Attention robustly gates a closed-loop touch reflex

Supporting information

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Model specifications

Number of elements in the model

The multiple loop model, like our former brainstem loop model, contains five rows of whiskers, with two rows of four whiskers and three rows of seven whiskers, corresponding to rows A-B and C-E in the rat. Each whisker is innervated by a separate pool of neurons that closes two loops between that whisker and the muscles attached to it, as shown in Figs. 1-2. The number of stations that compose the higher TIP-regulatory loop, as well as the number of cells in each station, vary between the different TIP-regulation model configurations, as indicated in Fig. 2. For all model configurations, the values indicated for the touch- and whisking-relaying cells are based on experimental data of the lemniscal- and paralemniscal pathways of the rats, respectively.

The number of neurons in each station along the loops are based on the followings:

1. Each whisker follicle in rats is innervated by approximately 200 trigeminal ganglion- (TG) (Welker and Van der Loos, 1986; Crissman et al., 1991), 200 trigeminal nuclei- (TN) cells (Jacquin et al., 1993; Timofeeva et al., 2003), 250 thalamic- (Land et al., 1995; Varga et al., 2002; Meyer et al., 2013), and 4500 cortical- (Meyer et al., 2013) neurons, which correspond to the SN1-, SN2-, H1- and H2 cells in the model.
2. **TG cells:**
   (1) The SN1s population is divided into four subpopulations according to the type of information relayed from the whisker: Whisking (SN1-W), Contact (SN1-C), Pressure (SN1-P) and Detach (SN1-D) cells (Szwed et al., 2003; Ahissar and Knutsen, 2008).
   (2) The number of TG Whisking- (SN1-W) and Touch- (SN1-C,P,D) cells is approximately equal (Szwed et al., 2003, Table 1).
   (3) The number of SN1-C, SN1-P, and SN1-D cells is approximately equal (Szwed et al., 2003, Table 1).
3. **TN-, H1- and H2 cells:**
   (1) Each SN2-, H1-, and H2 cell is innervated by exactly one type of SN1s, SN2s, and H1 cells, respectively (Yu et al., 2006; Deschenes and Urbain, 2009). The SN2s are assumed to relay all four types of information, and are divided into four subpopulations of SN2-W, SN2-C, SN2-P, and SN2-D cells.

The H1- (H2) cells are assumed to relay two types of information, and are divided into two subpopulations, whose types depend on the TIP regulation mechanism: H1-C and H1-W (H2-C and H2-W) in the whisking-based GATE+ (wGATE+) and GATE- configurations, and H1-C and H1-P (H2-C and H2-P) in the touch (pressure)-based GATE+ (pGATE+) configurations.

(2) Assume a similar ratio between the subtypes of SN2-, H1-, and H2 cells as those between the corresponding types of SN1s.

Notes:

- The number of cells of each population in the model was slightly changed in order to have a rounded number of cells in each of the subgroups.
- The number of the SN2-Ps was doubled in the pGATE+ configurations in order to have a similar number of SN2-Ps that innervate the H1- and MNs as in the wGATE+ and GATE- configurations.

The connectivity between pre- and post-synaptic cells along the loops are based on the followings:

1. Each SN1 cell innervates only one whisker follicle (Melaragno and Montagna, 1953; Renehan and Munger, 1986; Rice et al., 1986; Waite and Jacquin, 1992).
2. Each SN2-C,P,D is innervated by a pool of 2-4 SN1s of the corresponding type that innervate a single whisker (Jacquin et al., 1989a; Jacquin et al., 1989b; Jacquin et al., 1993; Veinante and Deschenes, 1999; Timofeeva et al., 2004; Furuta et al., 2008; Lo et al., 2011). Assume that each SN2-W is innervated by a pool of 20-40 SN2-Ws that innervate 1-12 whiskers (Fig. 3) (Jacquin, 1989; Jacquin et al., 1989a; Jacquin et al., 1989b; Furuta et al., 2006; Furuta et al., 2008) (assume one-order of magnitude higher number of pre-synaptic SN1-Ws than SN1-Cs).
3. Each SN2-P is innervated by a pool of H2-Ws or H2-Ps, according to the TIP-regulation configuration (wGATE+/GATE- or pGATE+, respectively). Assume that 5% of the H2 cells pool that innervate the same principal whisker as the SN2-P, innervate each SN2-P (Wise and Jones, 1977; Wise et al., 1979; Killackey et al., 1989; Furuta et al., 2010).
4. Each H1-C,P is innervated by a pool of 1-3 SN2-C,Ps that innervate the same principal whisker (Waite, 1973; Ito, 1988; Sugitani et al., 1990; Chiaia et al., 1991; Descheˆnes et al., 2003; Arsenault and Zhang, 2006). Assume that each H1-W is innervated by a pool of 10-30 SN2-Ws that innervate the same principal whisker (assume one-order of magnitude higher number of pre-synaptic SN2-Ws than SN2-Cs). Since each SN2-W receives inputs from 1-12 whiskers, each H1-W receives inputs from 1-12 whiskers as well (Diamond et al., 1992; Castejon et al., 2016).
5. Assume that each H2-C and H2-W is innervated by a pool of 2-4 H1-Cs and 20-40 H1-Ws that innervate the same principal whisker, respectively:
   (1) Based on anatomical data, a single H2-C is estimated to be innervated by ~80 H1-Cs (Bruno and Sakmann, 2006).

(2) However, functional results suggest that effectively a smaller number of H1-Cs converges on each H2-C (Timofeeva et al., 2003).

(3) Assume one-order of magnitude higher number of pre-synaptic H1-Ws than H1-Cs.

Since each H1-W receives inputs from 1-12 whiskers, each H2-W receives inputs from 1-12 whiskers as well (Mitrukhina et al., 2015; Castejon et al., 2016).

Note:

In order to allow the fastest response of high-threshold SN2-Ps in the pGATE+ model configurations, each high-threshold SN2-P is innervated by a group of cells from the higher loop's output station, whose activity is triggered by the same group of SN1-Ps that directly innervate the high-threshold SN2-P. For example, in the simplified pGATE+ configuration[1], the high-threshold SN2-P[40] is innervated by both SN1-P[0..2] and H1-P[0..4]. The latter are innervated by the low-threshold SN2-P[0], who receives inputs from SN1-P[0..2]. In the TTC pGATE+ configuration[1], the high-threshold SN2-P[40] is innervated by both SN1-P[0..2] and H2-P[0..75]. The latter are innervated by H1-P[0..4]; each of these H1-Ps is innervated by the low-threshold SN2-P[0], who receives inputs from SN1-P[0..2]. In the wGATE+ and GATE- configurations these requirements were not needed.

Model parameters

The parameters in the multiple-loop model are listed below[2]. Parameter values were set based on experimental data (indicated in the Reference column). For all model configurations, the values of the touch- and whisking-relaying cells' parameters were based on experimental data of the lemniscal- and paralemniscal pathways of the rats, respectively. When empirical data were not available, a genetic algorithm (GA) was used to evaluate values (see (Sherman et al., 2013), file S1, “Genetic algorithm”). The algorithm converged into several optimal solutions that produced the desired free-air whisking and TIP motions. The values of the most stable solution are displayed below.

Whisker

Parameter	Units	Value	Description	Source
θ_0	deg	60+5**index*	Angle at the beginning of simulation	(Towal et al., 2011)[3]
$\theta(t)$	deg	$\theta(0) = \theta_0$	Current angle	
$\dot{\theta}_0$	deg/sec	0	Angular velocity at the beginning of simulation	
$\dot{\theta}(t)$	deg/sec	$\dot{\theta}(0) = \dot{\theta}_0$	Current angular velocity	
$\dot{\theta}_{max}$	deg/sec	2000	Maximal angular velocity	(Simony et al., 2010)
side[4]	index	0-1	The whisker's side of the snout	

[1] Which contains 40 and 40 low- and high-threshold SN2-Ps, respectively.

[2] The values of the BS-loop model’s parameters are not displayed. Only a few values were changed following model’s expansion, and many were added (for the additional components of the H-loop and of the attentiveness module).

