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Chapter 1

**NEURAL MODELS FOR SOCIAL DEVELOPMENT IN
SHARED PARIETO-MOTOR CIRCUITS**

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ABSTRACT

This chapter reviews several computational models of the ontogenetic and epigenetic mechanisms that contribute to the construction and to the functioning of the shared sensory-motor circuits in the parieto-motor cortex. The primary role of these shared circuits, which include the so-called mirror neurons system, is found to transform the sensorimotor activity to deal with the real-time interaction in the environment. However, many evidences indicate that their role also pervade to social cognition, which makes them particularly important to study regarding their contributions to infant's motor and social development. We suggest that the special organization of the shared maps in the parieto-motor cortex that are capable to integrate multiple modalities and to avoid timing discrepancies, may present the characteristics of complex networks. Our simulations comfort the hypothesis that (1) the functional integration realized in those networks may be done by the reinforcement learning mechanism of spike timing-dependent plasticity and that (2) its regulation role may permit to understand the functions that sustain the neural representation of the bodily self –, like self-perception and body representation,– and of inter-subjectivity, like action understanding and self-other differentiation. Finally, these computational considerations may furnish some arguments for a decentralized (non motor-centric) view of the brain advantageously organized critically to allow functional integration within these circuits. Besides, any ontogenetic or epigenetic dysfunctions at one of these different stages could have dramatic consequence to later cognitive development as it is hypothesized to occur for autism.

Key Words: spiking neural networks, mirror neurons, sensorimotor integration, self-other representation
AMS Subject Classification: 92C42, 92C20, 68T05, 68T40.

INTRODUCTION

This chapter reviews some neural models developed in our laboratory to replicate the ontogenetic and the epigenetic construction of the sensorimotor circuits in the parieto-motor lobes. The shared circuits in the monkey and the human's parietal and motor areas are formed from reciprocal and anatomical connections that work in parallel for transforming sensorimotor information [Ferrari et al., 2009, Murata and Ishida, 2007]. Although their primary functions are aimed at interacting in the physical world by processing the multimodal sensory information about objects into motor commands, modern neurosciences attribute them a far broader role to engage oneself into the social world. The principal evidence comes from the finding by Rizzolatti and colleagues of a particular class of neurons in the monkey F5 motor area, which is firing both when the monkey executes one action *and* when he is observing someone else executing it [Rizzolatti et al., 1996, Gallese et al., 1996]. The metaphor of a mirroring mechanism between the sensory and motor apparatus for generating one action and for understanding those of others has been retained to name this special class of neurons found primarily in the motor circuits and then in the parietal cortex: like the F5 pre-motor area, the ventral intraparietal (VIP) area in the parietal cortex embeds also multimodal neurons that merge signals from visual, proprioceptive, auditory and somatopic systems [Sakata et al., 1997, Caggiano et al., 2009]. These VIP neurons are involved in the representation of the space within reach, the peripersonal space,

which encodes a body image at the skin surface aimed at locating the relative position of the body-parts and of the objects nearby in body-centered coordinates [Rizzolatti et al., 1997]. By extension, these mirror-like neurons describe not only how the body interacts *physically* in the environment but also how the bodily-self binds *socially* with others. These features of the mirror neurons (MN) have deep implications as they may furnish some grounds on how higher cognitive skills could have arisen from the neural extent of the body representation itself as it is argued for empathy [Decety and Sommerville, 2003, Decety and Jackson, 2004, Bufalari et al., 2007], “theory of mind” [Fogassi et al., 2005, Fujii et al., 2008], the roots of language [Rizzolatti and Arbib, 1998] and even corporeal awareness [Keysers and Gazzola, 2006, Rizzolatti and Fabbri-Destro, 2008]. One challenge for computational neuroscience is therefore to understand how these shared networks in the parieto-motor lobes have appeared and how they function to uphold the intersubjective self: how sensory and motor systems permit to represent oneself actions and to derive those of others? How they let oneself to perceive others as “like me”? Reversely, how structural dysfunctioning in parietal-motor connections are linked to functional impairments as it is hypothesized to occur for autism? This chapter will present works on the modeling of the functional and structural organization of the mirror neurons system [Pitti et al., 2008], its functioning for representating oneself actions and for understanding those of others [Pitti et al., 2009a], its possible development during infancy for constructing infant’s agency [Pitti et al., 2009b] and infant’s body image [Pitti et al., 2010].

0.1. mirror neurons systems as complex networks

The neuro-anatomy of the cortical circuits presents some specific properties that can permit us to figure out the neural mechanisms underlying their functioning, their development as well as the causes of their impairing. Conversely, these properties can serve us for engineering brain-like networks and to furnish as well some information theoretical considerations about their overall organization and efficiency [Sporns et al., 2004, Sporns, 2009]. For instance, the structural connectivity of the circuits in the parieto-motor lobes is found surprisingly sparse and distributed over large neural populations [Bullmore and Sporns, 2009], although they effectively integrate multimodal signals and support a broad range of cognitive functions [Murata and Ishida, 2007]. At the neuron level, many neuro-anatomical observations report that the mirror neurons represent a very few proportion of motor neurons with respect to the population of “pure motor neurons” that do not fire to action observation; mirror neurons represent up to 10% to 30% of these pure motor neurons which are not multimodal. Nonetheless, the small proportion of mirror neurons does not preclude the motor circuits to respond accurately to bodily and environmental events. One might wonder then how these networks achieve good responsiveness despite the scarcity of the mirror neurons (imbalanced distribution) and the density of their connections? We suggest that the efficiency of the MNS to respond so accurately to timely signals comes from a *critical* organization of its neural connectivity with a topology somewhat similar with the neural organization of a complex network [Sporns, 2010]. Our viewpoint may be supported by recent studies which indicate a hierarchical organization of the motor repertoire [Graziano, 2006, Lestou et al., 2008] and of the brain regions in general [Bullmore and Sporns, 2009]. Complex networks have been demonstrated to have remarkable information processing capabilities –e.g., coordi-

