A Model of Spatial Development from Parieto-Hippocampal Learning of Body-Place Associations

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Abstract

Infants' ability to orient their actions in space improves dramatically after their sixth month when they start to plan the correct motion of their hands for reaching objects. Recent developmental studies speculate that this enhancement of spatial memory corresponds to the activation of the hippocampal system that shapes the parieto-motor cortices for long-term spatial representation. We suggest that the mechanism of phase precession, which plays an active role in the para-hippocampal cortices to transform the continuous body signals into a precise temporal code could contribute as a key component for learning body-place associations. In a computer simulation of a nine-months old baby, we show how the hippocampal system transforms the input signals from the arm muscles into a phase code, the parietal system uses it then to build a topological map of reaching locations cells combined with eyes vision cells. It follows that one body posture can be retrieved back from estimating visually its location (e.g., for a reaching task).

keywords: phase precession, body-place association, peripersonal space, body image

1.   Introduction

The way infants perceive the space around them (i.e., infants' spatial representation) relies on two different mechanisms that mature separately during the first year (Bremner et al., 2008). Accordingly, the *earlier-developing* mechanism achieves a spatial correspondence of default body parts and the *later-developing* one remaps dynamically the position of the limbs. Piaget theorized that this developmental shift of spatial cognition during infancy corresponds to a stage-like transition from an egocentric representation to an allocentric one (Piaget, 1936). In this paper, we propose to model how such binding between the body dynamics and the external spatial cues emerges during development and the neural mechanisms it underlies.

Considering the earlier-developing mechanism, infants under six months of age learn to correlate the dynamics of their own bodily motions which permit them in return to build up simple physical rules and causal relationships for spatial tasks: e.g., solid objects cannot pass through other solid objects. During these perceptual experiences, infants appear to be sensitive to the temporal extent of their own sensory-motor activity by detecting the temporal contingencies across the modalities. These temporal associations shape a primitive representation of the spatial body, although not-yet mature. For instance, Rochat explains how simple it is to confuse infant's perception of its own body by adding just small delays to the visual feedback during self-observation (Rochat, 1998).

This peculiar situation nevertheless improves when 6 months-old children start to acquire an allocentric representation of their peripersonal space. During this period, infants become capable to categorize space from visual cues, to re-orient their body with respect to its own motion, to change viewpoints and to perform mental rotations (Newcombe and Huttenlocher, 2006). Some developmental studies attribute the spatial improvements of this period to the maturation of the hippocampal system and its surrounding cortex (Nelson et al., 2006). Indeed, the hippocampus is known to play an important role for processing the allocentric spatial information (O'Keefe and Burgess, 2005). Particular hippocampal neurons, known as place cells, have been found to respond to spatial locations where the animal is, whereas other types of hippocampal cells have been found to respond to the eye gaze direction (Rolls, 1999) or to the whole-body motion.

Interestingly, EEG's activity investigations on infants aged 2-11 months revealed an increase of theta synchrony – the natural rhythm of the hippocampus around $6\,Hz$– in the parietal and pre-

motor lobes during handling and reaching as well as during sucking and gazing (Futagi et al., 1998, Del Giudice et al., 2009). These observations suggest *(i)* that the hippocampal system could play a central role during the first year for constructing the spatial representation of the body into the sensori-motor networks (i.e., the body image) and *(ii)* that its theta rhythm could be involved in infant's preference for motion contingency and sensory-motor binding. The hippocampal processing of one body's action using the theta rhythm could shape the parietal cortex for body-place associations in the same way it shapes the hippocampal "place cells" for navigation purpose, by creating parieto-motor "reaching cells" for manipulation task (Graziano, 2006, Save and Poucet, 2009).

In contrast to more traditional memory systems, theta phase coding as done in the hippocampus is argued to facilitate the online memory storage of continuous signals (Hasselmo et al., 2009, Sato and Yamaguchi, 2009). When conventional memory models code spatio-temporal sequences with discrete states (e.g., nodes) and transition rules between these states for goal directed behavior (c.f., (Gaussier et al., 2002, Gabalda et al., 2007, Fuke et al., 2008, Nabeshima and Kuniyoshi, 2010)), theta phase coding forms associations between continuous states and continuous actions with the use of oscillations for encoding temporal intervals (Hasselmo et al., 2009); a neural mechanism particularly useful for updating the body posture in a continuous manner. Since motion coincidences between perceived actions and motor programs are hypothesized to be learnt through hebbian learning during self-observation (Del Giudice et al., 2009), we suggest that this later mechanism provides the ground for contingency detection and learning of one's body dynamics.

