Supplementary Material to the paper

Modulation of septo-hippocampal theta activity by $GABA_A$ receptors: An experimental and computational approach

Mihály Hajós, William E. Hoffmann, Gergõ Orbán, Tamás Kiss, Péter Érdi

Hippocampal CA1 pyramidal cell model

The model is a modified version of the model described in Varona et al. (2000). The model is a 256 compartmental, detailed morphological model of a CA1 pyramidal cell, where the somatic compartment is spherical, all other compartments are cylindrical with different anatomical length. The total effective area of the neuron was 66800 μm^2. For a compartment with membrane potential $V_{m,i}$ the discretized version of the cable equation holds:

$$C_{m,i}\, dV_{m,i}/dt = -\Sigma I_{i,j} - I_L - I_{syn} + I + R_{i,i+1}(V_{m,i+1} - V_{m,i}) + R_{i,i-1}(V_{m,i-1} - V_{m,i}), \quad (1)$$

where $C_{m.i}$ is the membrane capacitance of the ith compartment, $R_{i,j}$ is the cytoplasmic resistance between the ith and the jth compartments, $I_{i,j}$ represents the jth intrinsic current in compartment i, I_L is the leak current, and I_{syn} is the synaptic current.

The tonic depolarising current was set to a constant level, but the level was varied from cell-to-cell, and was picked form a Gaussian distribution. Width of the Gaussian was in the range of 0% up to 10% relative to the mean level (default 5%). Mean level of tonic depolarising current was between 500 and 700 pA (default was 600 pA).

Membrane resistance, axial resistance, membrane capacitance and reversal potential of the leakage current in the model were R_m=7.0 Ωm^2, $R_{i,j}$=1.5 Ωm for all i,j pairs and C_m= 0.75 $\mu F/cm^2$, E_l= –67 mV, respectively. Values of R_m and C_m at the dendritic compartments were compensated to take into account spine area: values varied in the range R_m=4.59 Ωm^2 and C_m= 1.144 $\mu F/cm^2$ R_m=5.6 Ωm^2 and C_m= 0.937 $\mu F/cm^2$, respectively along the apical dendritic region with increasing distance from the soma and were uniformly set to R_m=4.59 Ωm^2 and C_m= 1.144 $\mu F/cm^2$, respectively in the basal dendritic region.

Active ionic channels were described (Warman et al. 1994) mostly using the Hodgkin-Huxley formalism. V_m in the followings denotes transmembrane potential in a given compartment, E_X and g_X are the reversal potential and maximal ionic conductance for ion type X. The characters [*m*, *h*, *s*, *r*, *c*, *d*, *q*, *u*, *a*, *b*, *n*, *l*] describe gating variables, which are described by the equation

$$dx/dt = \phi_x[\alpha_x(V)(1 - x) - \beta_x(V)x] = \phi_x[x_\infty(V) - x]/\tau_x(V). \quad (2)$$

The sodium (Na) channel is described by the following set of equations:

$I_{Na} = g_{Na}\, m^3 h\, (V_m - E_{Na})$ (3.a)

$\alpha_m = -3.48 \cdot 10^3\, (V_m - 11) / \{\exp [(V_m - 11) / -12.94] - 1\}$ (3.b)

$\beta_m = 0.12 \cdot 10^3\, (V_m - 5.9) / \{\exp [(V_m - 5.9) / 4.47] - 1\}$ (3.c)

$\alpha_h = 3 / \exp[(V_m + 80) / 10)]$ (3.d)

$\beta_h = 12 / \{\exp[(V_m - 7.7) / -27] - 1\}$ (3.e)

E_{Na}= 45 mV, g_{Na} takes its maximal value, 90 mS/cm^2 at the soma and decreases to 0 mS/cm^2 with increasing distance from the soma on the apical and basal dendritic tree.

The delayed rectifier potassium (K_{DR}) channel is described by following set of equations:

$I_{DR} = g_{DR}\, n^4\, (V_m - E_K)$ (4.a)

$\alpha_n = -18\, V_m / \{[\exp (V_m / -25)] - 1\}$ (4.b)

$\beta_n = 3.6\, (V_m - 10\,\} / \{\exp [(V_m - 10) / 12] - 1\}$ (4.c)

E_K= –85 mV, g_{DR} takes its maximal value, 4.5 mS/cm^2 at the soma and decreases to 0.213 mS/cm^2 with increasing distance from the soma on the apical and basal dendritic tree.

