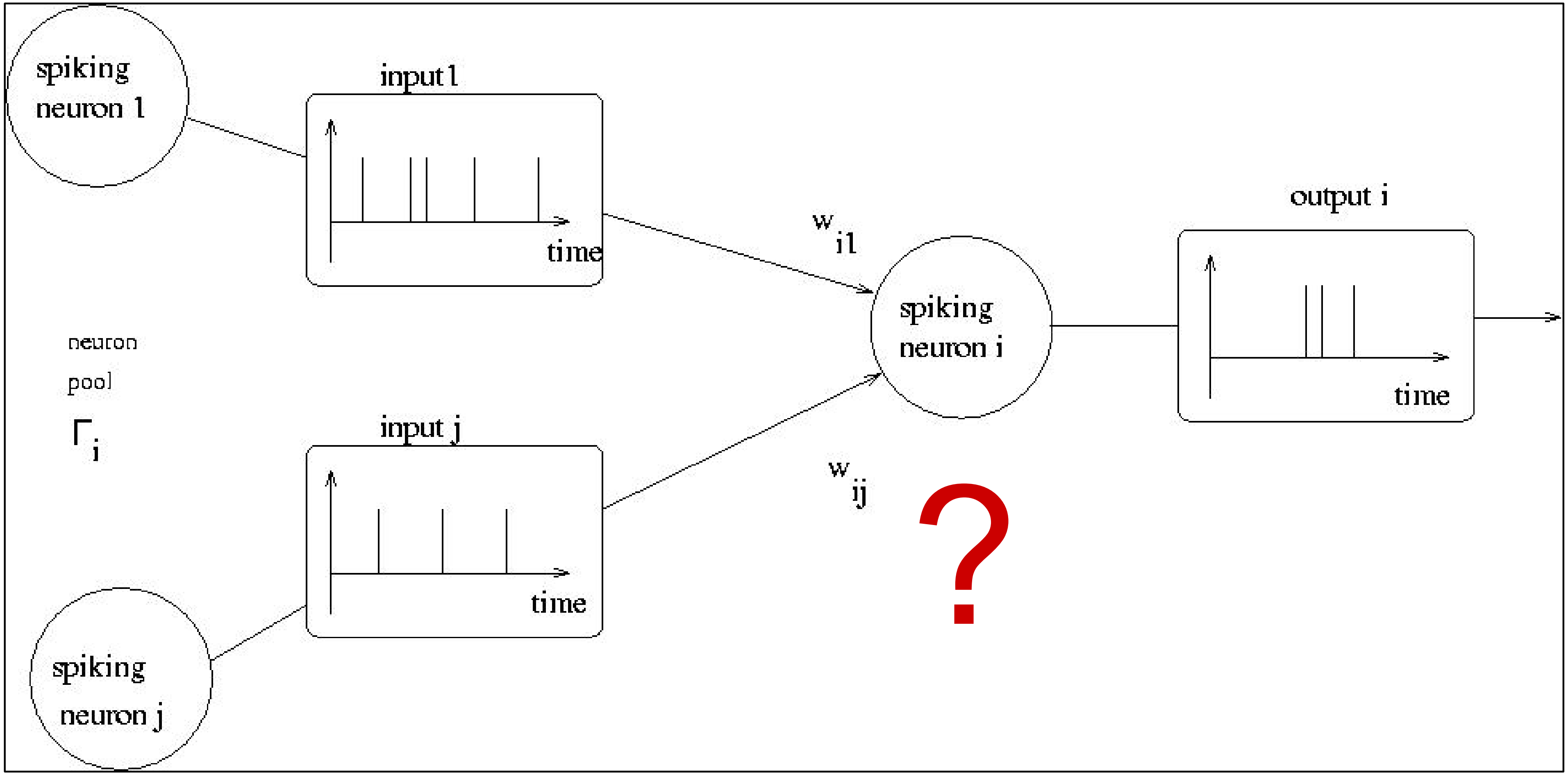
Neurons can use few spikes to solve complex tasks

- Simultaneous recordings of the firing times of 30 neurons from monkey visual cortex [Krüger and Aiple, 1988].
- Each spike is denoted by a vertical bar, with a separate row for each neuron.
- An interval of 150 msec is shaded. This time span is known to suffice for the completion of some very complex computations.