Based on these assumptions, we simulate the activity of the infant's hippocampal system to represent movements in continuous space and to learn the body image into the cortical network. We perform our experiments on a computer simulation presenting the common characteristics of a 9 month-old infant with an accurate model of its musculo-skeleton system and of its spinobulbar system, see (Kinjo et al., 2008). We constrain nonetheless our study to the body signals coming from the arms' muscles spindles, the joint angles from the shoulder-elbow-wrist system and the eye's vision cells. During sensory-motor exploration, the specific phase relation produced between the entorhinal cells – that is, the contingency matching across signals– organizes the cortical memory into a map of "reachable regions" cells via Hebbian learning. The visual cells finish to merge the neighbouring cells from each others and to refine
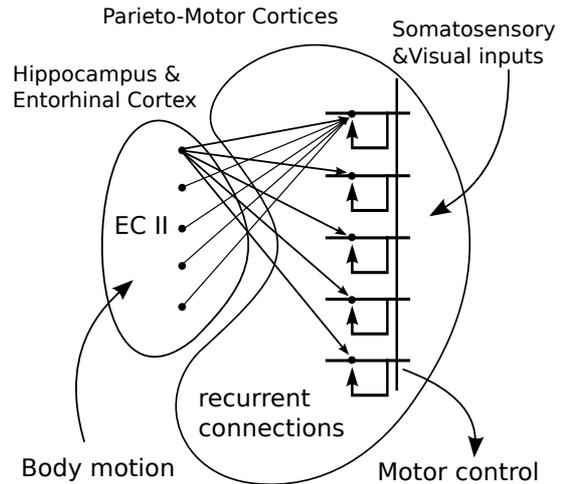
Figure 1: Basic structure of the parieto-hippocampal model. ECII retranscribes the amplitude's variations of the body signals into a temporal code and the cortical layer learns the associated postural cells that it binds recurrently with the visual signals via Hebbian learning.

their locations into the map.

The paper is organized as follows. In the first section, we describe the architecture of the cortico-hippocampal model formed by the ECII system and the parietal network with their respective neural architecture inspired by (Hasselmo et al., 2009, Sato and Yamaguchi, 2009, Izhikevich, 1999): ECII generates a theta phase code of the body posture and the recurrent links in the parietal network associate the reach-like neurons from each other into a topological map. We present then the characteristics of our baby simulator and the input/output body signals associated with it. At the body level, the spinal cords dynamics explore freely the sensory-motor configurations in a self-organized fashion, while at the brain level, ECII transforms the bodily changes into a temporal code that the parietal network learns afterwards. Over time, the parietal system constructs a topological map from the postural cells and the visual cells by linking the most congruent ones; e.g, like during hand-regard. We can estimate then the location of one reaching area and its associated postural configurations from visual information only. We discuss further the relevance of this framework to seize the statistics of the body and its links to social skills to discriminate self and others from a developmental and neurophysiological perspective.