The muscarinic potassim (K_M) channel is described by following set of equations:

$I_M = g_M\, u^2 (V_m - E_K)$ (5.a)

$\alpha_u = 0.016 / \exp [(V_m - 52.7) / -23]$ (5.b)

$\beta_u = 0.016 / \exp [(V_m - 52.7) / 18.8]$ (5.c)

g_M takes its maximal value, 3.75 mS/cm^2 at the soma and decreases to 0.167 mS/cm^2 with increasing distance from the soma on the apical and basal dendritic tree.

The A-type transient potassium (K_A) channel is described by following set of equations:

$I_A = g_A\, a\, b\, (V_m - E_K)$ (6.a)

$\alpha_a = -50\, (V_m + 20) / \{\exp [(V_m + 20) / -15] - 1\}$ (6.b)

$\beta_a = 0.1 \cdot 10^3\, (V_m + 10) / \{\exp [(V_m + 10) / 8] - 1\}$ (6.c)

$\alpha_b = 0.15 / \exp[(V_m + 18) / 15]$ (6.d)

$\beta_b = 60 / \{\exp[(V_m - 73) / -12] + 1\}$ (6.e)

g_A takes takes its maximal value, 60 mS/cm^2 at the soma and decreases to 0 mS/cm^2 with increasing distance from the soma on the apical and basal dendritic tree.

The calcium (Ca) current is described by following set of equations:

$I_{Ca} = g_{Ca}\, s^2\, r\, (V_m - E_{Ca})$ (7.a)

$\alpha_s = -0.016 \cdot 10^3\, (V_m + 26) / \{\exp[(V_m + 26) / -45] - 1\}$ (7.b)

$\beta_s = 4\, (V_m + 12) / \{\exp[(V_m + 12) / 10] - 1\}$ (7.c)

$\alpha_r = 0.6 / \exp[(V_m + 94) / 10]$ (7.d)

$\beta_r = 2.4 / \{\exp[(V_m - 68) / -27] + 1\}$ (7.e)

E_{Ca} was calculated from calcium concentration ratios of intra- and extracellullar concentrations, see below. g_{Ca} takes its maximal value, 5 mS/cm^2 at the soma and decreases to 0.22 mS/cm^2 with increasing distance from the soma on the apical and basal dendritic tree.

The calcium concentration dependent potassium (K_{AHP}) channel was implemented differently from other channels to better suit experimentally determined channel kinetics (Jose Manual Ibarz, personal communication).

$I_{AHP} = g_{AHP}\, q\, (V_m - E_K)$ (8)

Time constant τ_q was set to 48 ms and steady state activation, q_{inf} was determined by interpolating the following table:

[Ca^{++}] [nM]	*q*	[Ca^{++}] [nM]	*q*	[Ca^{++}] [nM]	*q*
0	0.004	1034	0.867	2069	0.979
103	0.035	1137	0.859	2172	0.982
206	0.111	1241	0.915	2275	0.984
310	0.231	1344	0.931	2379	0.986
413	0.372	1448	0.944	2483	0.987
517	0.508	1551	0.953	2586	0.989
620	0.622	1655	0.961	2689	0.990
724	0.712	1758	0.967	2793	0.991
827	0.780	1862	0.972	2896	0.992
931	0.830	1965	0.976	3000	1.000

*Table 1 Values used to describe the calcium concentration dependent activatioon variable (*q*) of the AHP channel*

g_{AHP} takes its maximal value, 0.9 mS/cm^2 at the soma and decreases to 0.04 mS/cm^2 with increasing distance from the soma on the apical and basal dendritic tree.

The calcium concentration and membrane potential dependent potassium (K_{CT}) channel is described by following set of equations:

$I_{CT} = g_{CT}\, c\, d\, (V_m - E_K)$ (9.a)

$\alpha_c = -7.7\, (V_m + V_{shift} + 103) / \{\exp[(V_m + V_{shift} + 103) / -12] - 1\}$ (9.b)

τ_c was set to 1.1 ms (9.c)

$\alpha_d = 1 / \exp[(V_m + 79) / 10]$ (9.d)

$\beta_d = 4 / \{\exp[(V_m - 82) / -27] + 1\}$ (9.e)

$V_{shift} = 40 \log([Ca^{++}] / 13.805 \cdot 10^{-3})$ (9.f)

g_{CT} takes its maximal value, 140 mS/cm^2 at the soma and decreases to 2 mS/cm^2 with increasing distance from the soma on the apical and basal dendritic tree.