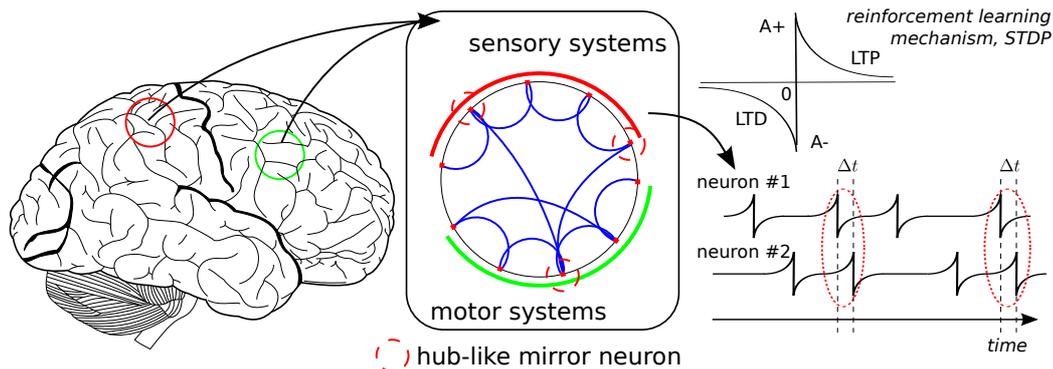


Figure 1. Proposed architecture for the functional organization and the multimodal integration in sensorimotor networks and in mirror neurons through Hebbian reinforcement learning mechanism (spike timing-dependent plasticity, STDP). The parsimony of mirror neurons with respect to their incredible ability to integrate multimodal signals suggests that the networks on which they rely are organized *critically*, alike complex networks. Like the mirror neurons, small-world networks display also high performance information processing with an organization structured around very scarce but well-connected hub-like elements.

nated dynamics organized over multiple sub-networks— *because* they exhibit efficiently distributed connections within hierarchical architectures. Certain types of complex networks, like small-world networks for instance, are found also to rely on a small fraction of *hubs*, which are nodes in the network with a relatively high number of connections [Watts and Strogatz, 1998, Newman, 2003]. Given that these networks are also sensitive to timing and that they are ubiquitous in the cerebral cortex, we think that they are pertinent models to simulate the functional integration of shared circuits in the parieto-motor cortices and that MNs-like circuits may encompass the common characteristics of default-brain networks [Bullmore and Sporns, 2009, Newman, 2003]. This may provide some information theoretical arguments to criticisms about the MNS [Dinstein, 2008, Hickok, 2009] and to the traditional motor-centric view of the brain. Therefore, rather than devising about the specific location and the numbers of MN (i.e., where the MN are), we may look instead at their connectivity and centrality within the global network in which they belong to (i.e., how well they are connected).

0.2. reinforcement learning of mirror neurons' connections

One key to integrating different types of information into a cohesive neural representation appears to lie in the encoding of the temporal relationships of cell firing. From a biological viewpoint, the regulation mechanism responsible for the functional integration in cortical neurons is the one of Spike Timing-Dependent Plasticity (STDP, cf. [Bi and Poo, 1998, Abbott and Nelson, 2000]). Information processing in distributed networks is performed with the precise timing due to STDP that reinforces the links of the most congruous neurons. Over time, the most congruous neural pairs aggregate them-

selves into coherent neural patterns whereas the less congruous ones delete their links. Keyzers first proposed that STDP could shape the specific connectivity and structural organization of the mirror neurons-like circuits to represent actions with millisecond order precision [Keyzers and Perrett, 2004]. In line with the learning hypothesis of the MN, we further develop that the functional integration in the learnt sensorimotor circuits sustains then the neural representation of the body in action [Lestou et al., 2008, Rizzolatti et al., 1996]. That is, various perceptual experiences in the environment will modulate differently the levels of integration in the sensorimotor circuits whereas the disrupting of sensorimotor integration will cause perceptual discrepancies. It follows that interacting with someone else, understanding his actions or imitating them should reconfigure the MNS and change the way it operates: experiences that differ from those typically encountered will re-activate one subject's own sensorimotor neurons branching from a different neural pathway whether the same modalities are available or not [Heyes, 2010]. This biologically-inspired mechanism based on reinforcement mechanism may furnish some indications on how a shared sensorimotor space is constructed to represent others and to engage with them. Moreover, it is in line with Gallese's simulation theory [Gallese, 2005] and Meltzoff's "Like me" theory [Meltzoff, 2007]). It supports furtherly the view that mirror neurons may be not innate systems, but rather acquired from learned perceptual-motor links during early development and that MN could have emerged from a mostly unstructured network of learning spiking neurons.

0.3. cortico-hippocampal scenario for the development of mirror neurons

Although no one knows where the mirror neurons come from, it is believed that they are acquired very early during development to endow infants with the necessary social abilities to interact with others [Heyes, 2010]. Meltzoff demonstrated for instance that newborns are capable to imitate facial gestures off-the-shelf which suggests that the bonding of human newborns is either innate or acquired from an early imprinting of the body image [Meltzoff and Moore, 1977]. He proposes that this mirroring mechanism may be based on a supramodal representation constructed from intra-uterine motor babbling experiences, which links the facial organs end-states contiguous with each others like tongue-to-lips, tongue-between-lips, tongue-beyond-lips [Meltzoff, 1997]. The successful replicating of neonatal imitation in monkeys by Ferrari argues furthermore for the commonality of an early recognition mechanism of self-other equivalences in mammals development which may be based on "mouth mirror neurons" for facial and ingestive actions [Ferrari et al., 2009]. Heyes proposes that this mirroring mechanism could be based on the reinforcement learning of sensorimotor contingencies which assumes that visual (sensory) representations of action simultaneously seen and executed become linked to motor representations (encoding somatosensory information and motor commands) through Hebbian learning [Brass and Heyes, 2005, Heyes, 2010]. Del Giudice and colleagues furtherly advance that the associative learning of sensorimotor circuits may involve the hippocampus since EEG's activity investigations on infants aged 2-11 months have revealed an increase of theta synchrony – the natural rhythm of the hippocampus around 6 *Hz*– in the parietal and premotor lobes during handling and reaching as well as during sucking and gazing [Futagi et al., 1998, Del Giudice et al., 2008].