2. Neural Models

We present in this section the basic structure of the parieto-hippocampal system which transforms the input signals (e.g., the body posture) into a temporal code and stores it as a topological memory.
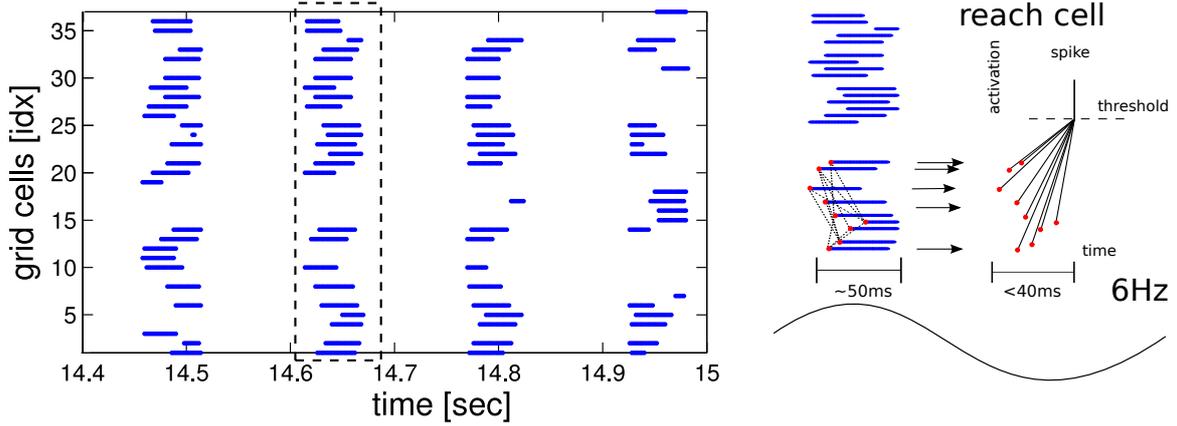
Figure 3: Parieto-hippocampal interface for coding spatial memory. The parietal system receives the temporal codes from the ECII layer (left), which trigger its associated "reach cells" above a certain threshold and every theta cycles (right). The recurrent links between the reach cells reinforced via the asymmetric Hebbian learning create a map.
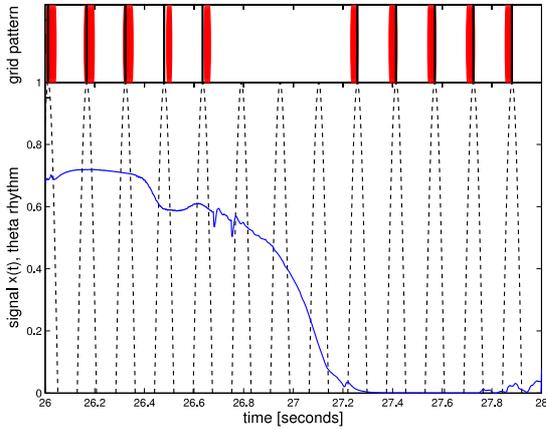
Figure 2: Phase coding in ECII. The speed signal $s(t)$ of the signal $x(t)$ (in blue) modulates the dendrite phase $\phi_D(t)$, the carrying signal, relative to the baseline phase of soma, $\phi_S(t)$ (dashed lines). Their respective sum produces a firing pattern (in red), in advance or in retard with respect to $\phi_S(t)$, used further for the read-out.

2.1   the ECII layer

The ECII layer is composed of individual cells that generate the phase code. Each cell consists of two oscillatory neurons, the soma and the dendrite, that realize a phase modulation function of an external signal (Hasselmo et al., 2009). The frequency of the soma f_S is the baseline frequency of the cell (i.e., the baseline theta rhythm) whereas the dendrite's frequency f_D carriers in its phase the speed signal $s(t)$ of a particular signal x: $s(t) = \Delta x / \Delta t$. The amplitude variation of one signal, which means its speed, modulates the phase of the dendrite.

In our experiments, the soma has the frequency $f_S = 6.42\,Hz$ and the dendrite's frequency f_D equals

to:

$$f_D(t) = f_S + s(t)B \tag{1}$$

where the constant B modulates the influence of the external input on the intrinsic frequency f_D. Under this scheme, the dendrite phase $\phi_D(t)$ varies along with $f_D(t)$ and proportionally to $s(t)$ and the baseline phase of the soma ϕ_S increases constantly at each time step:

$$\begin{cases} \Delta\phi_D = 2\pi f_D(t)\Delta t, \\ \Delta\phi_S = 2\pi f_S \Delta t \end{cases} \tag{2}$$

Using the temporal information from its two units, the cells can then efficiently represent the signals variations by embedding within their phase the phase difference between the modulated frequency of the dendrite and the static frequency of the soma. The cell function $g(t)$ is defined as follows:

$$g^{ECII}(t) = \Theta_D[\cos(\phi_D) + \cos(\phi_S)] \tag{3}$$

where Θ represents the Heaviside step function for any value above the threshold D set to 1.4. There, the cell $g(t)$ fires everytime the dendrite and the soma are near in phase, which achieves the read out into a discrete code. We plot in Fig. 2 the phase coding of a particular signal $x(t)$ (in blue) computed from its speed $s(t)$ by the dendrite and the soma (dotted lines) in the EC layer, and the cell $g(t)$ (in red). The dendrite frequency follows the variations of the signal speed and an interference pattern in the cell is produced every time the dendritic phase goes near the soma's one. The advance or retard in phase relative to ϕ_S retranscribes the signal's amplitude.