The hyperpolarization-activated non-specific cation current (h) is described by two interpolated tables, one for the membrane potential dependent time constant (τ_l), the other for the membrane potential dependent steady state value (l_{inf}) respectively.

V_m [mV]	τ_l [ms]	l_{inf}	V_m [mV]	τ_l [ms]	l_{inf}	V_m [mV]	τ_l [ms]	l_{inf}
–140.00	17	1.0	–96.36	30	0.90	–52.72	20	0.063
–129.09	17	1.0	–85.45	39	0.72	–41.81	16	0.040
–118.18	20	0.98	–74.54	47	0.40	–30.90	11	0.0
–107.27	24	0.96	–63.63	40	0.15	–20.00	8	0.0

Table 2 Values to describe time constant (τ_l) and steady-state values (l_{inf}) of the h channel

Reversal potential for this current was set to E_h= 0.0 mV, maximal conductance value, g_h, in the basal dendritic compartments were 0 mS/cm^2. The g_h value increased from the soma towards the distal apical dendrites from 1 mS/cm^2 to 10 mS/cm^2.

Intracellular calcium concentration ($[Ca^{++}]$*) and calcium reversal potential (*E_{Ca}*)* is described by following set of equations:

$$E_{Ca} = -13.3 \cdot \log([Ca^{++}]/1.2) \quad (10.a)$$

$$d[Ca^{++}]/dt = -[Ca^{++}]/\tau_{Ca} + B \cdot I_{Ca} \quad (10.b)$$

Following the work of Warman et al (1994) we used two calcium pools. The first one is used for calculating E_{Ca} and in I_{CT}, while the second is for I_{AHP}. Parameters for the first and second pools were $\tau_{Ca}= 9\cdot10^{-1}$ s, $B= 3\cdot10^{-7}$, and $\tau_{Ca}= 1\cdot10^{-3}$ ms, $B=3\cdot10^{-7}$ respectively.

Hippocampal and medial septal inhibitory neurons

Differential equation for a single-compartmental neuron is of the general form:

$$C_m \, dV_j/dt = -\Sigma I_i - I_L - I_{syn} + I \quad (11)$$

while gating variables were described by the equation

$$dx/dt = \phi_x[\alpha_x(V)(1-x) - \beta_x(V)x] = \phi_x[x_\infty(V) - x]/\tau_x(V) \quad (12)$$

In the former equation I_i stands for various intrinsic currents, I_L is the leakage current in the form

$$I_L = g_L(V - E_L), \quad (13)$$

I_{syn} is the sum of synaptic currents, and I is a tonic depolarizing current.

Horizontal o/a neurons

These interneurons projected both to the septum and to the *lacunosum molaculare* (O-LM neurons) were adapted from the model of Wang (2002), and were one

compartmental models, containing five intrinsic currents: sodium (I_{Na}), delayed rectifier potassium (I_K), hyperpolarization activated nonspecific cation current (I_h), high-threshold calcium current (I_{Ca}), and calcium-activated potassium current (I_{KCa}).

Sodium current was in the standard form:

$$I_{Na} = g_{Na} m_\infty^3 h (V - E_{Na}), \quad (14)$$

where the activation variable was replaced by its steady-state value

$$m_\infty = \alpha_m / (\alpha_m + \beta_m) \quad (15.a)$$

$$\alpha_m(V) = -0.1(V + 35)/\{\exp[-0.1(V + 35)] - 1\} \quad (15.b)$$

$$\beta_m(V) = 4 \exp[-(V + 60)/18] \quad (15.c)$$

$$\alpha_h(V) = 0.07 \exp[-(V + 58)/20] \quad (15.d)$$

$$\beta_h(V) = 1/\{\exp[-0.1(V + 28)] + 1\} \quad (15.e)$$

The delayed rectifier potassium current was

$$I_K = g_K n^4 (V - E_K) \quad (16.a)$$

$$\alpha_n(V) = -0.01 (V + 34) / \{\exp[-0.1(V + 34)] - 1\} \quad (16.b)$$

$$\beta_n(V) = 0.125 \exp[-(V + 44)/80] \quad (16.c)$$

The high-threshold calcium current was

$$I_{Ca} = g_{Ca} m_\infty^2 (V - V_{Ca}) \quad (17.a)$$

Again, m was replaced by its steady-state form

$$m_\infty(V) = 1/\{1 + \exp[-(V + 20)/9]\} \quad (17.b)$$

The voltage-independent, calcium-activated potassium current

$$I_{KCa} = g_{KCa} [Ca^{2+}]/([Ca^{2+}] + K_D)(V - V_K), \quad (18.a)$$

where the dynamics of calcium concentration was described by

$$d[Ca^{2+}]/dt = -\alpha I_{Ca} - [Ca^{2+}]/\tau_{Ca} \quad (18.b)$$

Finally, the form of hyperpolarization-activated current was

$$I_h = g_h H (V - E_h), \quad (19.a)$$

$$H_\infty(V) = 1/\{1 + \exp[(V + 80)/10]\} \quad (19.b)$$

$$\tau_H(V) = 200/\{\exp[(V + 70)/20] + \exp[-(V + 70)/20]\} + 5 \quad (19.c)$$

Parameters of the model neuron were: $g_L = 0.1$ mS/cm^2, $E_L = -65$ mV, $g_{Na} = 35$ mS/cm^2, $E_{Na} = +55$ mV, $g_K = 9$ mS/cm^2, $E_K = -90$ mV, $g_{Ca} = 1$ mS/cm^2, $E_{Ca} = +120$ mV, $g_h = 0.15$ mS/cm^2, $E_h = -40$ mV, $g_{KCa} = 10$ mS/cm^2, $\phi_h = \phi_n = 5$, $K_D = 30$ μM, $\alpha = 0.002$, $\tau_{Ca} = 80$ ms, I was 0 μA/cm^2. The membrane surface contributing to action potential generation was taken to be 1.25e3 μm^2, equivalent to the surface area of a sphere of 20 μm radius.

Basket neurons

These cells with somata residing in the pyramidal layer were single-compartmental realizations. The model was the same previously used by Wang and Buzsáki (1996), containing sodium (I_{Na}) and delayed rectifier potassium (I_K) currents.

Equations governing the sodium dynamics were:

$$I_{Na} = g_{Na} m_\infty^3 h(V - E_{Na}), \quad (20.a)$$

where m was substituted with its steady state form

$$\alpha_m/(\alpha_m + \beta_m) \quad (20.b)$$

$$\alpha_m(V) = -0.1(V + 35)/(\exp(-0.1(V + 35)) - 1) \quad (20.c)$$

$$\beta_m(V) = 4\exp(-(V + 60)/18) \quad (20.d)$$

$$\alpha_h(V) = 0.07 \exp(-(V + 58)/20) \quad (20.e)$$

$$\beta_h(V) = 1/(\exp(-0.1(V + 28)) + 1). \quad (20.f)$$

For the delayed rectifier potassium channel

$$I_K = g_K n^4 (V - E_K) \quad (21.a)$$

$$\alpha_n(V) = -0.01(V + 34)/(\exp(-0.1(V + 34)) - 1) \quad (21.b)$$

$$\beta_n(V) = 0.125 \exp(-(V + 44)/80) \quad (21.c)$$

Parameters of these equations were: $C_m = 1$ μF/cm^2, $g_L = 0.1$ mS/cm^2, $E_L = 65$ mV, $g_{Na} = 35$ mS/cm^2; $E_{Na} = 55$ mV, $g_K = 9$ mS/cm^2, and $E_K = -90$ mV, $\phi_h = 5$, and the tonic depolarizing current was set homogeneously, its level throughout the simulations was I was 1.4 μA/cm^2. Spatial dimensions of the cell were the same used for the horizontal o/a neuron.

Medial septal GABAergic neuron

This model neuron was the single-compartmental model previously described in Wang (2002). Besides I_{Na} and I_K, this model contained I_{KS} a slowly inactivating potassium current.