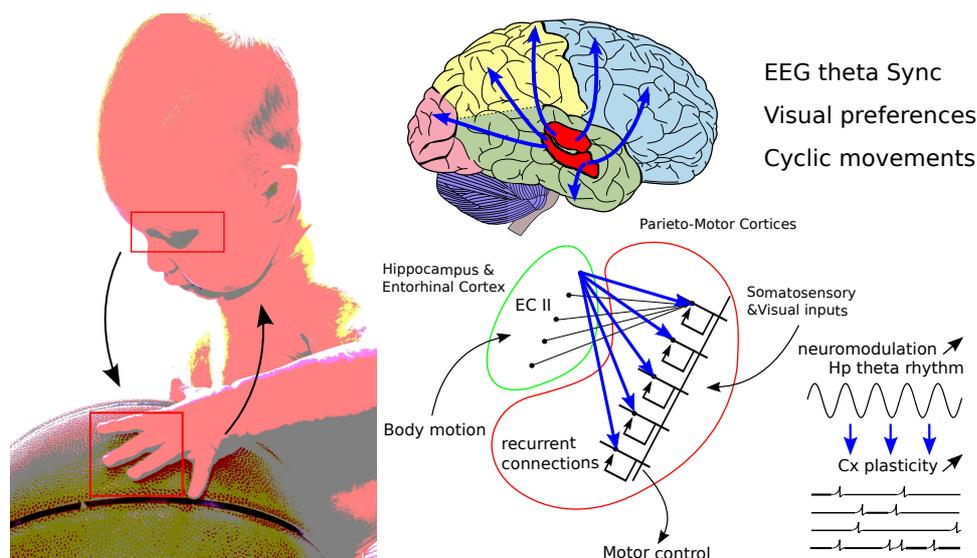


Figure 2. Proposed framework for sensorimotor learning and basic structure of the parieto-hippocampal model. The entorhinal region ECII retranscribes the amplitude's variations of the body signals into a temporal code and the cortical layer learns the associated postural cells that it binds recurrently with the visual signals via Hebbian learning.

This current proposal has the advantage to agree with the previous hypothesis and with other developmental theories which attribute also a prominent role to the hippocampal system for cortical development during the first year [McClelland et al., 1995, Nelson, 1995]. Considering mammals consolidation learning, it is known for instance that the hippocampus stores recent experiences in short-term memory and transfers them into long-term memory in the cortex for memory consolidation. The infant's preferences for motion contingency and sensory-motor binding could be explained then by the attentional signals coming from this subcortical area. It is known also that the neuromodulator acetylcholine (ACh) in the hippocampus contributes to the generation of the hippocampal theta rhythm and to cortical development by supporting attention and the learning of new memories [Hasselmo, 2006]; e.g., for the acquisition of new motor skills. If we reckon that the para-hippocampal system is an important center for processing spatial memory and transforming body signals, and that theta-burst stimulation –i.e. mimicking the hippocampal signals– is found to induce LTD-like plasticity in adult M1 for motor learning and retention [Huang et al., 2005], then these observations may suggest that hippocampal dynamics map or support the long-term spatial representation of the body (i.e., the body image) and the motor repertoire into the cortical sensori-motor networks. Thus, in the same way the entorhinal cortex transforms one body's actions and constructs “place cells” in the hippocampus for navigation purpose, we propose that the entorhinal cortex could shape “reaching cells” in the parieto-motor cortices for body-place associations and manipulation tasks [Graziano, 2006, Save and Poucet, 2009].

In the following, we show through simulations that hebbian learning can indeed leads

to the emergence of properties that resemble those of the MNS in networks mostly random but *embodied*; that is, through perception and action loops [Pfeifer and Bongard, 2006]. We organize this chapter as follows. We will present first how one efficient neural organization can emerge from mostly unstructured neural networks receiving bodily coherent inputs from different modalities with a timely-based reinforcement learning [Pitti et al., 2008]. The biologically plausible mechanism of Spike Timing-Dependent Plasticity rules out the contingency detection between neurons so that robust clusters distributed among the sensorimotor networks can assemble themselves during embodied interactions within the environment [Pitti et al., 2009a]. The associations between neurons of different modalities can serve then to predict or to simulate expected signals from other modalities. This can permit to reactivate one complete action pattern from partial information only, like during the observation of one action. We propose that the social features of the MNS –e.g., the perception of oneself body ownership and agency– are also based on these principles [Pitti et al., 2009b]. Moreover, we hypothesize that they may develop from hippocampal learning during early infancy which could structure the long-term spatial memory of the body in the cortical maps [Pitti et al., 2010]. Any ontogenetic or epigenetic dysfunctions in one of these particular stages could have then some dramatic consequences to later motor and cognitive skills learning as it is hypothesized to occur for autism.

RESULTS

1. Neural structure anatomy

The remarkable properties of the mirror neurons to fire either to actions performed or to actions observed and their attributed roles in social cognition question profoundly the classical views on the motor system’s organization. Parallely, the many researches and reviews done on the monkey MNS, its recent observation in the human nervous system [Keysers and Gazzola, 2010, Mukamel et al., 2010] as well as the arguments addressed lately [Hickok and Hauser, 2010, Rizzolatti and Sinigaglia, 2010] permit to dress an overall good picture of its characteristics and functionalities. Nonetheless, few is known about its underlying neural mechanisms and its functional organization, although many computational algorithms replicating its functions have been modeled [Oztop et al., 2006].

One genuine feature of MN we found worthy to investigate was its timing integration performance in regard to the rareness of this class of neurons: we mean by rareness that the mirror neurons are a relative small portion in comparison with the larger population of pure motor neurons –10 to 30 percents of motor neurons only present effective MN-like visuo-motor congruency, [Dinstein, 2008]– and we mean by timing integration performance or coherency performance that the mirror neurons population can be classified into two groups either as strictly congruent neurons (30 percents) or as broadly congruent neurons (60 percents) depending on their responses to the observation and execution of effective actions [Gallese et al., 1996]; i.e., the congruency to the strict motor action or to the broader goal of the action is translated into a rate code. It is remarkable that these features do not compromise their responsiveness either to executed and to observed actions, even when the action sequence’s end is occluded. Instead, we suggest that it is *because* they pos-

sess those characteristics that they can perform well. We propose therefore that, in order to rely on such an asymmetric distribution of neurons, the MNS must be critically organized as a complex network [Watts and Strogatz, 1998, Barabasi and Albert, 1999, Newman, 2003, Sporns, 2010]. Efficient neural connectivity may permit to supply critical neurons (i.e., the mirror neurons) fulfilling the functional integration in a network.

MN may suggest, *prima facie*, that few neurons are necessary to represent actions. However, such reasoning can only make sense if MN are understood parts of a larger network and belonging to many neural clusters merging different modalities. We propose that each of these clusters may generalize the spatio-temporal structure of one action sequence and the organization of these clusters could form the motor repertoire. In addition, they can be organized in a hierarchical manner at different description levels as observations of the motor system indicate it [Graziano and Aflalo, 2007, Lestou et al., 2008]. We can understand then that these mirror neurons must be efficiently connected within this network to support timing integration. Reversely, their damages can cause the degradation of the network performance and of its functional integration, which is considered one hypothesis of the cause for autism [Just et al., 2007].

