



## Spike transmission between electrically coupled sensory neurons is improved by filter properties

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#### Motivation: Neuromorphic circuits

"The human brain is the most energy-efficient processor around, so it is natural for hardware developers to try to mimic it.

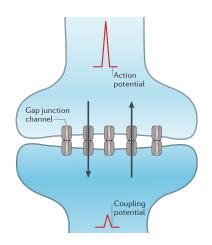
An approach called neuromorphic computing aims to do just that, with technologies that seek to simulate communication and processing in a biological nervous system."

Big data needs a hardware revolution.

Nature editorial, 6th Feb 2018

### Electrical synaptic transmission in biological neural networks Main properties

- Bidirectional
- ► Without delay
- Reliable: No transmission failures
- Analogic



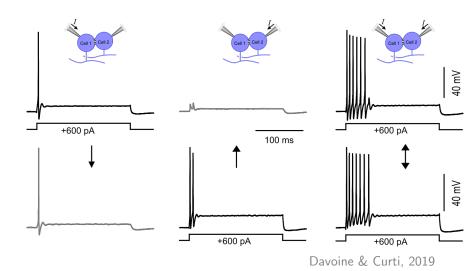
# Some emerging properties of electrical synapses in the nervous system

- Synchronization
- Lateral inhibition and excitation
- Coincidence detection
- Signal-to-noise ratio improvement

#### Coincidence detection

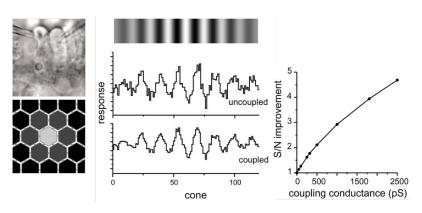
Sensory neurons from the mesencephalic trigeminal nucleus

Coincident inputs increase the effective input resistance in coupled neurons



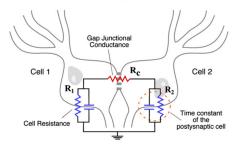
### Example: Signal-to-noise ratio improvement in the retina Cone photoreceptors

The cones of the retina have intrinsic noise, due to the phototransduction process. Electrical synapses between them attenuate the noise, without affecting the partially shared common visual input.

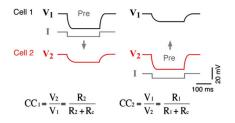


### Strength of electrical synaptic transmission DC signals

A Determinants of the strength of electrical transmission



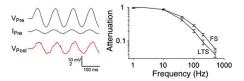
B Steady state Coupling Coefficient (CC):



#### Strength of electrical synaptic transmission

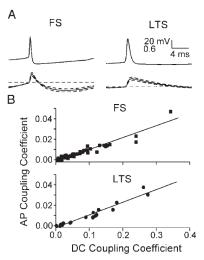
Frequency dependence for cortical neurons

Electrical synapses between Fast Spiking (FS) and Low-Threshold Spiking (LTS) cortical neurons act as lowpass filters



### Efficacy of electrical synaptic transmission Spikes vs DC

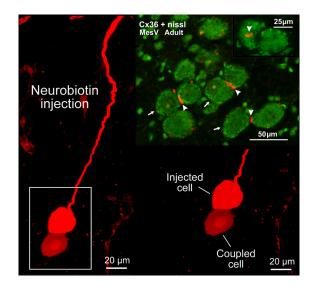
Electrical synapses transmit DC signals more efficiently than spikes in FS and LTS neurons.



Modified from Gibson et al., 2005

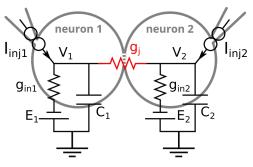
### Sensory neurons from the mesencephalic trigeminal nucleus

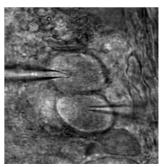
Neurons coupled in pairs, through their somas.



### Patch-clamp whole cell electrophysiological recordings

It is possible to record and stimulate electrically coupled cells, recording their membrane potentials and injecting currents.

