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Space impacts temporal processing via a visual-dependent spatially organized neural architecture

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Supplementary Materials

Space impacts temporal processing via a visual-dependent spatially organized neural architecture

Amadeo, Maria Bianca^{a*}, *Cuppini, Cristiano*^{b,1}, *Tonelli, Alessia*^{a,c,1}, *Tammurello, Carolina*^{a,d,1}, *Setti, Walter*^a, *Campus, Claudio*^a, *Signorini, Sabrina*^e, *Cocchi, Elena*^f, *Bonino, Margherita*^g, *Tinelli, Francesca*^h, *Camicione, Paola*ⁱ, *Serafino, Massimiliano*ⁱ & *Gori, Monica*^a

^aUnit for Visually Impaired People (U-VIP), Istituto Italiano di Tecnologia, Genoa, Italy

^bDepartment of Electrical, Electronic, and Information Engineering “Guglielmo Marconi”, University of Bologna, Bologna, Italy

^cSchool of Psychology, The University of Sydney, Sydney, Australia

^dDepartment of Informatics, Bioengineering, Robotics and Systems Engineering (DIBRIS), Università degli Studi di Genova, Genoa, Italy

^eDevelopmental Neurophthalmology Unit, IRCCS Mondino Foundation, Pavia, Italy.

^fFondazione Chiossone, Genova, Italy

^gScientific Institute, IRCCS E. Medea, Bosisio Parini, Lecco, Italy

^hDepartment of Developmental Neuroscience, IRCCS Fondazione Stella Maris, Pisa, Italy

ⁱIRCCS Istituto Giannina Gaslini, Genova, Italy

¹These authors contributed equally to this work.

* Corresponding author: Maria Bianca Amadeo, Unit for Visually Impaired People (U-VIP), Istituto Italiano di Tecnologia, Via Melen 83, Building B, 16152 Genova, Italia, mariabianca.amadeo@iit.it, +39 0108172232

Text S1

Mathematical implementation of the model architecture

Every element of the network has been described by means of a first order differential equation, which simulates the integrative properties of the cellular membrane, and a steady-state sigmoidal relationship that simulates the presence of a lower threshold and an upper saturation for neural activation. The saturation value is set at 1, i.e., all outputs are normalized to the maximum. The term “activity” is used to denote the output of each area.

In the following, each element will be denoted with a superscript, r , referred to a specific region of the model ($r = A, T, Ai, Ti, Af$, or Tf , where A refers to the auditory input area, T to the tactile input area, Ai , and Ti to the auditory interneurons and tactile interneurons, Af , and Tf to the output “auditory first” and “tactile first” neurons, responsible for the temporal processing of the external stimuli, respectively). $u(t)$ and $y(t)$ are used to represent the net input and output of a given neural element at time t , respectively. Thus, $y^r(t)$ and $u^r(t)$ represent the output and the net input of the neural element simulating the region r , respectively. A generic neural element of a region r is described by the following differential equation:

$$\tau^n \frac{dy^r(t)}{dt} = -y^r(t) + F(u^r(t)) \quad (1)$$

where τ is the time constant and $F(u(t))$ represents the sigmoidal relationship:

$$F(u^r(t)) = \frac{1}{1 + e^{-s(u^r(t) - \theta)}} \quad (2)$$

s and θ are parameters which establish the slope and the central position of the sigmoidal relationship, respectively. For the sake of simplicity, in this work all the neural elements are described by using the same parameters (s and θ) and the same time constant (τ^n).

The net input that reaches a specific neural element (i.e., the quantity $u^r(t)$ in Eq. (1)) depends on the region it belongs to.

Input areas

Elements in these regions, Tactile and Auditory in Fig 3, process separately auditory and tactile external stimuli ($r = A, T$). Their net input is the result of three components.

The first, the external component, is the unisensory input $e^r(t)$, coming from the external world. The second, the crossmodal component, is the input, $c^r(t)$, from the area processing the other sensory modality, transmitted to the target neuron through the crossmodal synapses. The last component is the contribution of the feedback inhibitory synapses, $I^r(t)$, which is the effect of the interneurons excited by the other sensory region that interacts with the target element through inhibitory synapses.