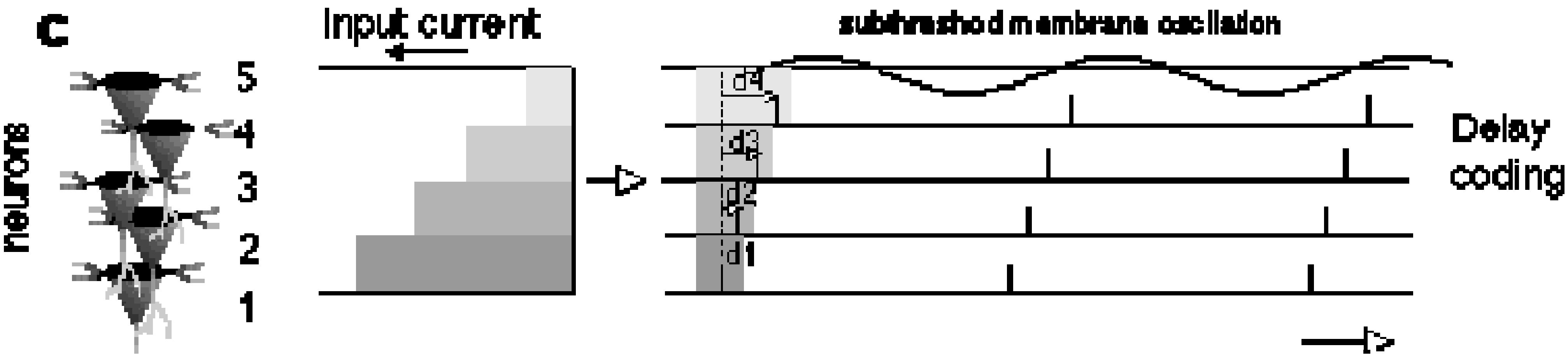


How is the information coded in the brain?

- What is the neural code (which links stimulus and response) that is used by the brain to send information from one neuron to another?



Spike delay code

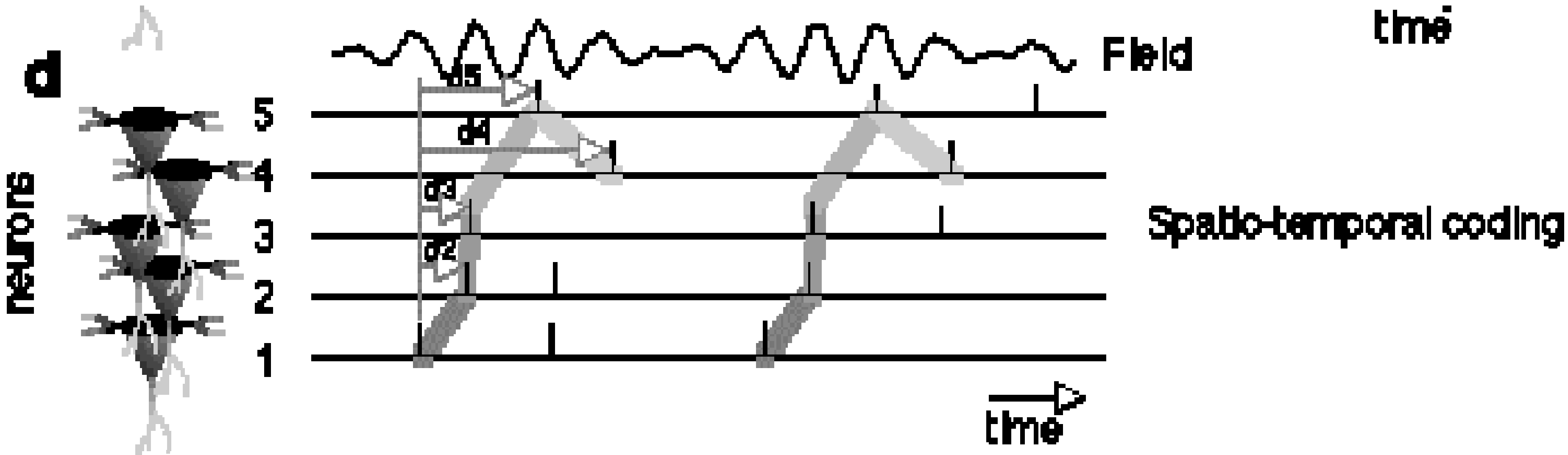


- Delay coding is based on the idea that neurons will respond to more energetic input signals by generating a spike earlier, and that this generated spike will arrive at the downstream neuron earlier than other spikes and will thus have a higher impact or 'ranking' relative to later incoming spikes.