2.2   the parietal layer

The architecture of the parietal system differs from the ECII layer by the recurrent connections it has
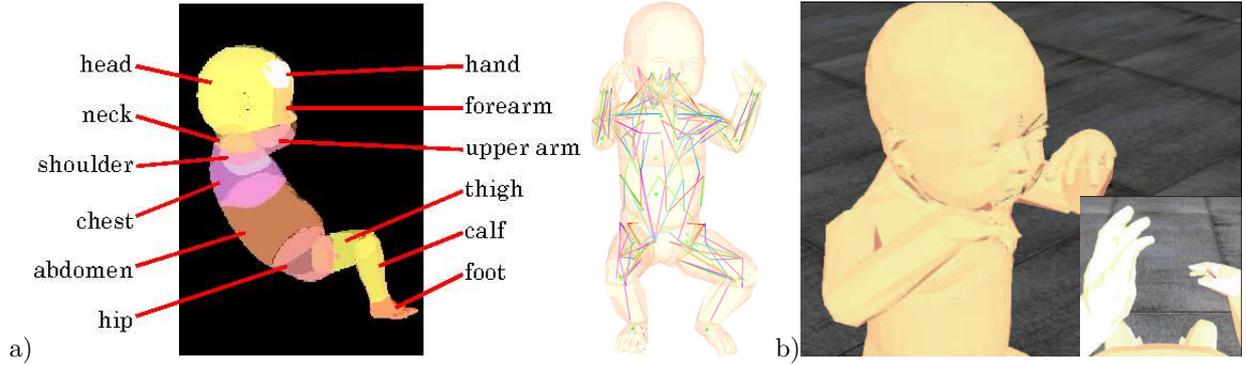
Figure 4: Overview of the infant model. (a) Body part name of the infant model with 198 muscles. In this paper, we control only the left and right arms (the hand, the forearm, the upper arm and the shoulder) which are constituted each by 37 muscles and 4 joint angles. (b) eye view and third person view of the infant model.

between its units. The network follows the principle of a self-organizing map that creates reach cells from the current body posture. Each ECII unit is connected to all the parietal cells with distinct plastic synaptic connections and each parietal cell learns a specific temporal code from a group of ECII units different from the other cells, see Figs. 1 and 3. Reinforcement learning relies on a Hebbian mechanism sensitive to the temporal delays Δt between the neurons firings; that is, sensitive to their phase relations. The temporal window is characterized by the time delay $\Delta t = t_j - t_i - \eta_{i,j}$ between the pre-synaptic ECII neuron spiking t_i and the post-synaptic parietal neuron firing t_j, where η represents the synaptic conduction delay between the two neurons. The plasticity of the synaptic weight $w_{i,j}$ between the ECII neurons i and the parietal cells j depends on the delay and the order of the firings $\eta_{i,j}$. A winner-take-all algorithm connects the most significant parietal cells j to the ECII cells i if the temporal firings Δt of all cells are circumscribed within an interval below $3\,ms$. If no parietal cells satisfy the new body configuration, a novel cell is added to the network.

Two concurrent mechanisms regulate the synaptic conductance (weight) between the parietal neurons, namely the long-term potentiation (LTP) that increases the synaptic strength between the neurons, and long-term depression (LTD) that decreases it. The LTP mechanism reinforces the synaptic links of the firing neurons (post-synaptic neurons) with the preceding ones that fired earlier (pre-synaptic neurons) in an interval range $\Delta t > 0$ whereas the LTD mechanism decreases those in the reverse order when $\Delta t < 0$. These two mechanisms produce a competitive and asymmetric learning. The synaptic weights w evolve according to eqs. 4 and 5:

$$\begin{aligned} w_{i,j}(t+1) &= w_{i,j}(t) + \Delta w, \\ \eta_{i,j}(t+1) &= \frac{\eta_{i,j}(t) + \Delta t}{2} \end{aligned} \quad (4)$$

$$\Delta w = \begin{cases} -A_- \exp\left(\ \Delta t/\tau_-\right) & \text{if } \Delta t < 0 \quad (LTD) \\ A_+ \exp\left(-\Delta t/\tau_+\right) & \text{if } \Delta t \geq 0 \quad (LTP) \end{cases} \quad (5)$$

with τ_- and τ_+ the parameters that bound the temporal window of synaptic activation (here, the phase angle), and A_- and A_+ their strength. We choose $\tau_- = \tau_+ = 5$ and $A_- = A_+ = 1$. The weights are circumscribed in the interval $[0, 10]$.