The sodium current was in the standard form:

$$I_{Na} = g_{Na} m_\infty^3 h(V - E_{Na}) \quad (22.a)$$

$$m_\infty = \alpha_m/(\alpha_m + \beta_m) \quad (22.b)$$

$$\alpha_m = -0.1(V + 33)/\{\exp[-0.1(V + 33)] - 1\} \quad (22.c)$$

$$\beta_m = 4 \exp[-(V + 58)/18] \quad (22.d)$$

$$\alpha_h = 0.07 \exp[-(V + 51)/10] \quad (22.e)$$

$$\beta_h = 1/\{\exp[-0.1(V + 21)] + 1\}. \quad (22.f)$$

The delayed rectifier potassium current was

$I_K = g_K n^4 (V - E_K)$ (23.a)

$\alpha_n = -0.01(V + 38)/\{\exp[-0.1(V + 38)] - 1\}$ (23.b)

$\beta_n = 0.125 \exp[-(V + 48)/80]$. (23.c)

The slowly inactivating potassium current

$I_{KS} = g_{KS} p\, q(V - E_K)$ (24.a)

was described with the steady-state form of gating variables:

$p_\infty = 1/\{1 + \exp[-(V + 34)/6.5]\}$ (24.b)

$\tau_p = 6$ ms (24.c)

$q_\infty = 1/\{1 + \exp[(V + 65)/6.6]\}$ (24.d)

$\tau_q = \tau_{q0}(1 + 1/\{1 + \exp[-(V + 50)/6.8]\})$ (24.e)

$\tau_{q0} = 100$ ms. (24.f)

The parameter values used were as follows: $C_m = 1$ μF/cm^2, $g_L = 0.1$ mS/cm^2, E_L=–50 mV, $g_{Na} = 50$, $g_K = 8$, $g_{KS} = 12$ (in mS/cm^2); $E_{Na} = +55$, $E_K = -85$ (in mV), $\phi_h = \phi_n = 5$, I =2.2 μA/cm^2, and was equal for each cell of the medial septal population. Spatial dimensions of the cell were the same used for the hippocampal interneurons.

Synapses and network structure

Synaptic currents for establishing synaptic contacts between neurons were either $GABA_A$ receptor mediated inhibitory postsynaptic currents (IPSCs) or glutamate receptor mediated excitatory postsynaptic currents (EPSCs).

$GABA_A$ IPSCs were described by the equation

$I_{syn} = g_{syn} s\, (V - E_{syn})$ (25)

and activation variable s was governed by first order kinetics

$ds/dt = \alpha F(V_{pre})(1 - s) - \beta s$, (26)

where the transmitter release probability ($F(V_{pre})$) was a function of the membrane potential of the presynaptic neuron

$F(V_{pre}) = 1/(1 + \exp(-(V_{pre} - \theta_{syn})/K))$ (27)

(Wang and Buzsáki, 1996). Parameters characterizing synaptic contacts between different pre- and postsynaptic neurons were as follows: for basket-to-pyramidal cell connections ($b \rightarrow p$): $\alpha = 10$ ms^{-1}, $\beta = 0.07$ ms^{-1}, K= 2 mV, E_{syn}= –80 mV; for basket-to-basket cell connections ($b \rightarrow b$), for medial septal-to-medial septal cell connections ($m \rightarrow m$), for medial septal-to-basket, o/a neuron connections ($m \rightarrow b$, $m \rightarrow o$): $\alpha = 10$ ms^{-1}, $\beta = 0.07$ ms^{-1}, K= 2 mV, E_{syn}= –75 mV; for o/a neuron-to-basket cell connections ($o \rightarrow b$) and o/a neuron-to-medial septal neuron

synapses ($o \rightarrow m$): α = 20 ms^{-1}, β = 0.05 ms^{-1}, K= 0.5 mV, E_{syn}= –80 mV; for o/a neuron-to-pyramidal cell connections ($o \rightarrow p$): α = 10 ms^{-1}, β = 0.07 ms^{-1}, K= 2 mV, E_{syn}= –85 mV; and for medial septal-to-medial septal cell connections ($m \rightarrow m$): α = 10 ms^{-1}, β = 0.07 ms^{-1}, K= 2 mV, E_{syn}= –75 mV. θ_{syn} was unanimously set to 0 mV at GABAergic synapses.