- Another variant of the spike delay code is that information is encoded in the phase relationship between the cell's firing activity and the underlying rhythmic oscillations of the whole population of neurons.

Image source: betarhythm.blogspot.co.nz/2009/04/

Spatio-temporal coding

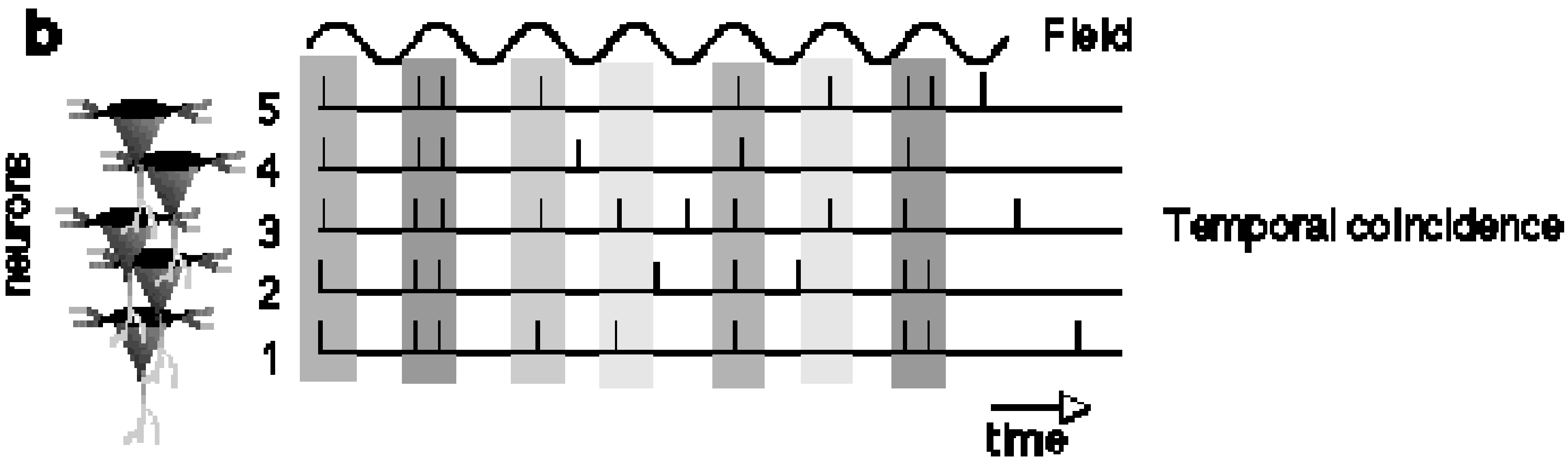


- Neurons respond to the same stimulus always with the same specific spatio-temporal pattern of spikes.

- Different stimuli evoke different spatio-temporal patterns of spikes in neuronal populations.

Image source: betarhythm.blogspot.co.nz/2009/04/

Synchrony code (coincidence detection)