3. Baby simulator

We use an extensive model of the musculo-skeleton system and spinal cord system reproducing the average characteristics of a 7-9 months-old infant (Kinjo et al., 2008), see Fig. 4 a). It is composed of 198 muscle spindles and tendons which comply to external pressure or to the position control of the spinal cords' central pattern generators (not presented here). In our experiments, we freeze the whole body motion except the arms to study only the postural mapping of the reaching locations along the visual signals. Each arm possesses 37 muscles controlled by the spindles length that can vary between a contraction mode and a release mode (position normalized between $[0, 1]$), and by the joint angles in the shoulder (3 d.o.f.) and the elbow (1 d.o.f.). The spindles and the joint angles provide thus the signal speed $s(t)$ to the ECII units (2×37 cells and 2×4 cells). We set $B = 1$ for the spindles signals and $B = 0.2$ for the joints signals.

The infant simulation's vision system treats the eye field visual information to watch its own hands motion, see Fig.4 b). The visual information from each eye is reduced to a 11×11 pixels square filtered by optical flow to detect the location of motion within the image, see Fig. 5. The pixels coordinates are transformed into one dimensional vector sent to the parietal system (2×121 cells). We set $B = 0.3$.

4. Experiments

We propose to study how the natural motor primitives are learnt along their spatial locations within the visual field during self-exploration of the arms motion, especially during hand-regard. The newly learnt body-place associations will permit then to re-active one muscle configuration of the arm from the estimated visual location; e.g., for reaching.

4.1 Calibrating the body image, encoding motor coordination

In our simulation, the physical embodiment of the central pattern generators in the spinal cords – their modelling is explained in (Kinjo et al., 2008)– self-organizes the motion behavior of the infant's arms. Over time, the muscles are contracting their dynamics to certain configurations only and the most redundant coordinations constitute then the repertoire of the motor primitives.

During this random exploration in the sensory-motor space, the hands move freely toward different spatial locations, crossing from time to time the eye field, see Fig. 5. There, the visual system tracks the motion and the location of the hand, while the motor system records the actual configuration of the muscles. Fig. 6 plots the activity of the visuo-motor system for a period of 3 seconds which corresponds to the evolution of the muscles activity of both arms (raster plot of the spindles' signal amplitude) and of the left eye visual information (raster plot of the activated pixels). One can observe from the graph that there is not a strict one-to-one correspondence between the patterns in the vision field with those of the muscles which indicates it will be difficult to learn some probabilistic rules based on the amplitude signals only and that one efficient learning system should encode the precise signal values. The hippocampal system plays such a functional role and encodes a precise snapshot of the body dynamics (i.e., the exact angle of each joint) that can be used further to reconstruct one trajectory of the body posture.

The encoding is realized in two steps: the entorhinal cortex remaps first the body signals into a phase code that the parietal cortex learns and combines after with the other sensory signals. Fig. 7 presents the phase code of the right hand signals only produced at the ECII level during self-motion; a close-up of the dynamics is given in Fig. 3. The relative advance or retard in phase to the baseline theta rhythm f_S retranscribes the correct length of the spindles; an advance in phase corresponds to the contraction of the spindle whereas a retard in phase corresponds to its elongation. Besides, the phase differences between the cells retranscribes their respective phase relations and thus, the actual arm's posture.