Altogether, these considerations suggest us that, in order to exhibit pragmatic neural representations exhibiting the tight links between perception and action, the MNS should follow a complex systems architecture exhibiting (i) a robust and redundant information processing relying critically on time, (ii) one asymmetric density distribution of the neurons connectivity, and (iii) a hierarchical and distributed representations. Those properties, summarized in table 1, are also an hallmark of scale-free and small-world networks (SWN, see Fig. 1). These networks have a characteristic nodes connectivity distribution which permit an efficient information propagation and synchronization at different time scales (i.e., hierarchical and scale-free dynamics). In these networks, the majority of units possesses few and short path lengths connections with their neighbors whereas a minority possesses many of them with long path lengths permitting to aggregate distant clusters with each others. These special neurons represent hub connectors that link the small-worlds to each other. Here, information exchange is particularly fast because of the hierarchical organization that combine centralization to the hubs and distribution from them, which makes the network robust to fault tolerance [Albert et al., 2000].

1.1. Neural mechanisms

The ability of the MN to bind various modalities exhibits in counterpart their sensitivity to timing in order to synchronize the modalities. To this respect, the mechanism of Spike Timing-Dependent Plasticity (STDP, [Bi and Poo, 1998, Song et al., 2000]) that dynamically regulates the synaptic plasticity for memory storage almost everywhere in the cerebral networks, is a rather good candidate to organize the MN connectivity as it has been suggested by [Keysers and Perrett, 2004]. STDP is based on a bidirectional mechanism of long-term potentiation (LTP) and long-term depression (LTD) that readjusts the synaptic weights to the precise timing interval between the initiating and the targeting neurons [Abbott and Nelson, 2000]. The time delay $\Delta t = t_{post} - t_{pre}$ between the pre-synaptic neuron spiking t_{pre} and the post-synaptic neuron firing t_{post} corresponds to the interval range of activation of their synaptic plasticity and weight adaptation Δw , see Fig. 3.

<i>Mirror neurons system</i>	<i>Small-world networks</i>
Mirror neurons merge different modalities and any problem in the global integration of modal processes can be dramatic. The impairing of the mirror neurons has been suggested as one of a cause of autism.	<p><i>Hub Connectors</i></p> <p>Complex networks rely on few but critical units integrating globally the local processes for which any defects can destroy the functional integrity of the ensemble.</p>
<p>Motor neurons distribution:</p> <p style="padding-left: 40px;">Pure motor neurons (60%)</p> <p style="padding-left: 40px;">Mirror neurons (30%)</p> <p>MNS distribution:</p> <p style="padding-left: 40px;">60% broadly congruent</p> <p style="padding-left: 40px;">30% strictly congruent</p>	<p><i>Power Law</i></p> <p>Connectivity distribution of the units in complex networks follow a power-law curve.</p>
The motor system represents actions at different description levels. The tight coupling between perception and action requires accurate timing.	<p><i>Scale-free dynamics & Critical timing</i></p> <p>Information is represented in hierarchies at multiple time scales and phase synchronization phenomena can be observed.</p>

Table 1. Qualitative and quantitative comparisons between the properties of the mirror neuron systems and of small-world networks.

The regulation of the neurons' weights depends directly on timing. Each time a post-synaptic neuron fires, its synaptic weights $w_{pre,post}$ are decreased by A_- (LTD), and each time a synapse receives an action potential, its synaptic weight $w_{pre,post}$ is incremented by an amount A_+ (LTP). The equations and the variables values used in our original papers [Pitti et al., 2009a, Pitti et al., 2009b] are reproduced below:

$$w_{pre,post}(t+1) = w_{pre,post}(t) + \Delta w \quad (1)$$

$$\Delta w = \begin{cases} A_+ \exp(-\Delta t/\tau_+) & \text{if } \Delta t < 0 \\ -A_- \exp(-\Delta t/\tau_-) & \text{if } \Delta t \geq 0 \end{cases} \quad (2)$$

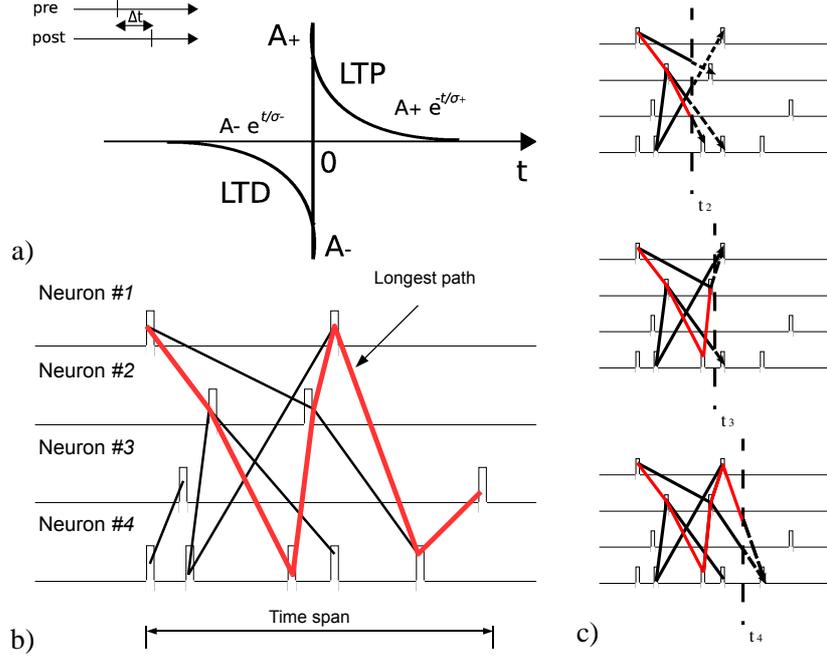


Figure 3. Mechanism of STDP. (a) Each time a post-synaptic neuron fires, its synaptic weights are decreased by A_- , and each time a synapse receives an action potential, its synaptic weight is incremented by an amount A_+ . (b) Based on this mechanism, different neural pairs can assemble themselves into asynchronous neuronal groups (polychronized groups c.f., [Izhikevich, 2006]). (c) The *scripts* do not only passively detect the contingency of external stimuli, but also activate new ones, anticipating further rewards.