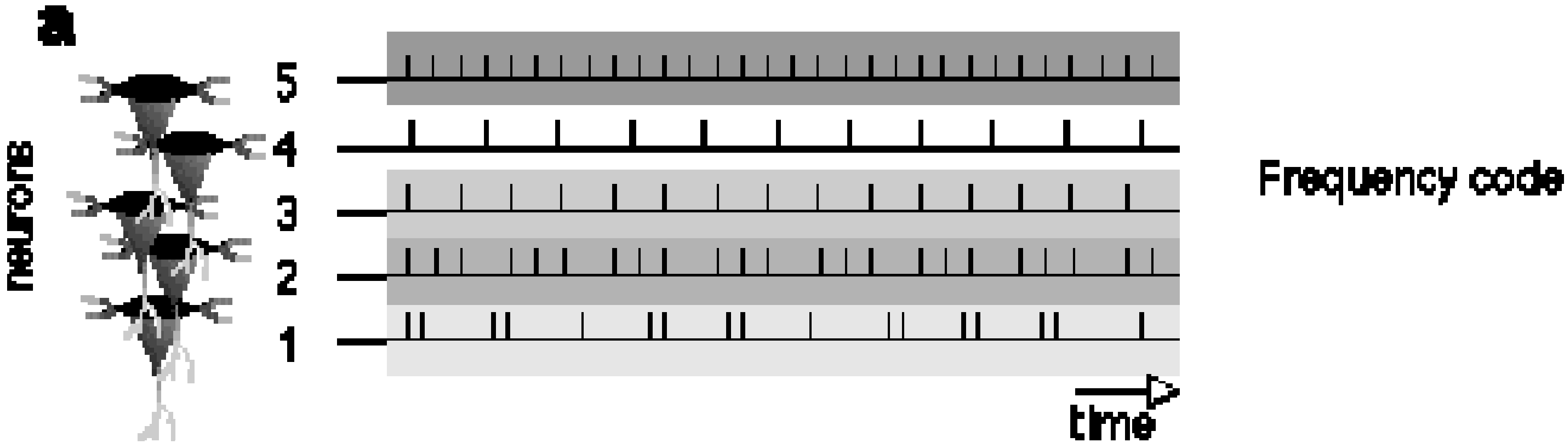


- Features that are represented by particular populations of neurons will synchronize the firing of these neurons if the features belong to the same object (binding by synchrony).

- Neurons act as coincidence detectors thus responding to and strengthening inputs that are active at the same time.

Image source: betarhythm.blogspot.co.nz/2009/04/

Rate or frequency code



- This hypothesis is based on the idea that a feature of an object is coded by the frequency of spikes. In the figure, each of the five neurons codes a different feature of an object.

- Each neuron sums inputs: it will only reach the firing threshold when the total number of spikes it receives exceeds some value.

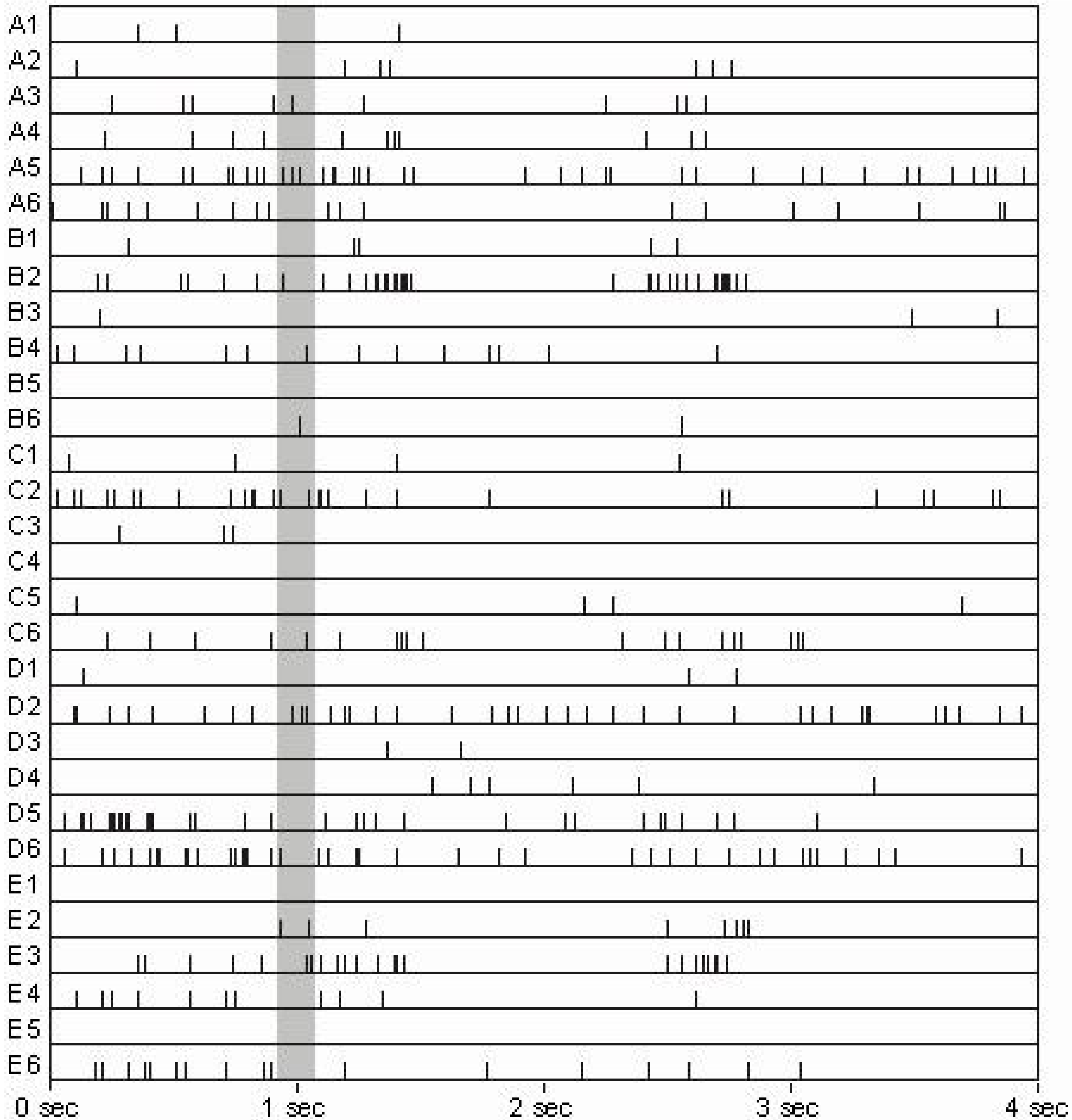
Image source: betarhythm.blogspot.co.nz/2009/04/