These temporal relations, which represent a pos-

Hand Regard - optical flow

$t_1 = 1.4\,sec.$ $t_3 = 1.6\,sec.$ $t_5 = 1.8\,sec.$
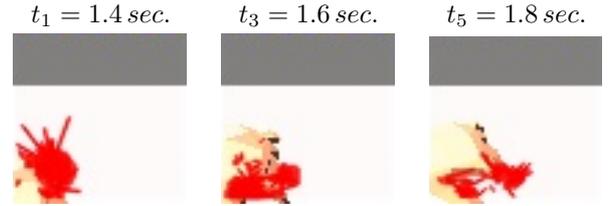
Figure 5: Hand regard. Visual sequence when the left hand moves in front of the eye field. The visual system detects the optical flow of the hand motion and its location in the eye field.
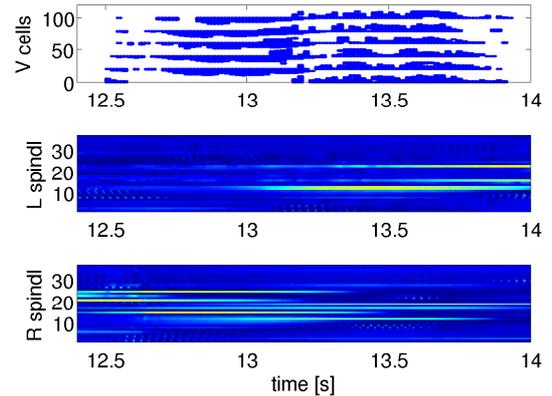
Figure 6: Raster plot of the arms muscles' activity during self-exploration in the sensory-motor space, when the infant moves its arms displayed in the lower-part. The graph in the upper-part reproduces the variations of the optical flow when the hands cross the vision field of the left eye. The correspondence problem between visual and motor modalities can be solved if the temporal relationships, the motion contingencies between body posture and optical flow, are learnt.

tural code, can then be learnt by the parietal system as a spatial code. During sensory-motor exploration, novel locations are explored by the hands and new postural cells are added to the parietal map.

We display in Fig. 8 the raster plot of the parietal map's reach cells and the trajectory in space of the left hand in which we superimposed the activity of four cells with different colors. Each cell fills out one specific region in space that sometimes overlaps with other regions. The code produced can serve then to shape the overall structure of the parietal system into a topological map where the neighbouring reach cells have a higher probability to fire contingently than those from farthest reaches, see Fig. 9 a). The connections between pre- and post-synaptic reach cells are reinforced with respect to their temporal order and the weights retranscribe the spatial relations between the cells. The graph in Fig. 9 b) reconstructed from the weight matrix models the cells' spatial relation presented in Fig. 8; i.e., the yellow and green
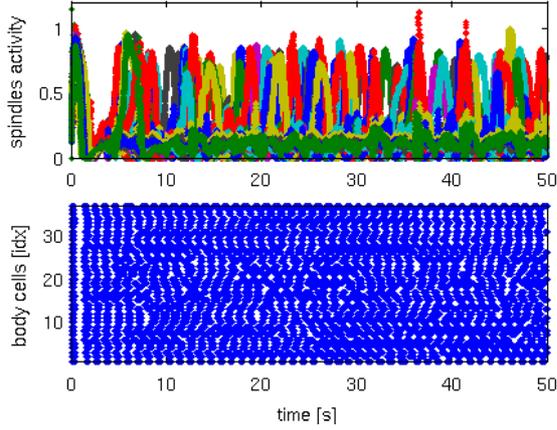
Figure 7: Raster plot of the muscles' activity from the body and grid cells firing in ECII. The advance in phase or the retard in phase of the grid cells reproduce the signal variations of the muscles spindles. The relative spatio-temporal patterns correspond then to the specific muscle configuration.
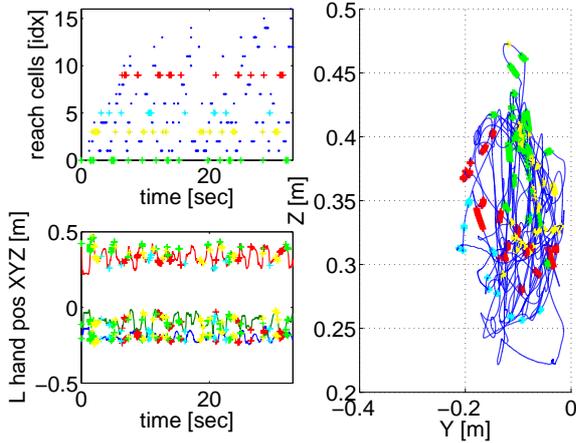
Figure 8: Raster plot of the reach cells relative to the spatial trajectory of the left hand. The superimposed colours indicate when the reach cells are firing in the upperleft raster plot and to which spatial regions they correspond to when the hand is moving around (right).

cells are far from the cyan and red cells.

4.2 Evaluating the body position from vision, reaching and retrieving visuo-motor associations

The neural map learns the body-place associations by detecting the contingencies between the proprioceptive signals. Its structure can be refined by re-estimating the body location in the visual field and by merging the redundant cells.