[3] Towal et al. (2011) show the following linear relation between whisker's column and its resting angle: A·col+B, where A=10.7, B=37.3. In our model, a linear relation with the following constants was implemented: A=5, B=60.

[4] Besides the whisker- and the object elements in the model, no other element requires this parameter. At the beginning of the simulation each whisker is attached to its SN1s, which are attached to their SN2, and so on, such that the side of each of the neurons composing the BS- and H-loops that innervate that whisker is indirectly set via the simulated connections.

			(0 and 1 correspond to left- and right sides)	
row	index	1-5	Row number (rows 1-5 correspond to rows A-E in the rat)	
index	index	1-7	Index of column in the row (up to 4 in four-whisker rows)	
xc	m	0.002*(*index* + 1)	Center of mass along the x-axis (caudal-rostral)	(Simony et al., 2010)
yc	m	0	Center of mass along the y-axis (ventral-dorsal)	(Simony et al., 2010)
L	m	0.03	Length	

Object

Parameter	Units	Value	Description	Source
x	m		Position along the x-axis (caudal-rostral)	
y	m		Position along the y-axis (medial-radial)	
z	m	1-5 (*row*)	Position along the z-axis (ventral-dorsal). The model assumes no whisker motion in this axis, thus z value simply indicates the row number in which the object is present	
present	logical	True/False	True when an object is present	
side	index	0-1	The side of the snout in which the object resides (0 and 1 correspond to left- and right sides)	
radialDistance	%	0-1	The radial distance of whisker-object contact, measured from the base of the whisker: $\frac{\sqrt{(x-xc)^2+(y-yc)^2}}{L}$ (xc, yc, L are whisker's parameters; see table above)	
*K**	N/m	$2\cdot10^{-5}\cdot$*radialDistance*	Spring constant.	

*Different from the BS-loop model, in the multiple-loop model the whiskers are assumed to be flexible bodies, and hence the base of the whisker continues to move forward following whisker-object contact. The object is assumed to act as a spring, applying a force, F_{obj}, that is perpendicular to the whisker at the contact point, at a size proportional to the radial distance of contact, measured from the base of the whisker. $F_{obj} = k \cdot (\theta(t) - \theta_{obj})$, where θ_{obj} is the whisker's angle upon whisker-object contact, when the whisker is straight.

Primary sensory Whisking cells (SN1-W)

Parameter	Units	value	Description	Source
$P_W(\theta,\dot{\theta})$	-	0-1	Firing probability: the current probability of the cell to fire. $P_W(\theta,\dot{\theta}) = 1-\left(1-\left(\frac{\theta_{range}-\lvert\theta-\theta_f\rvert}{\theta_{range}}\right)^{10}\right)\cdot\frac{\dot{\theta}}{\dot{\theta}_{max}}$ Set $P_W(\theta,\dot{\theta}) = 0$: (1) when $\dot{\theta} < 25$, (2) upon cell's firing. The above equation resulted in a much higher sensitivity of the cell to its whisker's angular velocity ($\dot{\theta}$) than its whisker's angle (θ), which resulted in its firings during the whisker's protraction period.	(Szwed et al., 2003)
threshold	-	0	The threshold to be crossed in order to successfully fire (P_W must be > 0)	
index	index	0-89	Each of the whisker's 90 SN1-Ws takes a different index	(Welker and Van der Loos, 1986; Crissman et al., 1991; Szwed et al., 2003)
θ_f	deg	θ_0+ *index**20/89	Favorite angle: its whisker's angle to which the cell is most sensitive, i.e., fires with highest probability. θ_0 is the resting angle of this cell's whisker, and 20 is the whisker's maximal amplitude[5].	(Szwed et al., 2003)
θ_{range}	deg	5	The range of angles of its whisker to which the cell responds. A cell can respond to the range: $[\theta_f-\frac{\theta_{range}}{2}, \theta_f+\frac{\theta_{range}}{2}]$	GA
$t_{response}$	msec	2-3	Time to generate action potential in response to whisker motion stimulus. At the beginning of the simulation, a delay of either 2 or 3 msec is set for each SN1-W, with an equal probability.	(Szwed et al., 2003)
t_{relay}	msec	1-2	Conductance time of the stimulus along the cell's axon to its post-synaptic target. At the beginning of the simulation, a delay of either 1 or 2 msec is set for each SN1-W, with an equal probability.	(Jacquin et al., 1986; Jacquin, 1989; Furuta et al., 2006)
APTransTimes	-		A linked list of the to-be-transmitted action potentials (see "model behavior in statecharts" below. Each link contains a value of future time at which the action potential generated by this neuron should reach its post-synaptic target.	
ARP	msec	1	Absolute refractory period duration	(Leiser and Moxon, 2007)
RRP	msec	3	Relative refractory period duration	Na^+ channels recovery time

Primary sensory Contact cells (SN1-C)

Parameter	Units	value	Description	Source
index	index	0-39	Each of the whisker's 40 SN1-Cs takes a different index	(Welker and Van der Loos, 1986; Crissman et al., 1991;

[5] Our transformation function that converts MNs' spikes to whisker movement supports a relatively small-amplitude whisker motion of up to 20° (see discussion in (Towal et al., 2011), and "Muscle forces & whisker motion" in file S1 of (Sherman et al., 2013)).

				Szwed et al., 2003)
$t_{response}$	msec	2-5 (2) [range (median)]	Time to generate action potential in response to contact stimulus. At the beginning of the simulation, a delay of either 2,3,4 or 5 msec is set for each SN1-C, with a decreasing probability.	(Szwed et al., 2003; Szwed et al., 2006)
t_{relay}	msec	1	Conductance time of the stimulus along the cell's axon to its post-synaptic target	(Furuta et al., 2006)
APTransTimes	-		A linked list of the to-be-transmitted action potentials (see "model behavior in statecharts" below. Each link contains a value of future time at which the action potential generated by this neuron should reach its post-synaptic target.	
ARP	msec	1	Absolute refractory period duration	(Leiser and Moxon, 2007)
RRP	msec	3	Relative refractory period duration	Na^+ channels recovery time

Primary sensory Pressure cells (SN1-P)

Parameter	Units	value	Description	Source
index	index	0-39	Each of the whisker's 40 SN1-Ps takes a different index	(Welker and Van der Loos, 1986; Crissman et al., 1991; Szwed et al., 2003)
threshold	-	8-18 (8) [range (median)]	The threshold to be crossed in order to successfully fire	
$t_{response}(x, y, L)$	msec	8-34	Time to generate action potential in response to contact stimulus. Changes for every cell according to its threshold, and to the radial distance of contact between its whisker and an object: $t_{response} = threshold * F(x, y, L)$ F(x,y,L) – a function of the radial distance of the object, measured from whisker's base ($\frac{\sqrt{(x-xc)^2+(y-yc)^2}}{L}$). F(x,y,L) = radialDistance + 1, and thus takes values in the range [1,2]. Note that for each cell, decreasing the radial distance of contact decreased $t_{response}$ and thus increased its firing rate.	(Szwed et al., 2003; Szwed et al., 2006)
t_{relay}	msec	1	Conductance time of the stimulus along the cell's axon to its post-synaptic target	Assume minimal relay time
APTransTimes	-		A linked list of the to-be-transmitted action potentials (see "model behavior in statecharts" below. Each link contains a value of future time at which the action potential generated by this neuron should reach its post-synaptic target.	
ARP	msec	1	Absolute refractory period duration	(Leiser and Moxon, 2007)
RRP	msec	3	Relative refractory period duration	Na^+ channels recovery time

Primary sensory Detach cells (SN1-D)

Parameter	Units	Value	Description	Source
index	index	0-39	Each of the whisker's 28 SN1-Ds takes a different index	(Welker and Van der Loos, 1986; Crissman et al., 1991; Szwed et al., 2003)
$t_{response}$	msec	1	Time to generate action potential in response to detachment of its whisker from an object	(Szwed et al., 2003)
t_{relay}	msec	1	Conductance time of the stimulus along the cell's axon to its post-synaptic target	Assume minimal relay time
APTransTimes	-		A linked list of the to-be-transmitted action potentials (see "model behavior in statecharts" below. Each link contains a value of future time at which the action potential generated by this neuron should reach its post-synaptic target.	
ARP	msec	1	Absolute refractory period duration	(Leiser and Moxon, 2007)
RRP	msec	3	Relative refractory period duration	Na^{+} channels recovery time