Glutamatergic transmission was mediated by AMPA receptors. The model for AMPA receptor-mediated current was described in Destexhe, (2000); briefly

$$I_{AMPA} = g_{AMPA}\, s\, (V - E_{AMPA}) \quad (28.a)$$

$$ds/dt = \alpha\, [T]\, (1 - s) - \beta\, s. \quad (28.b)$$

Here, α=1.1 mM^{-1}ms^{-1}, β= 0.19 ms^{-1}, E_{AMPA} = 0 mV. The transmitter release at an action potential was described by the equation

$$[T] = T_{max} / (1 + \exp(-(V_{pre} - V_p)/ K_p)), \quad (28.c)$$

where V_p= 2 mV and K_p=5 mV.

Strengths of synaptic contacts were tested in a wide range for probing the robustness of the observed phenomena; therefore both the ranges are given and default values (in parentheses) are shown. Deviations from default values are shown at corresponding figures. Strength of synaptic contacts was the same for neurons in a given pre- and postsynaptic population and changes in maximal synaptic conductance given in percentage refer to a ratio with respect to the default values.

When testing network size effect on oscillation generation convergence levels were kept constant. This way, overall depolarization of individual neurons were kept constant while network size was rescaled, preventing changes in firing rates resulting from altered strength of afferent connections.

Pattern of synaptic contacts was random: In the simulations convergence and divergence levels were set, pre- and postsynaptic neurons were selected in a random manner. Synaptic strengths and convergence/divergence levels are listed below:

- convergence of basket cells on pyramidal cells (Freund and Buzsáki 1996; Sik *et al.* 1995) varied between 8 and 20 (default 15), maximal synaptic conductance was 0.9 – 3 nS (default 1.38 nS);

- a single basket cell (Sik *et al*. 1995; Buhl *et al.* 1994) innervated 60 – 80 other basket cells (default 60), the tested range of maximal synaptic conductance was 0.125 – 0.5 nS (default 0.125 nS), in the simulations presented basket cell synapses were restricted to the somatic compartment;

- convergence of o/a neurons on pyramidal cells (Sik *et al.* 1995; Hájos and Mody 1997) was in the range of 8 – 20 (default 8) and were distributed on 3 distal apical dendritic compartments on different branches of the dendritic tree, maximal synaptic conductance varied between 0.8 – 1.1 nS (default 0.88 nS);

- convergence of o/a neurons on basket cells (Katona *et al*. 1999; Buhl *et al*. 1994) was in the range of 3 – 5 (default 5), maximal synaptic conductance was 0.7 – 1.1

nS (default 0.88 nS);

- pyramidal cells innervated 1.6 – 4 o/a cells (Lacaille *et al.* 1987; Blasco-Ibanez and Freund 1995) on average (default 2.4), maximal synaptic conductance was in the range of 0.6 – 1.5 nS (default 0.9) at AMPA receptors, and 0.3 – 0.75 nS (default 0.45 nS) at NMDA receptors;

- convergence of pyramidal cells on basket neurons (Freund and Buzsáki 1996; Kneisler and Dingledine 1995)was lower, could be as low as 0 and was increased up to 1.2 (default 0.25), maximal synaptic conductance was the same as for synapses connecting pyramidal cells to o/a neurons;

- medial septal neurons innervated 5 – 30 other medial septal neurons (Varga *et al*. 2002) (default 10), maximal synaptic conductance was varied between 0.12 – 0.88 nS (default was 0.25 nS);

- the amount of basket and o/a interneurons innervated by medial septal neurons (Freund and Antal 1988; Varga *et al.* 2002) was the same and varied between 3.5 – 10 (default 7), while maximal synaptic conductance was in the range of 0.38 – 1 nS (default 0.5 nS);

- finally, o/a neurons converged on 1.2 – 5 medial septal cells (Tóth and Freund 1992; Jinno and Kosaka 2002) on average (default was 2.5), maximal synaptic conductance was in the range of 0.38 – 1 nS (default 0.5 nS).

Number of neurons in a given type was 12, 50, 100, 50 for pyramidal cells basket neurons, o/a neurons, and medial septal cells, respectively. Individual simulations were also run with same network structure but increased number of neurons (48, 200, 100, 100) to test scalability.

Models were implemented in the GENESIS simulation software and run on two 16-node Beowulf clusters at KFKI RIPNP, Budapest, Hungary and at the Physics Department, Center for Complex Systems Studies, Kalamazoo College.

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