The external input is simulated by means of a spatial Gaussian function, to mimic the uncertainty in the detection of external sensory stimuli. Assuming a stimulus of sensory modality r ($r = a$ or t) presented in the position p^f , the consequent input to the network can be written as:

$$e_j^r(t) = \begin{cases} I_0^r \cdot e^{-\frac{(d_j^r)^2}{2(\sigma^r)^2}}, & 0 \leq t \leq D^r \\ 0, & t > D^r \end{cases} \quad (3)$$

characterized by its duration D^r , its effectiveness I_0^r , and σ^r , which defines the degree of uncertainty in sensory detection (which establishes the overall number of elements in region r , activated by the same external stimulus). d_j^r is the distance between the neuron at position j and the stimulus at position p^r . To avoid undesired border effects, the external inputs are implemented as having a circular structure; hence, the distance d_j^r is defined as:

$$d_j^r = \begin{cases} |j - p^r|, & \text{if } |j - p^r| \leq N/2 \\ N - |j - p^r|, & \text{if } |j - p^r| > N/2 \end{cases} \quad (4)$$

The crossmodal input, $c_j^r(t)$, obtained assuming that each element receives projections from the region processing the other modality, is defined as:

$$\begin{aligned} c_j^A(t) &= \sum_{k=1}^N W_{jk}^{AT} \cdot y_k^T(t - \Delta t) \\ c_j^T(t) &= \sum_{k=1}^N W_{jk}^{TA} \cdot y_k^A(t - \Delta t) \end{aligned} \quad (5)$$

where Δt is a delay which represents the latency with which crossmodal inputs are exchanged between the two regions and W_{jk}^{AT} , W_{jk}^{TA} are the weights of these reciprocal connections, defined by a Gaussian function:

$$W_{jk}^{cd} = W_{default} + W_0^{cd} \cdot e^{-\frac{(d_{jk})^2}{2(\sigma^{cd})^2}}, \quad cd = AT, TA \quad (6)$$

Where $W_{default}$ represents a uniform term mimicking the inhibitory default configuration among sensory modalities before the development of maps alignment. W_0^{cd} and σ^{cd} are the effectiveness and the standard deviation of the synapses among the unisensory input regions, and d_{jk} is the distance between the postsynaptic neuron at position j and the presynaptic one at position k . As previously described for the lateral synapses, to avoid undesired border effects, also the crossmodal synapses are implemented as having a circular structure, hence:

$$d_{jk} = \begin{cases} |j - k|, & \text{if } |j - k| \leq N/2 \\ N - |j - k|, & \text{if } |j - k| > N/2 \end{cases} \quad (7)$$

Finally, the inhibitory input, $l^r(t)$, a unisensory element which receives from the interneuron of the other modality defined as:

$$\begin{aligned} l_j^A(t) &= \sum_{k=1}^N LI_{jk}^{AT} \cdot y_k^{Ti}(t) \\ l_j^T(t) &= \sum_{k=1}^N LI_{jk}^{TA} \cdot y_k^{Ai}(t) \end{aligned} \quad (8)$$

where $y^{Ai}(t)$ and $y^{Ti}(t)$ are the activities of presynaptic auditory and tactile interneurons respectively, and LI_{jk}^{AT} , LI_{jk}^{TA} are the strengths of the inhibitory synapses, defined by a Gaussian function:

$$LI_{jk}^{cd} = LI_0^{cd} \cdot e^{-\frac{(d_{jk})^2}{2(\sigma^{cd})^2}}, cd = AT, TA \quad (9)$$

LI_0^{cd} and σ^{cd} are the effectiveness and the standard deviation of the synapses among the interneurons and the unisensory input regions, and d_{jk} is the distance between the postsynaptic neuron at position j and the presynaptic one at position k . Similarly to the crossmodal connections, to avoid undesired border effects, also the crossmodal synapses are implemented as having a circular structure as described by the Eq. (7). In the model, we did not incorporate a delay for the cross-sensory inhibition, because the dynamics of the inhibitory effect has been chosen much longer than any other mechanism of the network (see below *Dynamics of each input component*), so the effect of a delay is already included in the time constant chosen for these projections.

Inhibitory interneurons

Elements in these two regions ($r = A_i, T_i$) are excited respectively by the auditory and tactile input areas, and they exchange inhibitory projections. Their net input is the result of an excitatory stimulus, $I_{ex}^r(t)$, coming from the corresponding unisensory input region through excitatory synapses, and an inhibitory component, $I_{in}^r(t)$, produced by inhibitory synapses from the other interneuron.