Secondary sensory Whisking, Contact, Pressure and Detach cells (SN2-W,C,P,D)

<table>
<tr><th>Parameter</th><th>Units</th><th>Value</th><th>Description</th><th>Source</th></tr>
<tr><td>type</td><td>-</td><td>W,C,P,D</td><td>Cell type: whisking (W), contact (C), pressure (P), or detach (D)</td><td>(Yu et al., 2006; Deschenes and Urbain, 2009)</td></tr>
<tr><td>index</td><td>index</td><td>0-N</td><td>Each of the whisker's SN2s of each type takes a different index; N = 90,40,s2p,40 for SN2 of type W,C,P,D.
s2p depends on the TIP regulation configuration (a global parameter of the simulation), and is set to 40 and 80 in the whisking- and touch-based configurations (see Figs. 1-2).</td><td>(Jacquin et al., 1993; Timofeeva et al., 2003; Yu et al., 2006; Deschenes and Urbain, 2009)</td></tr>
<tr><td>$t_{response}$</td><td>msec</td><td>1-4</td><td>Time to generate action potential in response to stimuli from its pre-synaptic SN1s.
Not a parameter; results from simulation dynamics*</td><td></td></tr>
<tr><td>$t_{relayToMN}$</td><td>msec</td><td>1-4</td><td>Conductance time of the stimulus along the cell's axon to its post-synaptic MNs.
Delay of SN2-W = 1,2,3, or 4 with an equal probability.
Delay of SN2-C,P,D = 1.</td><td></td></tr>
<tr><td>$t_{relayToTh}$</td><td>msec</td><td>See table</td><td>Conductance time of the stimulus along the cell's axon to its post-synaptic thalamic cells. Relevant only for SN2-C cells in all model configurations, and for SN2-W or SN2-P cells in the whisking- or touch-based configurations.
<table>
<tr><td></td><td>Whisking-based</td><td colspan="2">Touch-based</td></tr>
<tr><td></td><td></td><td>Simplified</td><td>Adjusted</td></tr>
<tr><td>SN2-C</td><td colspan="3">22-26* or 4^</td></tr>
<tr><td>SN2-P</td><td>-</td><td>1</td><td>1-3*</td></tr>
<tr><td>SN2-W</td><td>4</td><td colspan="2">-</td></tr>
</table>
* An integer in the specified range, with an equal probability.
^ Depending on the rat's attentiveness mode: 4 when touch-attentive, 22-26 when touch-inattentive.</td><td>(Veinante et al., 2000; Minnery and Simons, 2002; Trageser and Keller, 2004; Yu et al., 2013)</td></tr>
<tr><td>APTransTimes</td><td>-</td><td></td><td>A linked list of the to-be-transmitted action potentials (see "model behavior in statecharts" below. Each link contains a value of future time at which the action</td><td></td></tr>
</table>

			potential generated by this neuron should reach its post-synaptic target.	
ARP	msec	2	Absolute refractory period duration	(Jacquin et al., 1986)
RRP	msec	3	Relative refractory period duration	Na^+ channels recovery time

* The delay in firing of an SN2 following pre-synaptic stimuli ($t_{response}$) depends on the time it takes the cell to cross a threshold. The time for crossing the threshold depends on the *threshold* (increased in the "RRP" state relative to "Rest"), strength of the pre-synaptic stimuli and time interval between stimuli:

$$A_{SN2-X}(t) = A_{SN2-X}(t-1) + \sum_{index=1}^{T} E_{SN1-X_{index}} + \sum_{index=1}^{N} E_{H-X_{index}} - C$$

where t is the elapsed time from the moment the SN2 enters the "GenerateAP" state,

$A_{SN2-X}(t-1)$ is the SN2 excitability value (arbitrary units) at time t-1,

X is the *type* of information the SN2 and its SN1s (and either thalamic or cortical cells; see below) relay, i.e., whisking (W), contact (C), pressure (P) or detach (D),

$E_{SN1-X_{index}}$ is the effect of a pre-synaptic "*index*" SN1 of the corresponding *type* (X), on its SN2 excitability,

$E_{H-X_{index}}$ is the effect of a pre-synaptic "*index*" H cell (thalamic and cortical cells in the 'ideal'- and TTC models, respectively) of the corresponding *type* (X), on its SN2 excitability; relevant to high-threshold SN2-Ps only (see Fig. 2),

T is the number of primary afferents of *type* X activated at time t,

N is the number of H cells of *type* X activated at time t; relevant to high-threshold SN2-Ps only (see Fig. 2),

C is a constant.

Once an SN2 crosses *threshold*, its excitability values are zeroed ($t = 0$; $A_{SN2-X}(0) = 0$).

Thus the effect of an SN1 firing (and of an H (H1 or H2) cell for the high-threshold SN2-Ps) on its SN2 excitability depends on the synaptic strength ($E_{SN1-X_{index}}$ and $E_{H-X_{index}}$), and decreases with time as moving away from the firing time of the SN1 (and H cell; embodied in C). Inputs from SN1-Ps alone allow the low-threshold SN2-Ps to cross *threshold*, while high-threshold SN2-Ps require inputs from both of their SN1s and H cells.

$A_{SN2-X}(t)$ value is not changed if the SN2 is at the "absolute refractory period" state.

Thalamic Whisking, Contact, and Pressure cells (H1-W,C,P)

<table>
<tr><th>Parameter</th><th>Units</th><th>Value</th><th>Description</th><th>Source</th></tr>
<tr><td>type</td><td>-</td><td>W,C,P</td><td>Cell type: whisking (W), contact (C), or pressure (P). H1-C were generated in all TIP regulation model configurations; H1-W and H1-P were generated in the whisking- and touch-based TIP regulation configurations (a global parameter of the simulation), respectively (see Fig. 2).</td><td>(Yu et al., 2006; Deschenes and Urbain, 2009)</td></tr>
<tr><td>index</td><td>index</td><td>0-N</td><td>Each of the whisker's H1 cells of each type takes a different index; N depends both on the H1 type and the TIP regulation configuration (a global parameter of the simulation):
<table><tr><th></th><th>Whisking-based</th><th>Touch-based</th></tr><tr><td>H1-C</td><td>80</td><td>86</td></tr></table></td><td>(Land et al., 1995; Varga et al., 2002; Yu et al., 2006; Deschenes and Urbain, 2009; Meyer et al., 2013)</td></tr>
</table>

<table>
<tr><td></td><td></td><td></td><td><table><tr><td>H1-P</td><td>-</td><td>174</td></tr><tr><td>H1-W</td><td>180</td><td>-</td></tr></table>See Fig. 2.</td><td></td></tr>
<tr><td>$t_{response}$</td><td>msec</td><td>1-2</td><td>Time to generate action potential in response to stimuli from its pre-synaptic SN2s.
Not a parameter; results from simulation dynamics*</td><td></td></tr>
<tr><td>t_{relay}</td><td>msec</td><td>See table</td><td>Conductance time of the stimulus along the cell's axon to its post-synaptic target (see Fig. 2). The value depends on the TIP regulation model configuration (a global parameter of the simulation):<table><tr><td></td><td colspan="2">Whisking-based</td><td colspan="2">Touch-based</td></tr><tr><td></td><td>Simplified</td><td>Adjusted</td><td>Simplified</td><td>Adjusted</td></tr><tr><td>H1-C</td><td>20</td><td>10</td><td>20</td><td>10</td></tr><tr><td>H1-P</td><td colspan="2">-</td><td>1</td><td>2-3*</td></tr><tr><td>H1-W</td><td>1-3*</td><td>4-6*</td><td colspan="2">-</td></tr></table>* An integer in the specified range, with an equal probability.</td><td>(Ahissar et al., 2000; Bruno and Sakmann, 2006; Castejon et al., 2016)</td></tr>
<tr><td>APTransTimes</td><td>-</td><td></td><td>A linked list of the to-be-transmitted action potentials (see "model behavior in statecharts" below. Each link contains a value of future time at which the action potential generated by this neuron should reach its post-synaptic target.</td><td></td></tr>
<tr><td>ARP</td><td>msec</td><td>1</td><td>Absolute refractory period duration</td><td>(Leiser and Moxon, 2007)</td></tr>
<tr><td>RRP</td><td>msec</td><td>3</td><td>Relative refractory period duration</td><td>Na^+ channels recovery time</td></tr>
</table>