The neurons dynamics of the spiking neuron can be defined with the integrate-and-fire neuron model proposed by Izhikevich [Izhikevich, 2003]:

$$\begin{aligned} v' &= 0.04v^2 + 5v + 140 - u + I \\ u' &= a(bv - u) \end{aligned} \quad (3)$$

with v representing the membrane potential of the neuron in mV and u a membrane recovery variable – v' and u' their respective temporal derivatives. The neurons are externally triggered by the signal I and their dynamics are reseted after any spiking

$$\text{if } v \geq +30mV, \text{ then } \begin{cases} v \leftarrow c \\ u \leftarrow u + d. \end{cases} \quad (4)$$

The variables set $\{a, b, c, d\}$ defines the neurons attributes whether excitatory $(a; b) = (0.02; 0.2)$ and $(c; d) = (-65; 8)$, or inhibitory; $(a; b) = (0.02; 0.25)$ and $(c; d) = (-65; 2)$. Further details in [Izhikevich, 2003, Izhikevich et al., 2004]. The external current I is the weighted sum of all the delayed incoming current I_{pre} from the presynaptic neurons that fired plus the external signal from one input ($I_{ext} \in [0, 20]$): $I = \sum w_{pre} I_{pre} + I_{ext}$.

We can envision the neural pairs $\{i, j\}$ as contingency detectors which can serve to encode local temporal *scripts*:

if NN_i fires at time t_i , then NN_j fires at time $t_j = t_i + \Delta t$.

This mechanism, although simple and local at the neurons level, can generate very complex dynamics as the neural pairs can aggregate themselves into long-range spatio-temporal clusters; see, Fig. 3 b), a phenomenon known as polychronization and by coined by Izhikevich [Izhikevich et al., 2004, Izhikevich, 2006]. Since these scripts activate also new ones in advance on the external signals, they are not passive systems, they can predict and anticipate future rewards, see Fig. 3 c).

In sensorimotor networks, we propose that these spatio-temporal patterns constitute a repertoire of commands or action primitives, for which the small scripts are the building blocks. Organized properly, the numerous scripts can furnish then a robust and redundant information of the sensorimotor coherency at the network level. In our experiments, the (mis)match between the external stimuli with these rules will modulate the level of sensorimotor coordination and therefore, any perceptual skills associated with them.

1.2. Neural dynamics & networks statistics

We analyze the networks statistics for the experiments performed in [Pitti et al., 2009a, Pitti et al., 2009b] and presented in section 2. The networks are typically a uniformly organized structure of thousands of excitatory and inhibitory neurons with random connections in average of 30 synaptic links. The links have variable lengths randomly chosen between 1 *ms* to 20 *ms* delays and equally weighted before learning. Each excitatory neurons receive a unimodal signal from the sensors (visual, somatic) or from the motors (proprioception) whereas the inhibitory neurons, which represent one third of the excitatory neurons, are all inter-neurons; that is, they receive indirectly the input signals from the excitatory neurons. In this section, we analyze in particular the networks characteristics with respect to the neural connectivity and the clusters distribution when the network's organization evolves and changes during learning: the functional integration within and between the unimodal circuits in terms of neural connectivity. The details of the experiences are given in Section 2.

Network structuring. During enactive interaction in the environment – i.e., when the embedded network is experiencing sensorimotor coordination– the incoming signals from the sensors combined with the reinforcement mechanism of STDP influence together the spontaneous activity of the neural dynamics so that the contingent neurons firing within $\Delta t = 40$ *ms* latency are wiring together. Since temporal congruency is the principal factor for linking the neurons from each other and not their location per se, the neurons can have either short-range and long-range connections. Therefore, the neurons can form coherent pairs and clusters associated to the particular sensorimotor experience with other neurons belonging to the same map or to others with different modalities. The functional integration across the modalities is analyzed in Fig. 4 where Fig. 4 a) displays the evolution of the synaptic weights distribution during the learning stage and Fig. 4 b) describes the level of segregation and integration between and across the maps. This second measure tries to capture quantitatively how the network organization evolves structurally. The level of specialization inside each network, I_{intra} , is measured as the number of (strong) synaptic

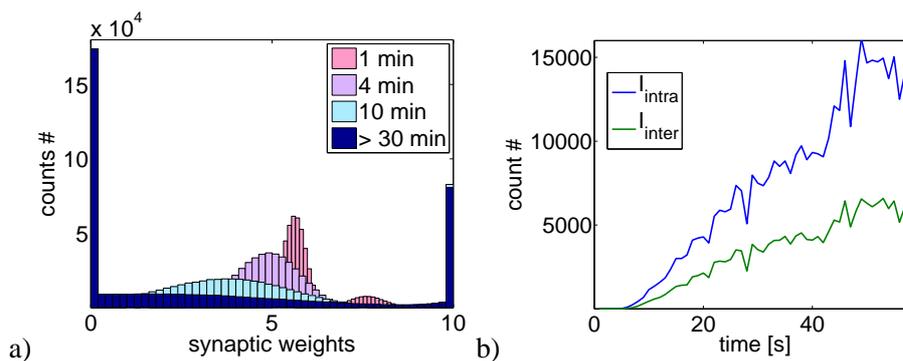


Figure 4. Network structuring. Evolution of the network synaptic weights distribution. (a) Histogram of the synaptic weights. The neural network achieves its self-organization by strengthening the most robust neural groups (weights' value > 9), and by deleting the inaccurate ones (weights' values < 1). (b) Evolution of the variables I_{intra} and I_{inter} computed the number of synaptic links between neurons within to same map or belonging to different ones.

links between neurons within the same map whereas the level of integration between the networks, I_{inter} , is measured as the number of (strong) synaptic links between neurons belonging to different maps. On the one hand, the network level of intra-modal integration, I_{intra} , corresponds to the information exchanged between the neurons belonging to the same maps (i.e., the number of synaptic links). On the other hand, the network level of inter-modal integration, I_{inter} , corresponds to the information exchanged between the neurons belonging to different maps (i.e., the number of synaptic links).