The excitatory components, $I_{ex}^r(t)$, targeting the auditory and tactile interneurons are defined as:

$$\begin{aligned} I_{ex_j}^{Ai}(t) &= \sum_{k=1}^N WI_{jk}^A \cdot y_k^A(t) \\ I_{ex_j}^{Ti}(t) &= \sum_{k=1}^N WI_{jk}^T \cdot y_k^T(t) \end{aligned} \quad (10)$$

where WI_{jk}^A and WI_{jk}^T are the weights of the excitatory connections from a unisensory input region to its corresponding interneuron element, implemented by a Gaussian function, as the previous connections:

$$WI_{jk}^r = WI_0^r \cdot e^{-\frac{(d_{jk})^2}{2(\sigma^r)^2}}, r = A, T \quad (11)$$

WI_0^r and σ^r are the effectiveness and the standard deviation of the synapses, and d_{jk} is the distance between the postsynaptic neuron at position j and the presynaptic one at position k . Similarly to the crossmodal connections, to avoid undesired border effects, also these synapses are implemented as having a circular structure as described by the Eq. (7).

The inhibitory input, $I_{in}^r(t)$, that an interneuron receives from the interneuron of the other modality, through inhibitory synapses, is constant and defined as:

$$\begin{aligned} I_{in}^{Ai}(t) &= LLI^{AiTi} \cdot y^{Ti}(t) \\ I_{in}^{Ti}(t) &= LLI^{TiAi} \cdot y^{Ai}(t) \end{aligned} \quad (12)$$

where $y^{Ai}(t)$ and $y^{Ti}(t)$ are the activities of presynaptic auditory and tactile interneurons respectively, and LLI^{AiTi} and LLI^{TiAi} are the strengths of the reciprocal inhibitory connections. These symmetrical synapses ($LLI^{TiAi} = LLI^{AiTi} = LLI$) implement the WTA mechanism between the two areas.

Output area

The two elements of this region ($r = Af, Tf$) receive a net input that is the sum of two stimuli: the first carried by long-range excitatory synapses, from the corresponding auditory and tactile input areas; the second, inhibitory, is the result of the reciprocal competition between the two elements.

The inhibitory input, $in^r(t)$, is defined as:

$$\begin{aligned} in^{AT}(t) &= L_{AT} \cdot y^{Tf}(t - \Delta t^m); \\ in^{TA}(t) &= L_{TA} \cdot y^{Af}(t - \Delta t^m); \end{aligned} \quad (13)$$

where $L_{AT} = L_{TA} = L$ are the weights of the reciprocal inhibitory connections among the units in the output region.

The excitatory input, $ex^r(t)$, is defined as:

$$ex^r(t) = \sum_{k=1}^N Wf^r \cdot y_k^r(t - \Delta t^m); \quad \forall r = A, T \quad (14)$$

where Wf^A and Wf^T are the weights of the excitatory connections from the unisensory input regions to the corresponding output element and are symmetrical: $Wf^A = Wf^T = Wf$. Δt^m is a delay, which represents the slightest latency with which stimuli from the pre-synaptic element are able to generate a response in the post-synaptic neuron.

Dynamics of each input component

The previous quantities, described by Eqs. (3, 8, 10, 12, 13 and 14), affect the input $u^r(t)$ of the corresponding postsynaptic element via a second order differential equation. By denoting with $o_i(t)$ the output of the differential equation for the generic input source $i(t)$ (described by any of Eqs. (3) to (9)) we have:

$$\begin{cases} \frac{d}{dt} o_i(t) = \delta_i(t) \\ \frac{d}{dt} \delta_i(t) = \frac{G_i^r}{(\tau_i^r)^2} i(t) - \frac{2 \cdot \delta_i(t)}{\tau_i^r} - \frac{o_i(t)}{(\tau_i^r)^2} \end{cases} \quad (15)$$

where G_i^r represents the gain and τ_i^r defines the time constant of the dynamics, for each region r , and input component i (Eqs. (3, 8, 10, 12, 13 and 14)). Eq. (15) implements a second-order impulse response with two coincident real poles. This is used frequently in neural modeling to mimic synaptic dynamics (Jansen and Rit 1995, Wendling, Bartolomei et al. 2002, Cuppini, Magosso et al. 2014, Cuppini, Ursino et al. 2020). In the model, in order to reduce the number of parameters, we choose the same values for G_i^r and τ_i^r , for the two sensory modalities (see Table 1S).