* The delay in firing of a thalamic cell following pre-synaptic stimuli ($t_{response}$) depends on the time it takes the cell to cross a threshold. The time for crossing the threshold depends on the *threshold* (increased in the “RRP” state relative to “Rest”), strength of the pre-synaptic stimuli and time interval between stimuli:

$$A_{H1-X}(t) = A_{H1-X}(t-1) + \sum_{index=1}^{T} E_{SN2-X_{index}} - C$$

where t is the elapsed time from the moment the thalamic cell enters the “GenerateAP” state,

$A_{H1-X}(t-1)$ is the thalamic cell’s excitability value (arbitrary units) at time t-1,

X is the *type* of information the thalamic cell and its SN2s relay, i.e., whisking (W), contact (C), or pressure (P),

$E_{SN2-X_{index}}$ is the effect of a pre-synaptic cell "*index*" of the corresponding *type* (X), on its thalamic cell’s excitability,

T is the number of secondary afferents of *type* X activated at time t,

C is a constant.

Once a thalamic cell crosses *threshold*, its excitability values are zeroed ($t = 0$; $A_{H1-X}(0) = 0$).

Thus the effect of an SN2 firing on its thalamic cell’s excitability depends on the synaptic strength ($E_{SN2-X_{index}}$) and decreases with time, as moving away from the firing time of the SN2 (embodied in C).

$A_{H1-X}(t)$ value is not changed if the thalamic cell is at the "absolute refractory period" state.

Cortical Whisking, Contact, and Pressure cells (H2-W,C,P)

<table>
<tr><th>Parameter</th><th>Units</th><th>Value</th><th>Description</th><th>Source</th></tr>
<tr><td>type</td><td>-</td><td>W,C,P</td><td>Cell type: whisking (W), contact (C), or pressure (P). H2-C were generated in the simplified TIP regulation model configurations; H2-W and H2-P were generated in the whisking- and touch-based TIP regulation configurations (a global parameter of the simulation), respectively (see Fig. 2).</td><td>(Yu et al., 2006; Deschenes and Urbain, 2009)</td></tr>
<tr><td>index</td><td>index</td><td>0-N</td><td>Each of the whisker's H1 cells of each type takes a different index; N depends both on the H1 type and the TIP regulation configuration (a global parameter of the simulation):
<table>
<tr><th></th><th>Whisking-based</th><th>Touch-based</th></tr>
<tr><td>H2-C</td><td>1400</td><td>1516</td></tr>
<tr><td>H2-P</td><td>-</td><td>3034</td></tr>
<tr><td>H2-W</td><td>3150</td><td>-</td></tr>
</table>
See Fig. 2.</td><td>(Yu et al., 2006; Deschenes and Urbain, 2009; Meyer et al., 2013)</td></tr>
<tr><td>$t_{response}$</td><td>msec</td><td>1</td><td>Time to generate action potential in response to stimuli from its pre-synaptic H1 cells.
Not a parameter; results from simulation dynamics*</td><td></td></tr>
<tr><td>t_{relay}</td><td>msec</td><td>See table</td><td>Conductance time of the stimulus along the cell's axon to its post-synaptic target (see Fig. 2). The value depends on the TIP regulation model configuration (a global parameter of the simulation):
<table>
<tr><th></th><th>Whisking-based</th><th>Touch-based</th></tr>
<tr><td>H2-C</td><td colspan="2">10</td></tr>
<tr><td>H2-P</td><td>-</td><td>1</td></tr>
<tr><td>H2-W</td><td>12-14*</td><td>-</td></tr>
</table>
* An integer in the specified range, with an equal probability.</td><td>(Matyas et al., 2010)</td></tr>
<tr><td>APTransTimes</td><td>-</td><td></td><td>A linked list of the to-be-transmitted action potentials (see "model behavior in statecharts" below. Each link contains a value of future time at which the action potential generated by this neuron should reach its post-synaptic target.</td><td></td></tr>
<tr><td>ARP</td><td>msec</td><td>1</td><td>Absolute refractory period duration</td><td>(Leiser and Moxon, 2007)</td></tr>
<tr><td>RRP</td><td>msec</td><td>2</td><td>Relative refractory period duration</td><td>Allows H2-Ws to fire at a maximal rate in response to thalamic stimuli, i.e., every 3 msec.</td></tr>
</table>

* The delay in firing of a cortical cell following pre-synaptic stimuli ($t_{response}$) depends on the time it takes the cell to cross a threshold. The time for crossing the threshold depends on the *threshold* (increased in the "RRP" state relative to "Rest"; value evaluated by GA), strength of the pre-synaptic stimuli and time interval between stimuli:

$$A_{H2-X}(t) = A_{H2-X}(t-1) + \sum_{index=1}^{T} E_{H1-X_{index}} - C$$

where t is the elapsed time from the moment the H2 enters the "GenerateAP" state,

$A_{H2-X}(t-1)$ is the cortical cell's excitability value (arbitrary units) at time t-1,

X is the *type* of information the cortical- and its thalamic cells relay, i.e., whisking (W), contact (C), or pressure (P),

$E_{H1-X_{index}}$ is the effect of a pre-synaptic cell "*index*" of the corresponding *type* (X), on its cortical cell's excitability,

T is the number of thalamic afferents of *type* X activated at time t,

C is a constant.

Once a cortical cell crosses *threshold*, its excitability values are zeroed ($t = 0;\ A_{H2-X}(0) = 0$).

Thus the effect of a thalamic cell's firing on its cortical cell's excitability depends on the synaptic strength ($E_{H1-X_{index}}$) and decreases with time, as moving away from the firing time of the thalamic cell (embodied in C).

$A_{H2-X}(t)$ value is not changed if the cortical cell is at the "absolute refractory period" state.

MN (ExtP, Int, ExtR)

Parameter	Units	Value	Description	Source
type	-	ExtP, Int, ExtR	MN *type*: extrinsic protractor, intrinsic, or extrinsic retractor	(Klein and Rhoades, 1985; Herfst and Brecht, 2008)
index	index	0-*N*	Each of the whisker's MNs of each *type* takes a different index; *N* depends on the MN *type*: ExtP_MN: 12 Int_MN: 30 ExtR_MN: 3	(Klein and Rhoades, 1985; Herfst and Brecht, 2008)
$t_{response}$	msec	1-4	Time to generate action potential in response to stimuli from its pre-synaptic sources (SN2s, CPG). Not a parameter; results from simulation dynamics*	
t_{relay}	msec	1	Conductance time of the stimulus along the cell's axon to its post-synaptic target	(Yetiser et al.; Martin and Biscoe, 1977)
APTransTimes	-		A linked list of the to-be-transmitted action potentials (see "model behavior in statecharts" below. Each link contains a value of future time at which the action potential generated by this neuron should reach its post-synaptic target.	
ARP	msec	2	Absolute refractory period duration	(Martin and Biscoe, 1977)
RRP	msec	3	Relative refractory period duration	Na^{+} channels recovery time

* The delay in firing of an MN following pre-synaptic stimuli ($t_{response}$) depends on the time it takes the cell to cross a threshold. The time for crossing the threshold depends on the *threshold* (increased in the "RRP" state relative to "Rest"; value evaluated by GA), strength of the pre-synaptic stimuli and time interval between stimuli:

$$A_{MN}(t) = A_{MN}(t-1) + E_{CPG} + \sum_{index=1}^{T} E_{SN2-X_{index}} - C$$

where t is the elapsed time from the moment the MN enters the "GenerateAP" state,

$A_{MN}(t-1)$ is the MN excitability value (arbitrary units) at time *t*-1,

E_{CPG} is the effect of the pre-synaptic CPG on its MN excitability,

X is the *type* of information the SN2 relays, i.e., whisking (W), contact (C), pressure (P) or detach (D)**,

$E_{SN2-X_{index}}$ is the effect of a pre-synaptic SN2-X number "*index*" on its MN excitability,

T is the number of secondary afferents of *type* X activated at time t,

C is a constant.