Before any learning, the uniform distribution of the neurons' synaptic weights with arbitrary connections between the neurons warrants that the network's organization is initially random. During learning, this situation typically changes when the network receives contingent sensorimotor signals (e.g., visuo-somatosensory signals like in Section 2.1. and Section 2.2. or visuo-motor signals like in Section 2.3. and Section 2.4.). In this stage, STDP synchronizes the neural dynamics that receive signals from different modalities and starts to structure the network, see Fig. 4 a). The process of specialization *within* the maps is observed by the evolution of the variable I_{intra} , and the one of integration *across* the maps is observed by the evolution of the variable I_{inter} in Fig. 4 b). These two processes indicates that the network self-organizes itself from a random map into a complex network with a hierarchical architecture: two processes are taking place in parallel, one "horizontal", inside the maps and the other "vertical", between them.

Clusters statistics. We extract from the network's connectivity matrix the clusters consistent with Izhikevich's definition of polychronized groups which are the time-locked firing patterns [Izhikevich, 2006]. Fig. 5 summarizes the clusters' analysis done where one cluster is defined as a neural group with a time span and a path length measured from its *longest* neural path colored in red in Fig. 5 a). Fig. 5 (b) plots the density distribution of the neurons connectivity inside the network which means the proportion of neurons connected to $[1, 2, \dots, N]$ neurons whereas Fig. 5 (c) displays the clusters' group length distribution and Fig. 5 (d) shows the relation between the clusters' group length and their time length.

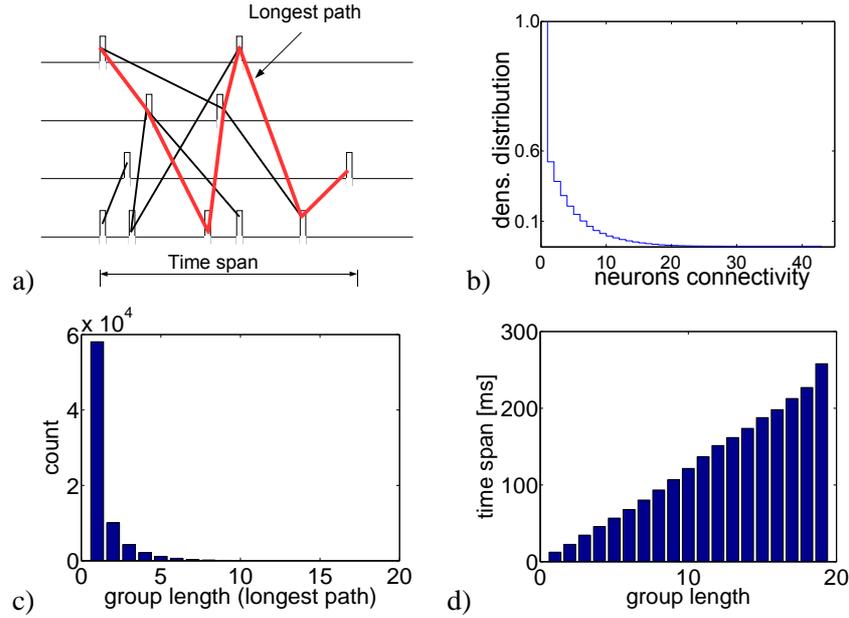


Figure 5. Clusters statistics. Density distribution of the neurons connectivity (b), ordered by the length of the clusters (c) and by their time span (d) [resp. the longest path of cluster defined and their time span in (a)]. The density of the neurons connectivity follows the characteristic power-law curve typical of small-world networks. The network produces scale-free dynamics.

Taken together, these measures describe the network functional properties. For instance, a significant feature is the power-law curves displayed in b) and c) – respectively. the clusters group length and the neurons connectivity– which indicates a scale-free organization inside the network, characteristic to complex systems. The power-law means that few units densely integrate the network and drive its activity whereas the majority is less critical to its functioning [Buzsaki, 2006]. The density distribution of the neurons connectivity in b) indicates that ninety percents of the neurons possess really few connections with their siblings, lesser than 3 links. Besides, the 10 percents most connected neurons have more than fifteen strong synaptic connections. These few neurons are particularly important to connect the small clusters with each others. Therefore, those 10% of neurons are the most critical neurons within the network, they correspond to the hub connectors. The average length of the neural clusters is of 2 or 3 neurons (small clusters) and few clusters have constituted of five or more neurons (long clusters). Depending on their length, the neural clusters have a time span varying from few milliseconds to 250 milliseconds. The longer the clusters, the more coherent is the neural response with respect to the external dynamics.

We propose that MNS follows the organization of complex networks which develop small-world connections and are found to generate efficient inter-regional communication, enhanced signal propagation speed, computational power, and synchronizability [Watts and Strogatz, 1998].

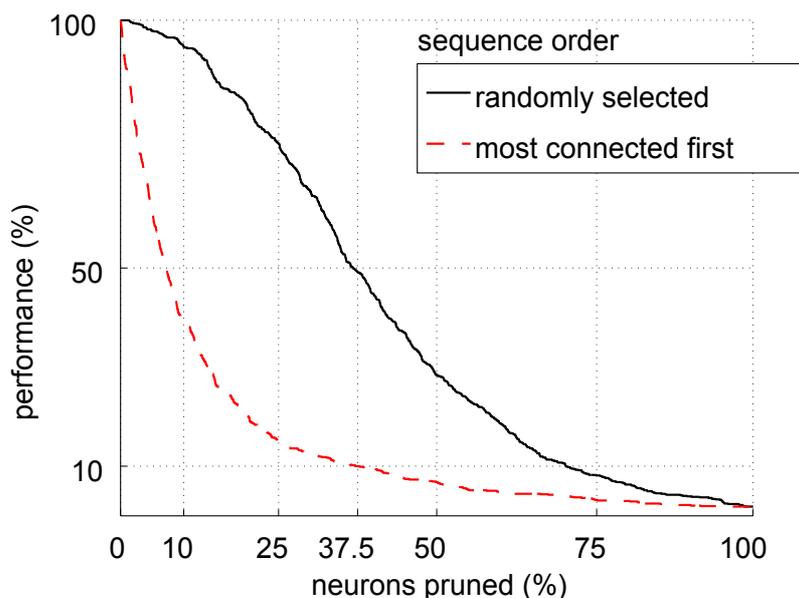


Figure 6. Network Performance. The network robustness varies dramatically whether the most connected neurons (the most critical ones) are pruned first (dashed line) or if the neurons are pruned in a random sequential order (continuous line).