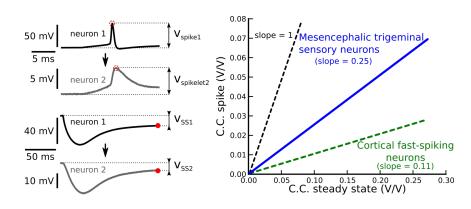




#### Efficacy of electrical synaptic transmission

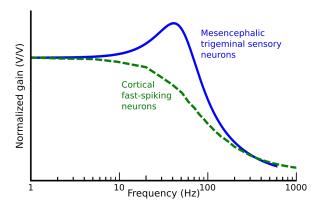
Comparative between the attenuation of action potentials and DC signals

Sensory neurons from the mesencephalic trigeminal nucleus are more efficient at spike transmission than FS neurons.



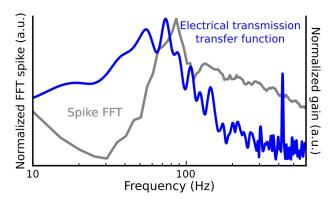
### Filter properties of electrical synaptic transmission

The enhanced efficacy of spike transmission is due to the bandpass properties of electrical synaptic transmission in sensory neurons.



#### Frequency content of spikes

The bandpass filter is better suited to the frequency contents of the spikes.



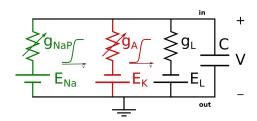
# How these sensory neurons improve their efficacy in spike transmission?

### Reduced electrical model of a sensory neuron

First, we built a simplified model of one sensory neuron:

Operating close to the Resting Membrane Potential (RMP = -55 mV; set point of the neuron) the main ion currents are the leak  $I_L$  and:

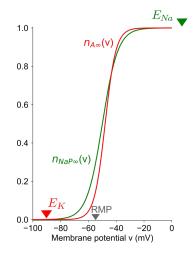
- ► Persistent sodium I<sub>NaP</sub>
- $\triangleright$  A-type potassium  $I_A$



### Reduced electrical model of a single sensory neuron

$$\begin{cases} \frac{dv}{dt} &= \frac{1}{C} \left( -I_L - I_{NaP} - I_A \right) \\ I_L &= g_L \left( v - E_L \right) \\ I_{NaP} &= \overline{g}_{NaP} \cdot n_{NaP\infty} \left( v - E_{Na} \right) \\ I_A &= \overline{g}_A \cdot n_A \left( v - E_K \right) \\ \frac{dn_A}{dt} &= \frac{n_{A\infty} - n_A}{\tau_A} \end{cases}$$

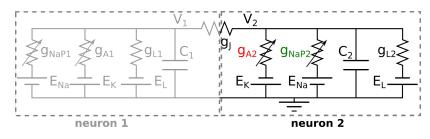
where the asymptotic activation curves  $n_{NaP\infty}$  and  $n_{A\infty}$  are sigmoid functions of v and  $\tau_A = 3.4$  ms.



#### Reduced model of electrical transmission

Equivalent circuit

To study synaptic transmission close to the resting membrane potential, two simplified neuron models were coupled through a linear conductance  $g_J$ , which represents the electrical synapse.



### Reduced model of electrical transmission Transfer function

Bandpass behavior in control conditions:

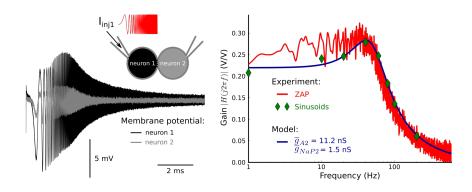
$$H(j\omega) = \frac{g_J(1+j\omega\tau_A)}{(j\omega)^2 \tau_A C_2 + (C_2 + \Gamma_\infty \tau_A)j\omega + \Gamma_0}$$

where  $\Gamma_{\infty}$  and  $\Gamma_{0}$  depend on the ion conductances, the activation curves  $n_{NaP\infty}$  and  $n_{A\infty}$  and their voltage derivatives.

### The reduced model explains the filter properties of electrical transmission

#### Control conditions

The membrane potentials of both neurons were recorded while injecting ZAP (chirp) or sinusoidal currents to one of them. The transfer function was obtained as the ratio of their FFT.