Modelling spiking neural networks (SNN)

- To study SNN we need some simple yet accurate models of input-output functions of biological neurons.

- There are a number of such models available, each being a more or less drastic simplification of the original complexity of biological neurons.

- These simple abstract models are known as **integrate & fire neurons**.

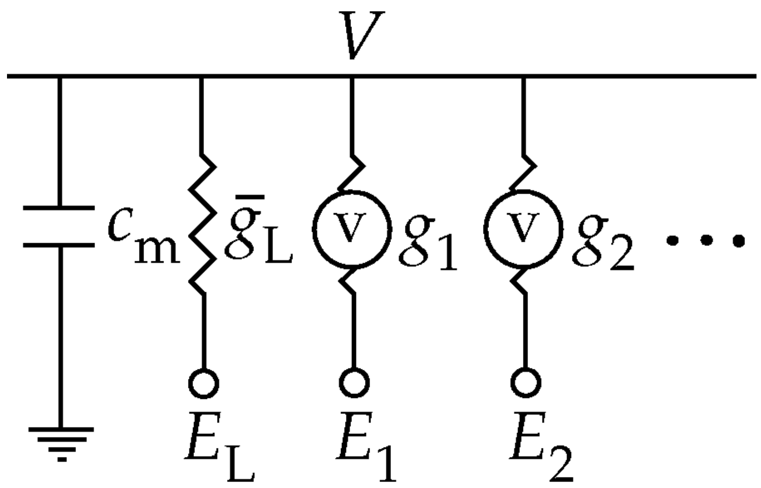


Integrate and fire (I&F) models

- Soma plus dendrites are modelled as a single compartment.
- Action potentials occur when the membrane potential V reaches a firing threshold θ.
- Leaky I&F: after firing, the membrane potential is reset to the value of resting potential V_0.
- I&F can be modelled at various levels of rigour depending on simplifying assumptions used.

Single compartment model

Electric scheme equivalent to one integrate and fire (I&F) neuron model



- Rate of change of the membrane potential V is proportional to the electric current entering into neuron;
- By convention capacitance current is 'plus' while membrane current is 'minus':

$$c_m \frac{dV}{dt} = -i_m$$

Membrane current

- Membrane current i_m is the sum of leakage current and all the currents flowing through all the currently open ion channels per unit area of the membrane (where k = Na, K, and Cl):

$$i_m = i_L + \sum_k i_k$$

- Each current component is equal to driving force (difference between the membrane potential V and the equilibrium potential E_k) multiplied by the corresponding ion channel *conductance* g_k:

$$i_k = g_k (V - E_k)$$

$$i_L = \overline{g}_L (V - E_L)$$

"Passive" integrate & fire model

Simplest model is a passive model, which assumes NO voltage-gated conductance. Therefore:

$$c_m \frac{dV}{dt} = -\bar{g}_L (V - E_L) + I_e$$

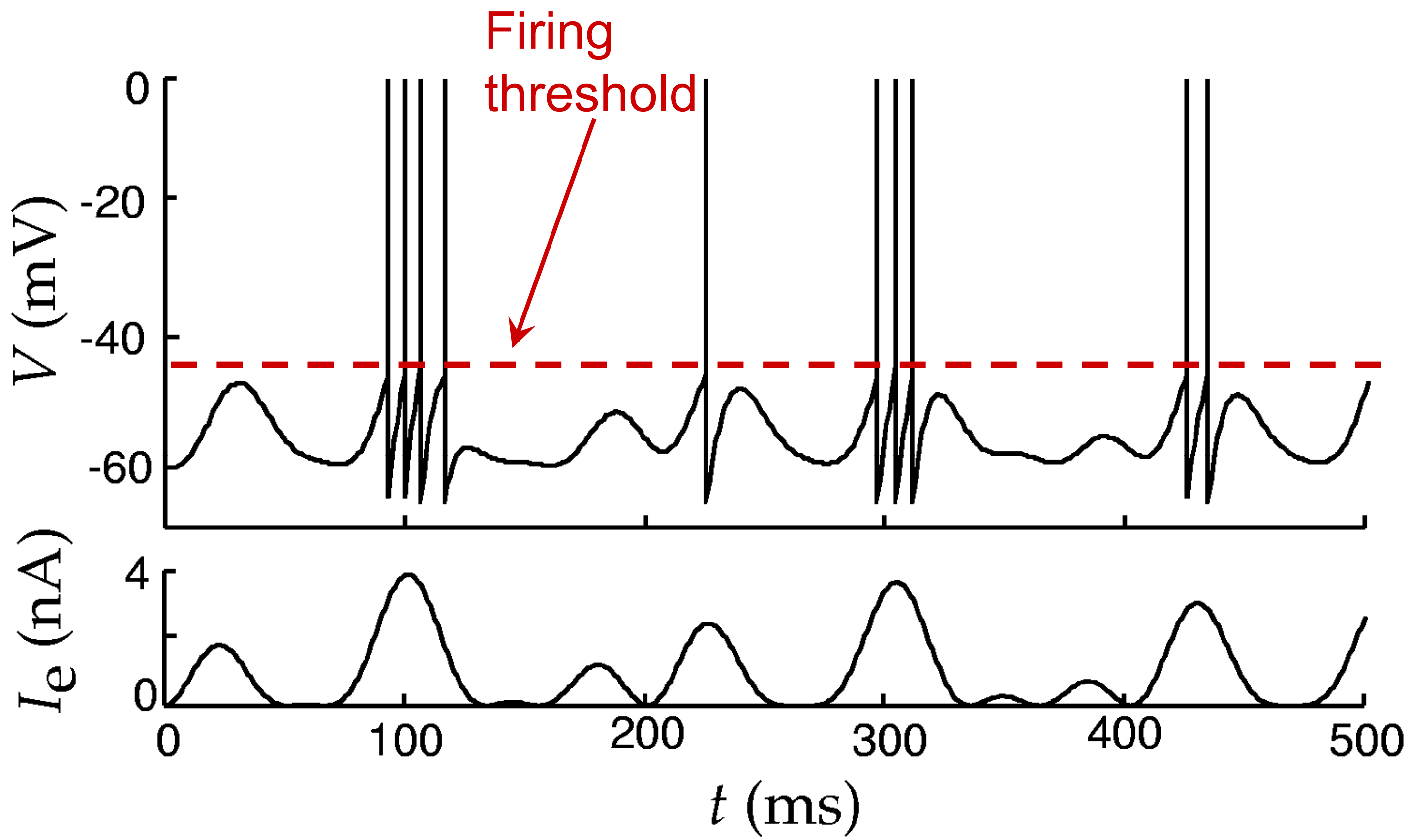
Where all synaptic currents are denoted by I_e. Multiplying through by $r_m = 1/g_L$ we get the so-called **cable equation**:

$$\tau_m \frac{dV}{dt} = E_L - V + r_m I_e$$

If $V \geq \theta$ a spike is fired. The spike HH process is not explicitly modelled.

If $I_e = 0$, V decays exponentially to E_L with time constant $\tau_m = c_m r_m$

“Passive” integrate & fire model



Spike waveforms are simply superimposed upon underlying waveform of membrane potential

Differential equation for V can be solved numerically for different time course of synaptic current I_e as in the figure above.