According to the previous description, the total input (namely $u^r(t)$) received by a neuron in region r , is computed as follows:

- i For the input regions, it is the sum of the external component (Eq. (3)), crossmodal term (Eq. (5)), and inhibitory feedback (Eq. (8)), filtered through the second order equation (Eq. (15)):

$$u^r(t) = o_e(t) + o_c(t) + o_l(t); \quad \forall r = A, T \quad (16)$$

- ii For the inhibitory interneurons, it is the sum of the excitation from the input region (Eq. (10)), and the effect of the WTA mechanism (Eq. (12)), filtered by Eq. (15):

$$u^r(t) = o_{I_{ex}}(t) + o_{I_{in}}(t); \forall r = Ai, Ti \quad (17)$$

- iii For the output region, it is the effect of the effect of the reciprocal inhibition (Eq. (13)) and the feedforward excitatory synapses (Eq. (14)), filtered by the differential equation previously described (Eq. (15)):

$$u^r(t) = o_{ex}(t) + o_{in}(t); \forall r = Af, Tf \quad (18)$$

Parameters assignment

The values of model parameters (see Table 1S) were assigned according to the criteria summarized below, based on findings reported in the literature. Parameters describing the elements of the network were assumed equal for the two sensory modalities, with the only exception of the external inputs, to reduce the number of ad hoc assumptions. Moreover, the values of the synaptic weights were adjusted to achieve the best fit between the model and the empirical behavioral data.

Parameters of individual neurons

The central abscissa, θ , was assigned to have negligible neuron activity in basal conditions (i.e., when the input was zero). The slope of the sigmoidal relationship, s , was assigned to have a smooth transition from silence to saturation in response to external stimuli. The time constant agreed with values (a few ms) normally used in deterministic mean-field equations (Treves 1993, Ben-Yishai, Bar-Or et al. 1995).

External input

Physiological evidence shows that in the brain, auditory and tactile processing are very fast, and exhibit short latencies (e.g., Recanzone, Guard et al. 2000). So, we set the time constants, τ_i^A and τ_i^T , for both modalities, used to reproduce the temporal evolution of the process of an auditory and a tactile stimulus in the early cortical areas, so that the input areas are activated by an external input 20-30ms after the stimulus, hence $\tau_i^T = \tau_i^A = 3\text{ms}$ has been chosen.

The strength of the external tactile and auditory stimuli (parameters I_0^T and I_0^A) are chosen so that the overall input elicits a response, in the input regions, in the linear part of the sigmoidal static characteristic (i.e., a slightly below saturation), while the standard deviations (σ_0^T and σ_0^A) are chosen to mimic the different sensory uncertainty in spatial detection associated to the two modalities, where the auditory is characterized by a lower spatial proficiency with respect to the tactile, hence $\sigma_0^A > \sigma_0^T$. The duration of the stimuli, $D^r = 10\text{ms}$, has been chosen to mimic stimuli used in Experiment 2.

Synaptic connections

The effectiveness of the feedforward excitatory connections targeting the output region (W^T and W^A) and the interneurons (WI^T and WI^A) is set so that an effective unisensory stimulus of sufficient strength (i.e., able to lead input areas close to saturation) evokes an activity in the upper part of the linear region of the sigmoidal activation function (i.e., close to the maximum activity in this area). These parameters were set to mediate an effective competition among the stimuli of different sensory modalities to mimic the experimental task of temporal discrimination.

These feedforward connections are characterized by a fast dynamic ($\tau_i^r = 3\text{ms}$; with $i = A, T, Af, Tf$). Moreover, feedforward connections to the output area present a delay Δt^m , to mimic the latencies of sensory processing from primary cortical regions to higher order prefrontal cortices and the lower detectable temporal asynchronies between sensory stimuli. We assigned to Δt^m a value $\Delta t^m = 50\text{ms}$.

Interneurons reciprocal inhibition, $I_{in}^r(t)$, implement the WTA competition. The effectiveness of the reciprocal synapses, LLI , is chosen high enough so that the “winner” interneuron is able to turn off almost completely the “loser” element. This element is characterized by a fast dynamic as well ($\tau_i^r = 3\text{ms}$). To set up the parameters of the inhibitory feedback synapses from the interneurons to the input regions, we considered the empirical results in the literature from (Crosse, Foxe et al. 2022) showing that two stimuli of different sensory modalities would compete with each other if presented temporally misaligned. The strongest cross-sensory inhibitory effect occurs for inter-stimulus intervals as short as 1000ms, but this effect decays slowly for longer time intervals between the stimuli. To simulate this result, the feedback inhibitory synapses in the model have slow dynamics, implemented by time constants for the feedback projections as large as to 180ms ($\tau_l^{Ai} = \tau_l^{Ti}$). In fact, with such a time constant, the inhibitory component provides the most significant contribution to the input regions of the other modality after almost 1000ms after stimulus presentation.