# The reduced model explains the filter properties of electrical transmission

 $I_{NaP}$  and  $I_A$  blocked

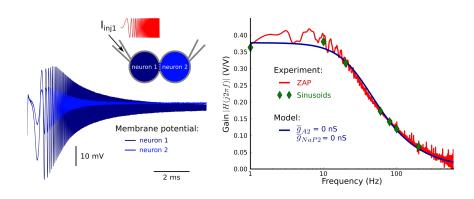
If  $I_{NaP}$  and  $I_A$  are blocked, the filter becomes lowpass:

$$H_{\text{passive}}(j\omega) = \frac{g_J}{g_J + g_{L2} + j\omega C_2}$$

## The reduced model explains the filter properties of electrical transmission

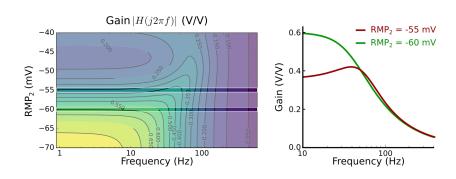
 $I_{NaP}$  and  $I_A$  blocked

When  $I_{NaP}$  and  $I_A$  are pharmacologically blocked, the electrical synapse becomes a lowpass filter.



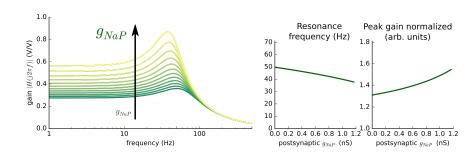
# Bandpass behavior is displayed at the resting membrane potential of the neuron

The filter properties depend on the set point of the neuron. If it changes (as may happen in pathological conditions), the bandpass turns into a lowpass.



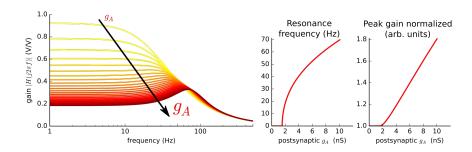
### The persistent sodium current $I_{NaP}$ amplifies the gain

 $I_{NaP}$  acts as an amplifying mechanism, without modifying the shape of the filter.



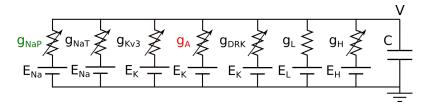
# The A-type potassium current $I_A$ is responsible for the bandpass behavior

 $I_A$  introduces the resonance. DC signals become more attenuated than faster ones, like the spikes.



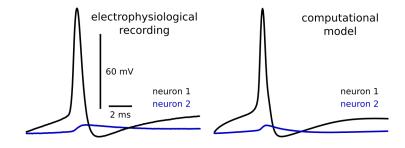
### Realistic neuron model from electrophysiological recordings

We added more ion currents to the reduced model, in order to have a realistic model with spikes.



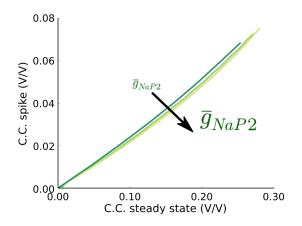
### Realistic neuron model from electrophysiological recordings

The parameters of the realistic model were obtained by fitting electrophysiological recordings, using an evolutionary multi-objective optimization algorithm.



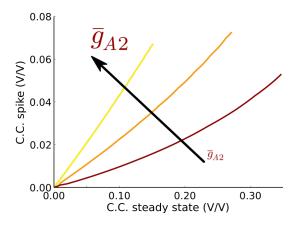
### I<sub>NaP</sub> doesn't change spike transmission efficacy

 $I_{NaP}$  amplified the gain of the filter in the whole frequency range: DC signals and spikes are transmitted with the same relative efficacy.



### 1<sub>A</sub> improves spike transmission efficacy

According to the filter analysis,  $I_A$  increased the relative attenuation of DC signals vs faster ones. Thus, it enhances the efficacy of the transmission of spikes vs steady-state.



#### Conclusions

► Electrical synapses endow biological neural networks with rather sophisticated computational capabilities.

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- Spike (digital) transmission can be selectively improved by voltage-dependent resonant currents, like I<sub>A</sub>.
- Amplifying currents such as  $I_{NaP}$  boost the gain, to compensate for the attenuation caused by resonant currents.

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