We plot in Fig. 10 the spatio-temporal patterns in the vision map and the respective raster plots of the left and right reach cells when the hands move
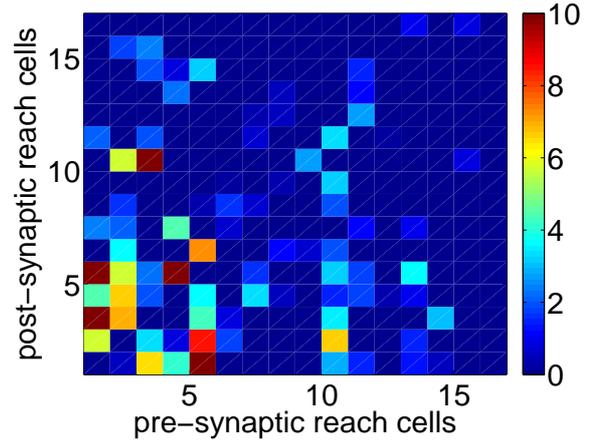
a)
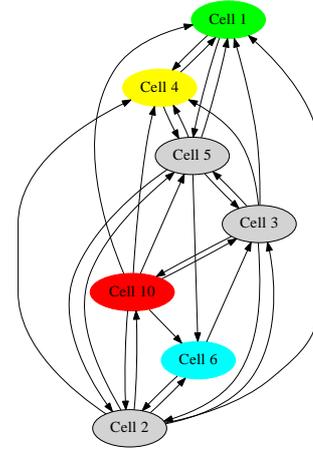
b)

Figure 9: Reach cells' connection matrix w between pre- and post-synaptic neurons in the parietal layer. In a), The asymmetric Hebbian learning constructs a topological map where the weights indicate the relative distance between the cells. In b), sub-graph reconstructed from the weight matrix.

in front of the eye field. Over time, the vision cells reinforce their links with the contingent reach cells. The reach cells not-yet wired, which are close in the peripersonal space but distant in the postural space – i.e., when two postural configurations completely different, from the same hand or from the other, reach the same point– can then be binded from the vision information; see Fig. 11.

These associations can permit then to estimate the location of the arm and its limbs configuration from the visual stimuli only as it is the case during reaching when an object is entering inside a particular region. We stop the learning stage and start the retrieval task. In this mode, ECII does not receive anymore the signals from the body and we control the body signals directly from the learnt synaptic connections. The visual inputs activate their asso-
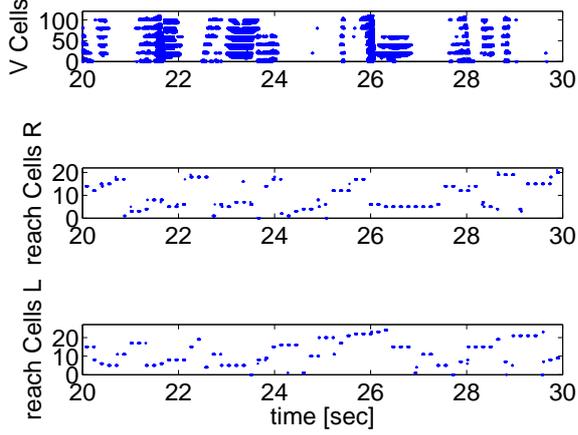
Figure 10: Specific spatio-temporal patterns in the parietal system of the left-arm and the right-arm during motion in front of the eye field. The vision map can refine the parietal organization by discriminating the reach cells from each other or by combining them if they occupy the same visual region.

a)