Deterministic versus stochastic neuron model

- Deterministic: the philosophical doctrine that every state of affairs is the inevitable consequence of preceding states of affairs.
- Thus we can calculate the exact value of membrane voltage V based on injected current I_e, initial conditions and values of model parameters.
- In addition, it is not only deterministic but also predictable.
- However, in neural system (brain) there are many sources of noise.
- Sources of noise are: random opening and closing of ion channels, random release of neurotransmitter, spontaneous firing of some types of neurons, and as a result of all this, an ongoing spontaneous spiking activity in the neural networks (sometimes called background activity).

Deterministic versus stochastic neuron model

- Deterministic solution (forward Euler) of cable equation:

$$V(t+\Delta t) = V(t) + \frac{dV}{dt}\Delta t$$

- To incorporate noise into the model we can add a stochastic term to the membrane equation, i.e.:

$$V(t+\Delta t) = V(t) + \frac{dV}{dt}\Delta t + \sigma \Delta W(t)$$

- Where Δt is the time step of numerical integration and ΔW(t) is a random variable drawn from a Gaussian (normal) distribution with a zero mean and variance Δt, and σ parametrises the level of noise.

Deterministic versus stochastic neuron model

- Another way to incorporate noise into the model is to add a stochastic term to the firing threshold (with the same meaning of symbols), i.e.:

$$\theta(t + \Delta t) = \theta(t) + \sigma \Delta W(t)$$

- It is still a deterministic model: if $V \geq \theta$, the spike is **always** fired.

- Thus a true randomness can be modelled by making the spiking itself probabilistic, i.e. if $V \geq \theta$, the spike is generated with certain probability, which is a function of ΔV, i.e. P = 1/(1+exp(–ΔV)), where $\Delta V = V \geq \theta$, or the spiking can be entirely random, i.e.

$$P\{n \text{ spikes during } \Delta t\} = e^{-r\Delta t} \frac{(r\Delta t)^n}{n!}$$

Izhikevich's model of spiking neuron

- reproduces firing behavior of many types of cortical neurons. It combines the biologically plausibility of Hodgkin-Huxley-type dynamics and the computational efficiency of integrate-and-fire neurons. (http://www.izhikevich.org/publications/spikes.htm)

$$\dot{v} = 0.04v^2 + 5v + 140 - u + EPSP$$

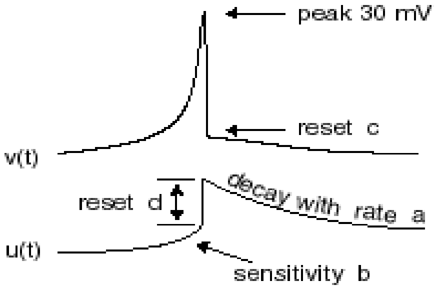
$$\dot{u} = a(bv - u)$$

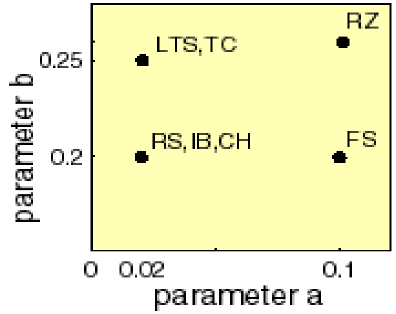
$$\text{if} \quad v \geq \text{AP}, \quad \text{then} \begin{cases} v \leftarrow c \\ u \leftarrow u + d \end{cases}$$