We analyze the network’s tolerance when confronted to an attack (i.e., neurons pruning) which can permit to identify the centrality of the neuron within the network or its importance and to model also the impairing caused during the developmental stage, see Fig. 6. We hypothesize that the 10% most connected neurons may correspond to the “strictly congruent” MN neurons within the network, which can be robust against a random pruning of its neurons but weak against a non-arbitrary pruning. For the case of a random pruning (continuous line), the network’s performance decreases linearly when we suppress neurons one by one selected in an aleatory order and the overall features of the network are preserved. For the case of pruning the most connected neurons (i.e., the hub connectors in dashed line), the network’s performance falls drastically and the performance of the network when 7% of the most connected neurons are suppressed corresponds to the situation of suppressing 37.5% of the neurons randomly selected in the first case. Thus, each neuron does not have the same importance within the network and a relatively few numbers sustain the network functional integrity. This result can give some arguments to the point that mirror neurons can be statistically few relative to pure motor neurons but are in contrast much well connected (multimodality): the scarcity of the hub connectors warrants the network’s efficiency for information processing because they are also well connected within the global network. We have shown how an apparent hierarchical structure possessing some of the characteristics of the MNS can emerge from hebbian learning in an apparent random recurrent network. We apply in the following this mechanism for modeling cognitive functions exhibited by mirror neuron-like systems for visuo-tactile integration and anticipation, contingency perception and agency perception and spatial representation of the body.

2. Cognitive functions

After comparison of the quantitative properties of the mirror neurons, we present in this section the cognitive functions that illustrate their qualitative aspects, realized in sensorimotor networks: cross-modal association and contingency perception for action understanding, agency perception and spatial representation of the body. Beyond simply controlling motion, mirror neurons reflect how the body relates to others, physically and socially. We propose that this is done through temporal contiguity, at the neural level, by exploiting the efficient organization in complex sensorimotor networks.

2.1. visuo-tactile integration during grasping

The experiences conducted by Rizzolatti on action representation showed the tight coupling that exists between perception and action, between neurons in the motor system with those from other modalities in the sensory networks. We investigate the conditions for such situation to occur in embedded networks of spiking neurons between visuo, tactile and motor modalities and regulated by STDP, to perceive oneself actions as well as those of others. The details of the experimental setup are detailed in [Pitti et al., 2009a] but it can be explained as follows. We would like to simulate the multimodal integration during the act of grasping between somatosensory information and visual information within the network

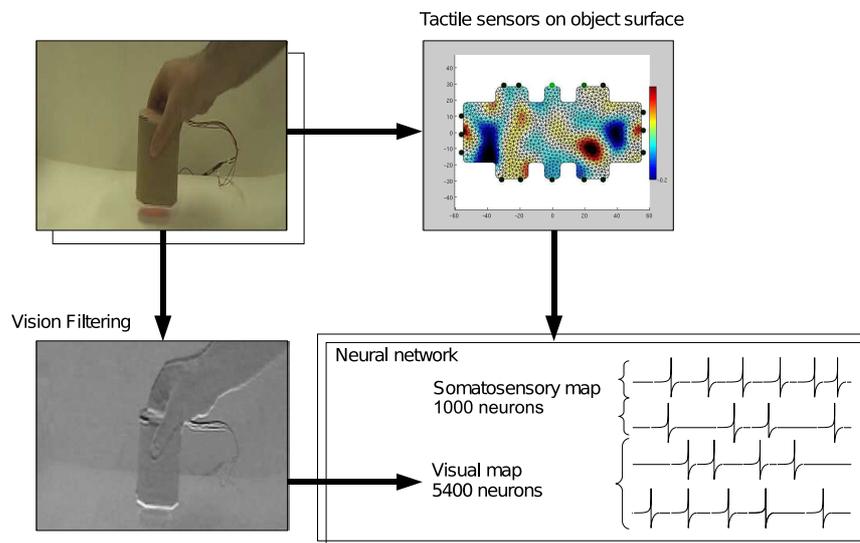


Figure 7. Schematic of the grasping experiment. The experiencing of co-occurrent visuo-tactile perception during grasping (in the upper-left corner) by the network (bottom-right corner) is done by receiving the incoming information from the camera and from the pressure sensitive device.

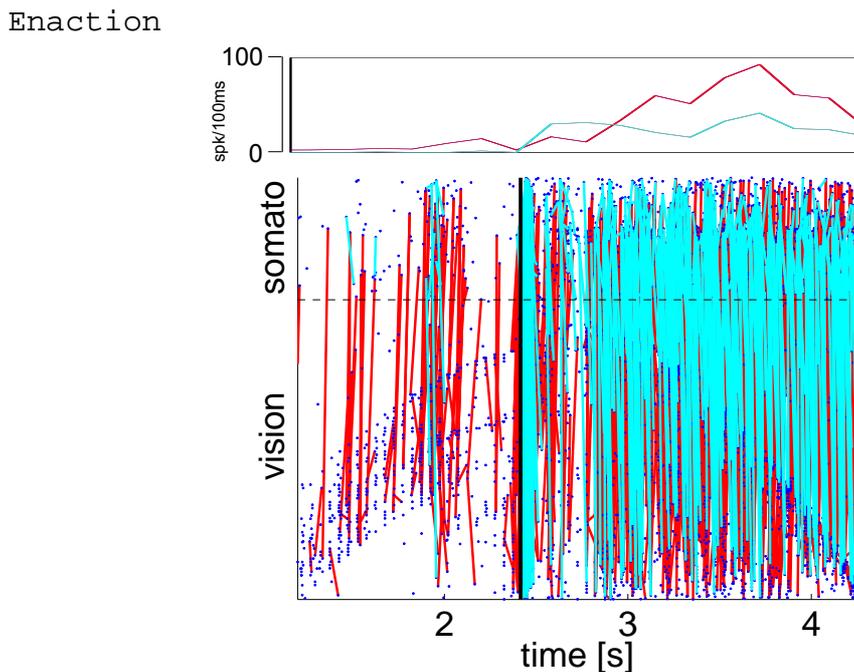


Figure 8. Spike rate and neural dynamics in the visual and tactile maps during physical interactions (resp. top and bottom). The whole action sequence is exposed from seeing, reaching the cup, the time to contact, then touching and grasping (see also Fig. 9). In red (resp. cyan), the synaptic activation from the neurons of the vision map (resp. tactile map). Processes done in the network are constituted from the parallel neural firings between the two maps. The visuo-haptic patterns are not randomly activated but synchronized and functionally assembled.

receiving those two modalities. The tactile sensors covering the surface of an object are sent to their respective somatosensory neurons in the neural network so that those neurons trigger when they receive external input. In parallel, the visual information coming from the fixed camera is sent to the visual map after being binarized with a motion detection filtering. The somatosensory neurons represent 1000 of the excitatory neurons within the network and the visual neurons represent 5400 of them, to which 1000 more inhibitory neurons are added. Each neuron is allocated with 30 synaptic links connected randomly to other neurons with random lengths and delays below 20 *ms*. The network is initialized with a uniform synaptic weight distribution so that its organization is mostly unspecific from the beginning; see Fig. 7.