** Assume the 'direct excitation of retractor MNs' (E–R) configuration, i.e., SN2-Ws innervate all three types of MNs, SN2-Ps innervate the ExtR_MNs, and SN2-Ds innervate ExtP_MNs (see (Sherman et al., 2013, Fig. 3E)).

Once an MN crosses threshold, its excitability values are zeroed ($\mathrm{t} = 0;\ \mathrm{A_{MN}}(0) = 0$).

Thus the effect of a pre-synaptic source (CPG or SN2) firing on its MN excitability depends on the synaptic strength (E_{CPG} or $E_{SN2-X_{index}}$) and decreases with time, as moving away from the firing time of the pre-synaptic source (embodied in C).

$A_{MN}(t)$ value is not changed if the MN is at the "absolute refractory period" state.

Muscle (ExtP, Int, ExtR)

Parameter	Units	Value	Description	Source
type	-	ExtP, Int, ExtR	Muscle *type*: extrinsic protractor, intrinsic, or extrinsic retractor	(Haidarliu et al., 2010)
Ca_0	M	10^{-7}	Concentration of Ca^{2+} ions in muscle cytoplasm at rest	(Simony et al., 2010)
$Ca(t)$	M	$\frac{r_0\tau_c}{\tau_c-\tau_r}\left[e^{\frac{-t}{\tau_c}} - e^{\frac{-t}{\tau_r}}\right] + Ca(t-1)e^{\frac{-t}{\tau_c}}$	Concentration of Ca^{2+} ions released from the SR to the cytoplasm; $Ca(0) = Ca_0$	(Simony et al., 2010)
r_0	-	2.55	A constant	(Simony et al., 2010)
$r(t)$	-	$e^{\frac{-t}{\tau_r}}$	The fraction of open ryanodine receptors (RyRs); $r(t) = r_0$	(Simony et al., 2010)
t	msec		Elapsed time following MN stimulation. Initialized to zero at stimulation onset time	
τ_c	msec	7.4	Time constant of the decay of intracellular Ca^{+2} ions	(Simony et al., 2010)
τ_r	msec	5	Decay time constant of *r*	(Simony et al., 2010)
A	-	*	Force scaling factor	GA
stimuliNum	-	0-(size of innervating MN pool)	Number of MN stimuli in the last 4 msec	
threshold	index	$\frac{1}{3}$ of the innervating MN pool	Minimal number of *stimuliNum*, during a time-window of 4 msec, required for muscle contraction	

* Muscles force scaling factor:

Muscle *type*	Value	Description
Intrinsic	0.4	
Pseudo intrinsic	0.7	
Extrinsic protractor	$A = \begin{cases} 0.05, \text{CPG} - \text{induced activation} \\ f(x), \text{sensory feedback} - \text{induced activation} \end{cases}$	i.e., muscle's ExtP_MNs triggered by ExtP_CGP. i.e., muscle's ExtP_MNs triggered by SN2-D. When activated by SN2-D, *A*=f(x), is a function of the activated number of SN2-Ds (x) in response to whisker-object contact. f(x) ~ x (size principle of motor units recruitment); 0.05 ≤ f(x) ≤ 0.5
Extrinsic retractor	0.05	

Once a muscle successfully crosses its *threshold*, its parameters' updated values are passed to a Matlab function, which calculates muscle's force and transforms it into whisker motion. The calculation is beyond the scope of this study and is describes in detail in (Simony et al., 2010). Briefly, total muscle force, *F*, is composed of two components: $F = F_c + F_l$, where the F_c component depends on $Ca(t)$ and *A* as follows: $F_c = A\frac{Ca(t)^4}{1+Ca(t)^4}$, and the F_l component depends on muscle's length (See formulas (6)-(7) in (Simony et al., 2010)).

CPG (ExtP, Int, ExtR)

Parameter	Units	Value	Description	Source
type	-	ExtP, Int, ExtR	CPG *type*: extrinsic protractor, intrinsic, or extrinsic retractor	(Hill et al., 2008)
cycleDuration	msec	4	Time interval between successive stimuli of the corresponding type of MNs. Corresponds to CPG's firing rate.	GA
currentCycle	index	0-cyclesNum	Current cycle's number. Only at initialization, *currentCycle* gets a non-positive value*: 0,-2,-21 for ExtP, Int, ExtR CPGs	
cyclesNum	index	9,18,16	Number of successive stimuli by ExtP, Int, and ExtR CPGs. Corresponds to "Activate" state's duration**	(Hill et al., 2008)
silenceDuration	msec	114,78,86	for the ExtP, Int, and ExtR CPG, respectively. *silenceDuration* = 150 - *cycleDuration* * *cyclesNum* (150 msec is whisk cycle duration, i.e., protraction + retraction)	(Hill et al., 2008)

* At the beginning of the simulation *currentCycle* gets a non-positive value, resulting in a delayed activation of the CPG (delayed by |*currentCycle*|**cycleDuration*, i.e., by 0,8,84 msec for the ExtP, Int, ExtR CPGs (Hill et al., 2008)).

** Model execution results in the following periods of activity of the different CPGs throughout a whisking cycle:

CPG *type*	Active period [msec]
ExtP	0-36
Int	8-80
ExtR	84-148

Attentiveness module (X)

Parameter	Units	Value	Description	Source
minPerceivingTime	msec	0	A constant. The minimal period of time during which X will not respond to incoming contact events following convergence on object perception.	
lastPerceivingTime	msec		The last simulation time at which X converged on object perception.	
objectAccuracy		0-1	Current accuracy of perception of the inspected object.	
confidenceLevel		0.95	A constant. The minimal accuracy level above which the rat converged on the perception of the inspected object.	
deltaConfidence		0.33	A constant. The increase in *objectAccuracy* upon a single whisker-object contact.	

* The above values resulted in the whisker trajectories presented in Fig. S1A, i.e., three successive cycles of TIP generation, followed by one cycle with no TIPs. Note that for each whisker-object contact *objectAccuracy* is increased by *deltaConfidence* only at contact **onset** time.

Model behavior in statecharts

Neurons

Since the behavior of all types of neurons in the model is very similar, the behavior of a generic neuron is described. The statechart that defines the behavior of a generic neuron is displayed in (Sherman et al., 2013, Fig. 4B) and is explained in the text. Two orthogonal states were added (Fig. 4A, left and right areas, separated by a dashed line): one that represents the cell body's state and which contains four sub-states – those described in (Sherman et al., 2013, Fig. 4B), and one that represents the cell axon's state and which contains two sub-states: (1) "No transmission" (noTransmit) – in which the neuron does not have any action potential (AP) to transmit to its post-synaptic target, (2) "Transmit action potential" (transmitAP) – in which the neuron has one or more APs to transmit to its post-synaptic target. At any moment the neuron can be in exactly one sub-state of each of the two orthogonal states, such that the transitions between the sub-states at each side occur independently of the other side. Each time the neuron fires, i.e., moves from the "Generate action potential" to the "Absolute refractory period" state, a new transmission time, t_{trans}, is added to the end of a APTransTimes list, where t_{trans} = current simulation time + t_{relay} (see model parameters above). In addition the neuron sends a fire event to itself, which triggers a transition to the "Transit AP" state if the neuron is in the "No transmission" state. While in the "Transit AP" state, once the simulation time reaches the first t_{trans} in the APTransTimes list a stimulus is sent to the neuron's post-synaptic target. In the model, each type of neuron has its own statechart, which is very similar to the diagram in (Sherman et al., 2013, Fig. 4B), but with two major differences between the different types of neurons:

(1) Type of stimulus that triggers a neuron to fire:

Cell type	Firing depends on…
SN1-W	Whisker's angle and angular velocity
SN1-C	Contact time - upon touch
SN1-P	(1) Contact time - upon and during touch period (2) Radial distance of contact (stimulus strength)
SN1-D	Detachment time - upon detachment
SN2s,H1,H2, MNs	Strength of stimulus - must reach threshold

The firing probability of the above cells is specified in detail in Model parameters.