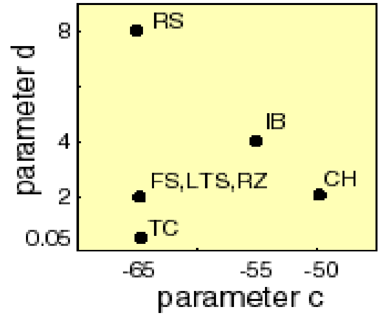
Simple spiking model of Izhikevich

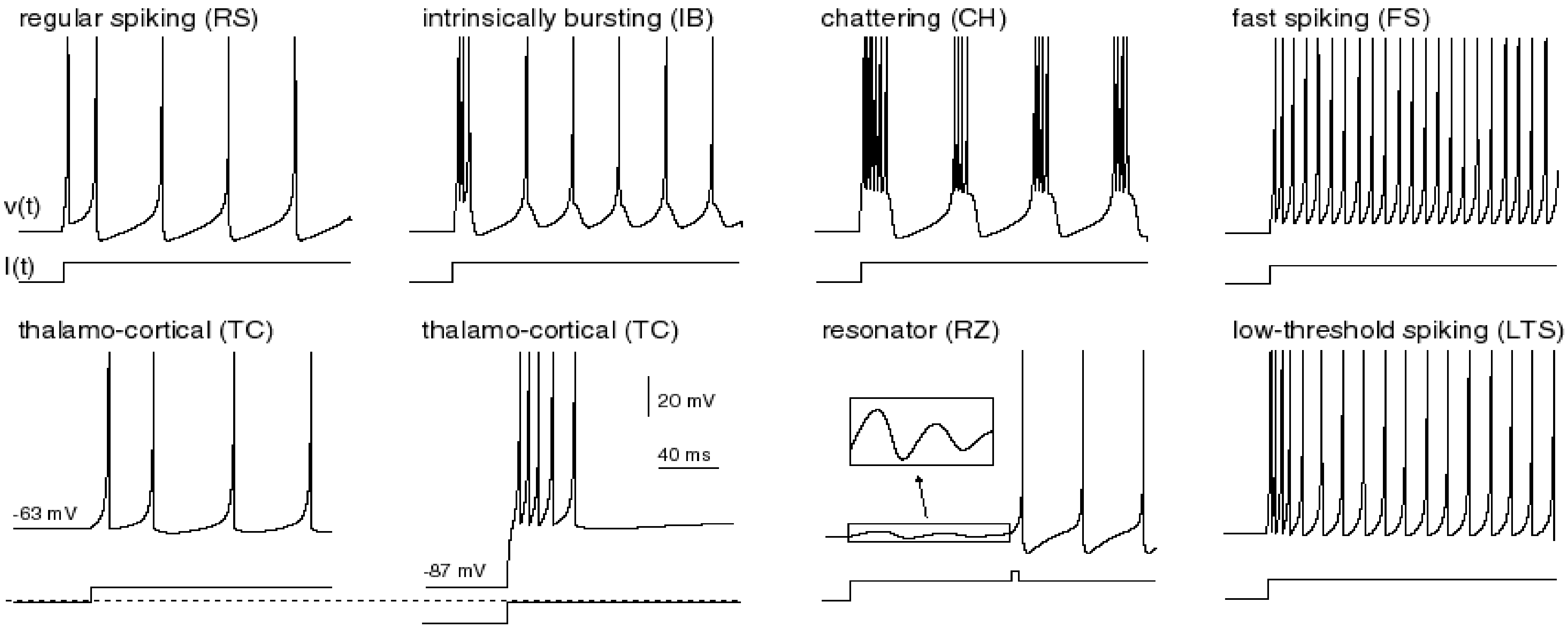
$v' = 0.04v^2 + 5v + 140 - u + I$
$u' = a(bv - u)$

if $v = 30$ mV,
then $v \leftarrow c, \quad u \leftarrow u + d$









Eugene Izhikevich's book & company

- Author: Dynamical System in Neuroscience, MIT Press, 2007: www.izhikevich.org/publications/dsn.pdf
- Director of the Brain Corporation: http://www.artificialbrains.com/brain-corporation, the goal of which is "to build artificial brains for commercial applications".
- The **vision project** aims to recreate the mammalian visual system in a large-scale model. The **motor control project** is developing spiking models of action selection, reinforcement learning, and motor control for robots.
- E.I. already built a large-scale simulation of the human brain. The model contained 1 million spiking neurons and 500 million synapses. It represented 300 x 300 mm of thalamo-cortical surface and nuclei. 1 s of simulation took 1 m on a Beowulf cluster of 27 processors running at 3 GHz each.

How do we fix the model parameter values?

- Step 1: Fix the known parameters (e.g. V_0, E_L, etc) and make educated guesses for the remaining unknown parameter values.
- Step 2: Use the model to simulate experiments, producing model data.
- Step 3: Compare the model data with experimental data.
- Step 4: Adjust one or more parameter values and repeat from Step 2 until the simulated data sufficiently matches experimental data.
- Step 5: Use the model to simulate new experiments not used in the steps above and compare the resulting model data with the new experimental data to verify that the chosen parameter values are robust.