As stated above, the values of the inhibitory feedback connections (LI^{AT} , LI^{TA}), as well as parameters of crossmodal synapses, were set to reproduce the empirical data of Experiment 2.

The parameters of crossmodal synapses were defined based on empirical findings showing cortico-cortical interactions in case of audio-tactile tasks as early as 40ms after the stimulus presentations, both in animal models and in human studies (Kayser, Petkov et al. 2005, Zhang, Kwon et al. 2020, Fu and Riecke 2023). These authors, analyzing EEG data and high-resolution fMRI recordings, studied crossmodal activations and audio-tactile interactions in the auditory cortex (belt and parabelt regions) and in the tactile regions (S2) at very early post stimulus latencies. Empirical evidence supports the notion that crossmodal stimulation affects the sensory processing in different cortical regions, previously defined as modality specific. To simulate these results, we used the input to the neurons (i.e., quantity $u(t)$ in Eq. (1)) since this is indicative of field potentials, detected through EEG or MEG techniques, and/or synaptic metabolic activity, detected through fMRI. The dynamics of the reciprocal crossmodal projections have been chosen fast and symmetrical for both sensory modalities. Their time constant ($\tau = 15\text{ms}$) and the delay in crossmodal synapses, $\Delta t = 16\text{ms}$, simulating the latency with which the influence of a unisensory stimulus was detected in the area processing the other sensory modality, were selected so that the crossmodal component produces an effect with a rapid time course, affecting “the other region” after further 30-40ms.

For all the above elements, G_i^r the values have been chosen so that the elicited activity in the post-synaptic elements is in the linear portion of the sigmoidal relationship: as shown in Table S1, $G_i^r = 75$ for every synapse ($i = e, c, I_{ex}, I_{in}, in, ex$), except for the inhibitory feedback ($i = l$) where $G_l^r = 750$.

Neurons			
$\theta = 25$	$s = 0.3$	$\tau = 3 \text{ ms}$	
External inputs			
$I_0^A = 3$ $\sigma^A = 32$	$I_0^T = 2.6$ $\sigma^T = 4$	$D^r = 10 \text{ ms}, r=A,T$	
Synapses			
$G_i^r = 75; i = e, c, I_{ex}, I_{in}, in, ex$ $G_l^r = 750; \tau_l^r = 180 \text{ ms}$	$\tau_k^r = 3 \text{ ms};$ $k = e, I_{ex}, I_{in}, in, ex$	$\tau_c^r = 15 \text{ ms}$	
Input Regions		Interneurons	Output area
$W_0^{AT} = W_0^{TA} = 2$	$LI_0^{AT} = LI_0^{TA} = 0.5$	$WI_0^A = WI_0^T = 2.5$	$L = 10$

$\sigma^{AT} = \sigma^{TA} =$ $0.5W_{default} = -0.25$ $\Delta t = 16 ms$	$\sigma^{AT} = \sigma^{TA} = 5$	$\sigma^A = \sigma^T = 0.5$ $LLI = 10$	$Wf = 0.25$ $\Delta t^m = 60 ms$
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Table S1. Parameters value

Text S2

Results

Experiment 1

Predictors	X ² (degree of freedom = 1)	p
Hand	0.04	0.8
Distance	1.04	0.3
Age	0.03	0.9
Hand * Age	0.09	0.8
Distance * Age	0.13	0.7
Hand * Distance	3.34	0.07
Hand * Distance * Age	1.98	0.2

Table S2 Results of the model PSE~Hand(*Same, Different*) * Distance(*Far, Close*) * Age + (1|subject)

Experiment 2

Predictors	X ² (degree of freedom = 1)	P
Hand	1.56	0.2
Group	0.16	0.7
Age	1.52	0.2
Hand * Age	1.32	0.3
Hand * Group	0.05	0.8
Age * Group	0.01	0.9
Hand * Group * Age	2.12	0.1

Table S3 Results of the model PSE~Hand(*Same, Different*) * Group(*Sighted, Blind*) * Age + (1|subject)