(2) Post-synaptic target*:

Pre-synaptic cell	Post-synaptic target
SN1, H2	SN2
SN2	H1, MN
H1	H2
CPG	MN
MN	Muscles

* The different types of pre-synaptic cells of each station innervate post-synaptic cells of different types (Figs. 1-2). Both pre- and post-synaptic cells usually relay the same type of information, except for the H2-SN2 connections in the wGATE+ model configurations. Assume the 'direct excitation of retractor MNs' (E–R) configuration for SN2-MN connections (see (Sherman et al., 2013, Fig. 3E)).

CPG, Muscle and Whisker

The statecharts of these elements are described in (Sherman et al., 2013, see text and Figs. 4A,C-D).

Two orthogonal states were added to the whisker's statechart (Fig. 4B, left and right areas, separated by a dashed line): one that regards whisker motion's state and which contains two sub-states – those described in (Sherman et al., 2013, Fig. 4D), and one that regards whisker-object contact's state and which contains two sub-states: (1) "Free" – in which the whisker does not touch any object, and (2) "Balked" – in which the whisker touches an object. At any moment the neuron can be in exactly one sub-state of each of the two orthogonal states, such that the transitions between the sub-states at each side occur independently of the other side. As explained in (Sherman et al., 2013), the angle and angular velocity of a whisker are constantly updated each time a muscle that is attached to the whisker transmits a move event. Every whisker can receive a move event from several muscles, and upon the first stimulation event, the whisker exits its initial "Rest" state and enters the "Move" state, in which it stays until its angle and angular velocity return to their resting values (i.e., $\theta(t) = \theta_0$ and $\dot{\theta}(t) = \dot{\theta}_0$). Independent of the "Rest"-"Move" transitions, each time the whisker receives a move event, it compares its angle to the objects' angles and calculates whether or not it is touching an object, and acts accordingly: if found in the "Free" (or "Balked") state and its angle is larger (or smaller) than that of the object, the whisker moves to the "Balked" (of "Free") state while sending a stimulus event to its post-synaptic Contact (or Detach) SN1s; otherwise, it stays in its current state.

Object

The statechart of this element is described in (Sherman et al., 2013) (see file S1 and Fig. 4B).

Manager

The Manager's behavior is not described here, as it basically helps overcome technical issues, such as synchronization between instances. This component does not have any equivalent biological entity.

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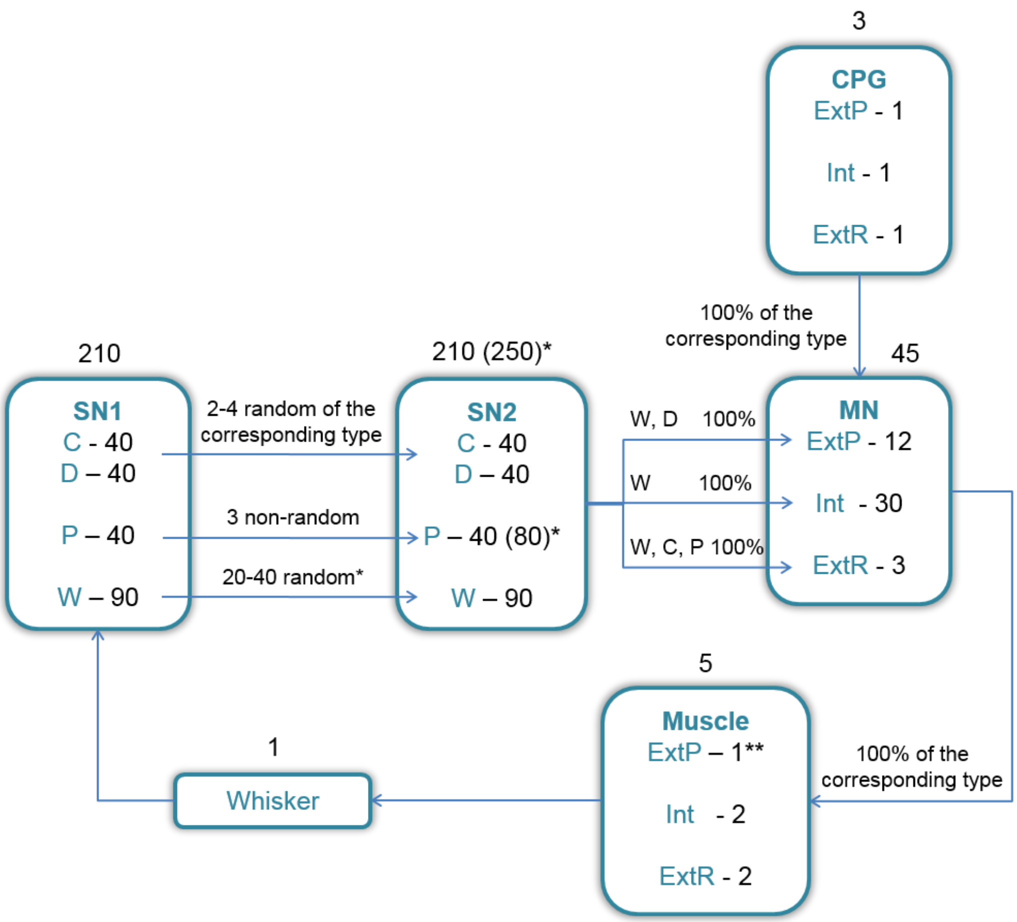
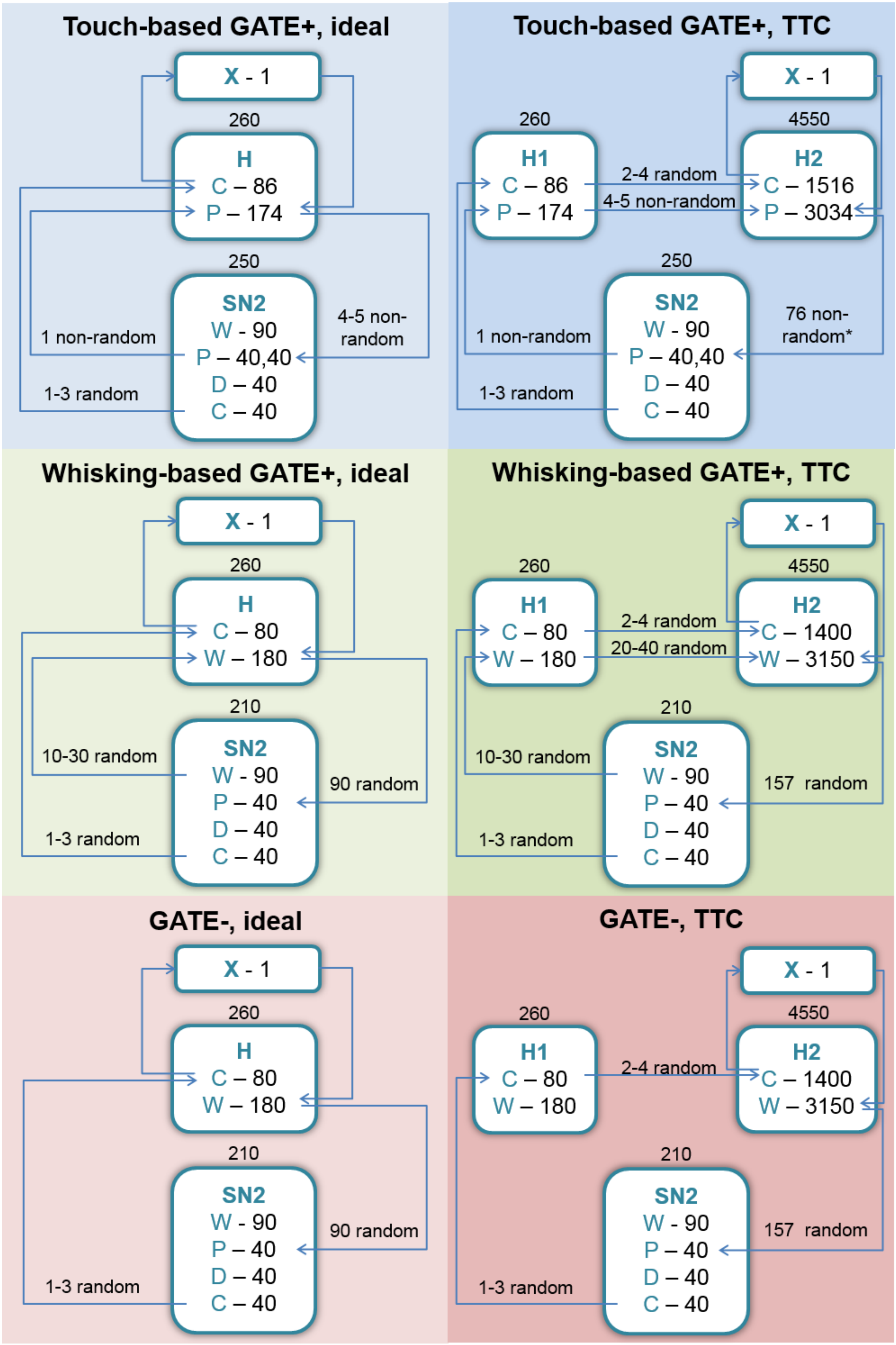