b)
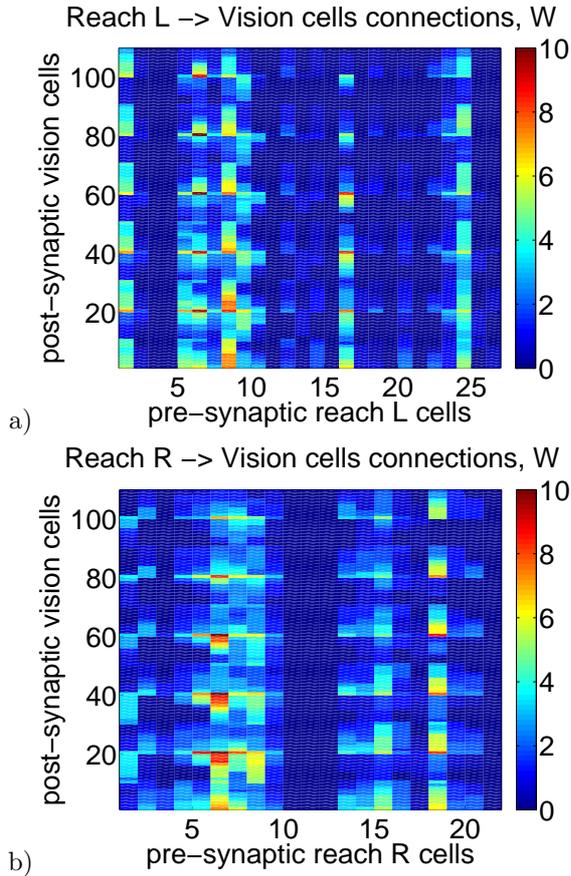
Figure 11: Synaptic conduction matrices between reach cells and visual cells. Reach cells of the left and right arm that occupy the same visual regions are combined with respect to others; respectively a) and b).
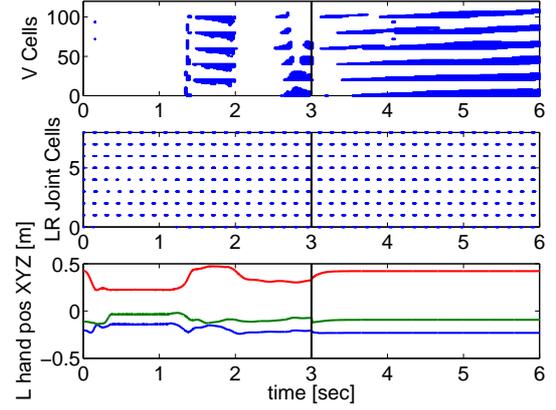
Figure 12: Activation of one selected reach cell from visual inputs at $t = 3.0\,sec$ and retrieval of the arms joint angles and hand position.

ciated reach cells which trigger at their turn their respective postural configurations. The reactivation of a specific phase code is done with the equations set below that synchronizes the phase of one specific reach cell j to the one of its pre-synaptic ECII neuron i (Izhikevich, 1999) relative to its synaptic conduction delay $\eta_{i,j}$ and synaptic strength $w_{i,j}$, such that if the cell i fires, then we have:

$$
\begin{cases}
H_{i,j} &= \phi_D^i(t) - 2\pi f_S\,\eta_{i,j} - \phi_D^j(t), \\
\Delta\phi_D^j &= \Delta\phi_S + w_{i,j}H_{i,j}.
\end{cases}
\tag{6}
$$

where $H_{i,j}$ is the phase distance between the two cells. Over time, $\phi_D^j(t)$ synchronizes to a certain period and the body signal x_j from the joint angle can be retrieved back then by demodulation using the formula:

$$
x_j(t) = \frac{\phi_D^j(t) - \phi_S(t)}{2\pi B}
\tag{7}
$$

It follows that the stimulation of the vision cells located in the left-side of the vision field triggers the associated reach cells as specified by the connection matrix in Fig. 11 a). Slowly, the compound network converges to a specific phase code in few hundreds of milliseconds and the hand stabilizes to a specific configuration and spatial location, see Fig. 12.

5. Discussion

Adults perceive space as a seamlessly reliable modality which permits them to be unaware of the complex neural machinery behind the manipulation of objects or the reaching to one location. It is however a competence that newborns lack at birth. To succeed in these spatial tasks, infants have to learn first how to combine various kinds of signals to intrust the position of the body limbs and to transform the whole-body activity into spatial coordinates.

Some recent developmental studies speculate that this enhancement of spatial memory could correspond to the activation of the hippocampal system that maps a spatial representation of the environment in an allocentric fashion (Newcombe and Huttenlocher, 2006, Nelson et al., 2006). We suggest that the mechanism of phase precession in the para-hippocampal cells could be essential for sensory-motor integration and the construction of the spatial representation of the body during the first year. The hippocampus could shape then the parieto-motor cortices that include the mirror neurons system (Del Giudice et al., 2009) and the visual receptive fields, which remap dynamically the frames of reference of the peripersonal space: the *reachable* space around the body.

The ability to perceive the spatial boundaries of *oneself* body parts will serve later on to self-other differentiation, self-perception and to higher cognitive skills in general such as social interaction and imitation, which require the imitator to solve the correspondence problem by mapping visual information into into his own body space.

Acknowledgments

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