Figure 1. The number of elements that compose a single whisker's brainstem- (TIP generating) loop. Each whisker is innervated by a separated pool of primary afferent- (SN1), secondary afferent- (SN2)*, and motor efferent- (MN) cells, which contain tens of neurons of several subtypes, as indicated in the scheme. For example, a single whisker is directly innervated by 210 SN1s which include 40 contact (C), 40 detach (D), 40 pressure (P), and 90 whisking (W) cells. Each type of SN1s innervates the corresponding type of SN2s, where a single SN2 is innervated by a certain group of SN1s of the corresponding type as follows: a SN2 Contact (C) or Detach (D) cell is innervated by randomly chosen 2-4 SN1s; a SN2 Pressure (P) cell is innervated by 2-4 similarly responding SN1s; a SN2 Whisking (W) cell is innervated by randomly chosen 20-40 SN1s that innervate 3-13 whiskers, as shown in Fig. 3. Assuming the "E-R" TIP-inducing configuration (see (Sherman et al., 2013, Fig. 3E)), different types of SN2s innervate different types of MNs, with each MN innervated by all SN2s of the matched type. Each type of MNs innervates the corresponding type of muscle/s attached to the whisker (Sherman et al., 2013). In addition to this closed loop, all whiskers' MNs are innervated by the model central pattern generators (CPGs), with each CPG innervating all MNs of the corresponding type (Sherman et al., 2013). Note that no connections exist between sub-populations of neurons of a certain type (e.g., between primary afferent whisking (SN1-W) and pressure (SN1-P) cells).

* The pGATE+, wGATE+, and GATE- models contain 80, 40 and 40 SN2 Pressure cells, respectively (see Model parameters).

** Two (instead of one) extrinsic protractor muscles are attached to the most rostral whisker in rows A-B (Sherman et al., 2013, Fig. 1B).



Touch-based GATE+, ideal
X - 1
260
H
C – 86
P – 174
250
SN2
W - 90
P – 40,40
D – 40
C – 40
1 non-random
1-3 random
4-5 non-random
Touch-based GATE+, TTC
X - 1
260
H1
C – 86
P – 174
4550
H2
C – 1516
P – 3034
2-4 random
4-5 non-random
250
SN2
W - 90
P – 40,40
D – 40
C – 40
1 non-random
1-3 random
76 non-random*
Whisking-based GATE+, ideal
X - 1
260
H
C – 80
W – 180
210
SN2
W - 90
P – 40
D – 40
C – 40
10-30 random
1-3 random
90 random
Whisking-based GATE+, TTC
X - 1
260
H1
C – 80
W – 180
4550
H2
C – 1400
W – 3150
2-4 random
20-40 random
210
SN2
W - 90
P – 40
D – 40
C – 40
10-30 random
1-3 random
157 random
GATE-, ideal
X - 1
260
H
C – 80
W – 180
210
SN2
W - 90
P – 40
D – 40
C – 40
1-3 random
90 random
GATE-, TTC
X - 1
260
H1
C – 80
W – 180
4550
H2
C – 1400
W – 3150
2-4 random
210
SN2
W - 90
P – 40
D – 40
C – 40
1-3 random
157 random

Figure 2. The number of elements that compose a single whisker's higher- (TIP regulatory) loop in the different models. Each whisker is innervated by a separated pool of cells that composes the higher loop (H-loop), which contain tens of neurons of several subtypes, as indicated in the scheme. In the pGATE+ models (light- and dark blue), the SN2 Pressure (P) cells are divided into two subgroups such that one (40 low-threshold cells) projects to the input station of the H-loop, and the other (40 high-threshold cells) is innervated by the output station of the H-loop. In the wGATE+ models (light- and dark green), the SN2 Whisking (W) cells project to the input station of the H-loop, and the output station of the H-loop innervates the SN2 (high-threshold) P cells. In the ideal-loop configurations (light blue/green/red) the H-loop is composed of one station (H), which functions as both the input- and output station. In the trigemino-thalamo-cortical- (TTC) configurations (dark blue/green/red) the H-loop is composed of two stations such that the input station (H1) corresponds to the thalamic station-, and the output station (H2) to the cortical station of the paralemniscal/lemniscal pathway. In all models the attention-affecting cells of the output station of the H-loop (H2-att) innervate a single component, an attentiveness module (X), which projects back to the pressure- (pGATE+) or whisking- (wGATE+ and GATE-) relaying cells of the output station. Touch cells (C and P) along the H-loop are innervated by a few pre-synaptic cells, as occurs in the lemniscal pathway of the rats, and whisking-relaying cells (W) are assumed to be innervated by one order of magnitude more cells, as no data are available for the paralemniscal pathway (see Model specifications).

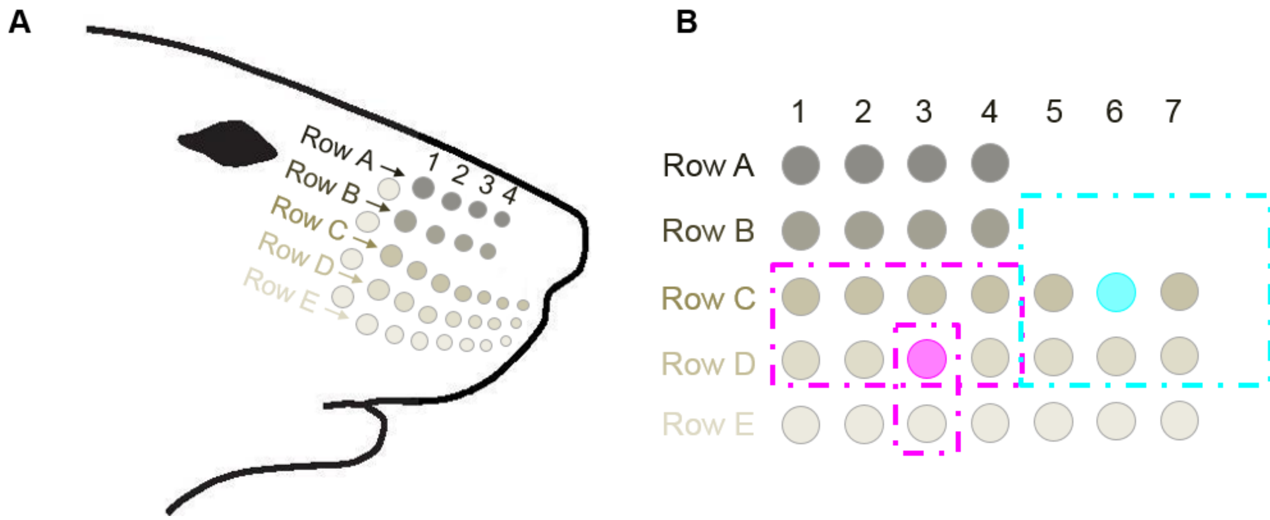
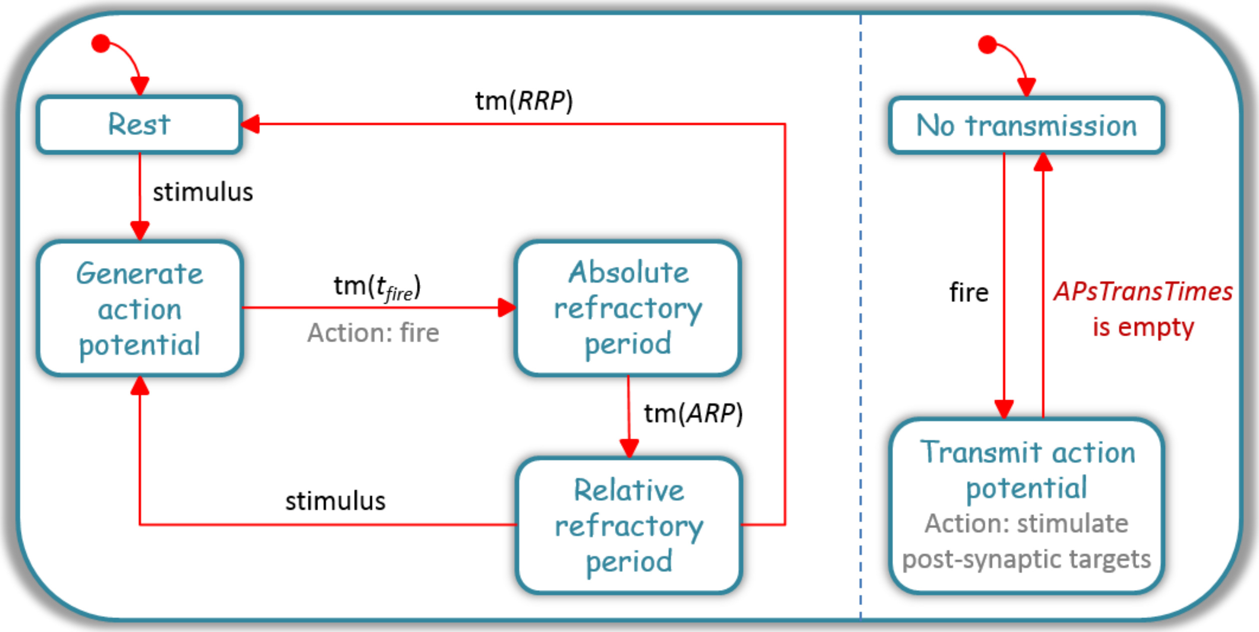


Figure 3. The receptive field of the whisking-relaying cells in the model. (**A**) One- of the two whisker pads simulated by the multiple-loop model. Each is composed of five rows of whiskers. (**B**) Exemplary receptive fields of whisking-relaying cells in the model. Each whisking-relaying primary afferent (SN1-W) directly innervated a single whisker. Each whisking-relaying secondary afferent (SN2) was innervated by a group of 20-40 SN1-Ws that innervated a matrix of 1-12 adjacent whiskers (see Model specifications). The matrix included the principal whisker (PW) of the SN2-W, positioned at row R_i and arc A_j, and 1-3 and 1-4 adjacent rows and arcs, respectively, whose numbers were raffled at the beginning of the simulation with equal probabilities. If one or three rows (arcs) were raffled, the closest rows to the PW were chosen, i.e., R_i (A_j) or R_{i-1}, R_i, R_{i+1} (A_{j-1}, A_j, A_{j+1}); if two rows (arcs) were raffled, the row (arc) of the PW was chosen together with one of the two adjacent rows (arcs) with an equal probability, i.e., R_{i-1}, R_i or R_i, R_{i+1} (A_{j-1}, A_j or A_j, A_{j+1}); if four arcs were raffled, the arc of the PW and its adjacent neighbors were chosen, together with one of the two 1-arc distant arcs, raffled with an equal probability, i.e., A_{j-2}, A_{j-1}, A_j, A_{j+1} or A_{j-1}, A_j, A_{j+1}, A_{j+2}. Discarded raffled adjacent rows (arcs) if these did not exist. For example, in one model execution the group of SN1-Ws that innervated whisker D3 (pink circle) could be raffled from a group of 90*8 SN1-Ws that innervated whiskers 1-4 in rows C-D (upper pink rectangle), and in another simulation from a group of 2*90 SN1-Ws that innervated whiskers D3-D4 (lower pink rectangle). For whiskers that did not have both upper and lower adjacent rows (or the 1-2 left and right arcs), the non-existent whiskers were discarded, e.g., the group of SN1-Ws that innervated whisker C6 (cyan circle) could be raffled from a group of 90*6 SN1-Ws that innervated whiskers 5-8 and 8 in rows B and C-D, respectively (cyan rectangle). Each whisking-relaying thalamic and cortical cell (H1-W and H2-W, respectively) was innervated by a group of 10-30 SN2-Ws and 20-40 H1-Ws, respectively, which innervated the same PW. Thus, the SN1-Ws in the model had single-whisker receptive fields, and the SN2-Ws, H1-Ws, and H2-Ws had multiple-whisker (1-12) receptive fields.

Note: the receptive fields described for the H1-W and H2-W are relevant only for whisking-based TIP-regulatory GATE+ models, with the latter relevant only for the trigemino-thalamo-cortical (TTC) configuration.

A



B

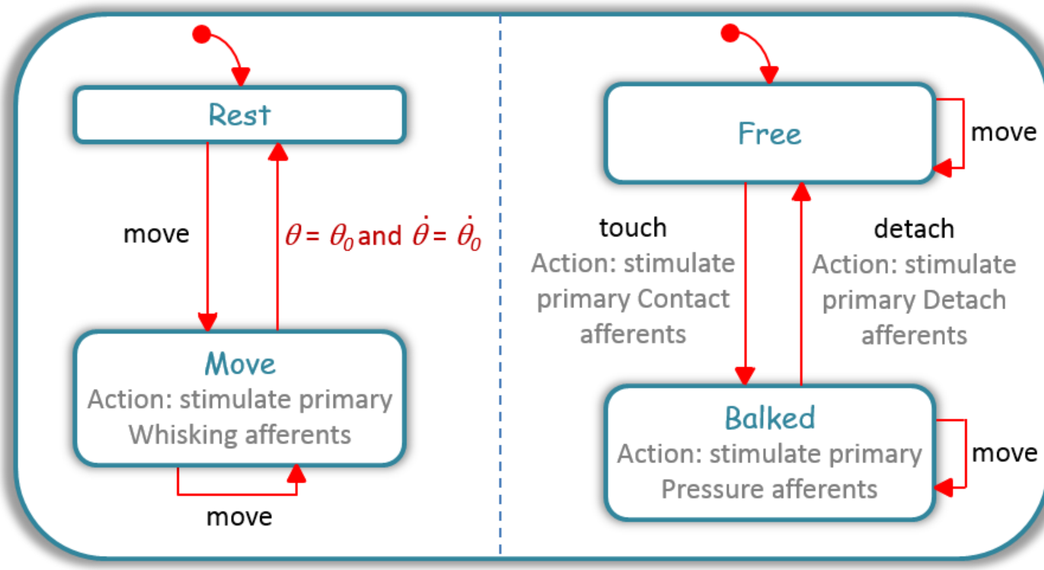


Figure 4. The statecharts in the multiple-loop model that were changed following the brainstem-loop model. Each statechart describes the behavior of an element of a certain type: (**A**) Neuron (**B**) Whisker. The blue boxes indicate the states of the element. The red arrows, together with the triggering events (black) and/or the conditions (red) written next to them, describe the transitions between the states. Actions are indicated in gray. ●→ points to the initial state upon model execution. © indicates a condition connector. tm(*X*) indicates a timeout of *X* ms; the values of the different *X* parameters are specified under Model parameters. When the model is executed, many copies of each statechart are generated, one for each of the actual components of the parent element. As the simulation advances, each component responds to various events by changing its states and parameter values accordingly, and by transmitting events to itself/other components.