The perceptual experiences consist of the execution of visually perceived actions (i.e., seeing and touching one object) during which the network learns to associate the somatosensory signals and vision modalities via hebbian learning and STDP. The learning period within the network is similar to the situation presented in Section 1.2. and the network evolves into a complex network structure by reinforcing the links between the neurons that are correlated and by pruning the others, see Fig. 4. Over time, a specific organization is shaped through multimodal integration with a log-curve neurons connectivity indicating a

Time-to-contact

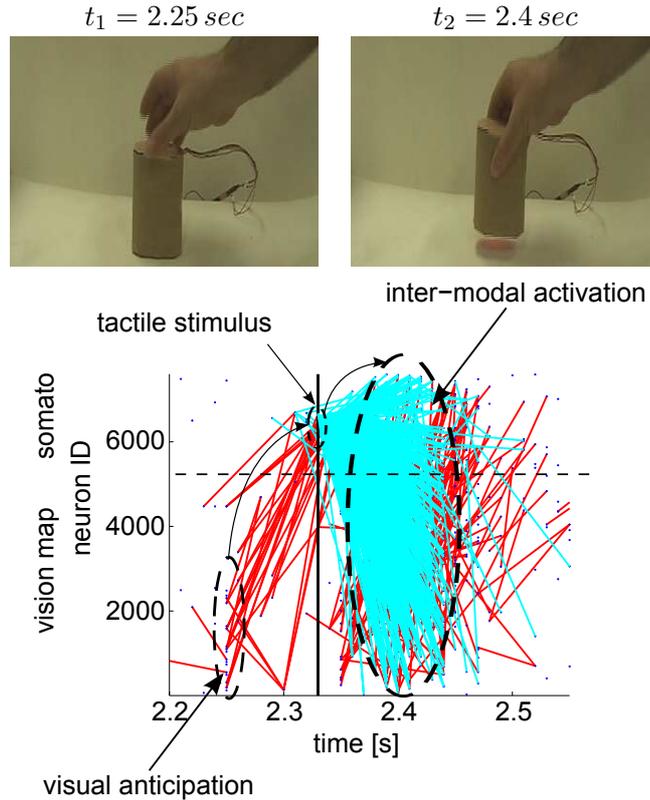


Figure 9. Neural dynamics of the visuo-tactile maps during physical interactions. In red (resp. in cyan) the synaptic activation from the neurons of the vision map (resp. the tactile map). At time-to-contact ($t = t_1$), the retina *anticipates* only the temporal changes about the hand motion in the direction of the cup: the spatial information about the cup is filtered. When grasping the object ($t = t_2$), joint detection of hand motion contingent to the cup motion and the haptic activity corresponding to a coordination in the neural dynamics (synchronization among the maps).

small-world network hierarchy and the presence of hub-like neurons, see Fig. 5. The associations learnt between the networks will permit to anticipate (or simulate) the neural activity in one modality from the basis of another, like it is the case during action observation when no tactile information is received.

The neural activity in the vision and tactile maps during grasping is plotted in Fig. 8 where the black line at $t = 2.3 \text{ sec.}$ indicates the precise time-to-contact. The superimposed synaptic links in red correspond to the neural activity generated by the neurons from the vision map and the links in cyan represent the one generated by the neurons from the tactile map. The firing rate of each variable is plotted at the top.

Despite the very broad activity in the network, one can see some strong inter-modal interactions between the maps at the time-to-contact, which indicates that the two maps intensively exchange information from each other. It is not clear whether or not functional integration and efficient neural connectivity are effective. However, the whole network

behaves as a kind of contingency detector due to the STDP links: the analysis of the neural activity before and after the time-to-contact $t \in [t_1; t_2]$ in Fig. 9 shows that the visual neurons trigger *before* the time-to-contact and anticipate the future tactile information at the time of contact. Hence, the neural pairs do not detect passively the contingent signals, instead they actively estimate and anticipate expected signals, even from other modalities. A situation called *anticipated contact* by [Berthoz, 1997] which is a form of spatial-visual proximity with the area of the body that will be touched [Rizzolatti and Sinigaglia, 2006]. At the time-to-contact, it is the turn of the somatosensory neurons to trigger a different pattern of activity by triggering a burst of neurons synchronized in the tactile map and in the visual map. As it has been shown in [Siri et al., 2007], the recurrent network is sensitive to the input pattern due to its small-world connectivity organized by the strongest synapses. We can envision therefore these neural scripts as a repertoire of highly sensitive contingency detectors, always re-activating the learnt combinations from external stimuli. By doing so, they emphasize also the importance of timing and synchronization which are important to identify oneself actions by anticipating the rewards and to estimate those of others.

2.2. Action understanding and retrieval as re-activation

The associative and anticipatory skills acquired by the neural network and showed in Fig. 9 can serve for example to reconstruct one missing modality (or to reactivate it) from other modalities that are available; e.g., when we are observing actions performed by others and simulate the perceptual sensation of the other. In this situation, vision is enough to sense and simulate the missing tactile and proprioceptive information, or when we manipulate objects in hidden conditions and we reconstruct its shape mentally (i.e., simulation of the missing visual information).

We propose to reproduce Rizzolatti’s experiment exhibiting the MN ability to trigger with precise timing to observed actions [Rizzolatti et al., 1996]. We consider to this end to reconduct the grasping experience in the same experimental conditions as the one previously done with the same device to be grasped, the same position on the visual field with the same camera angle and with an overall similar execution speed, but this time with *no* tactile information sent to the network. We display in Fig. 10 the neural activity during action observation with the same color code as used in the previous section, the time-to-contact is at $t = 2.5 \text{ sec}$ (plain line). After $t > 2.8 \text{ sec}$ and despite the missing modality, the neural maps do reproduce similar dynamics as during enaction, when all modalities were available (to compare with Fig. 8). The visual patterns in red activate the neurons belonging to the tactile map from the previously learnt associations. Reversely, the tactile neurons in cyan fire back the vision neurons as if the tactile information was effectively provided. The massively parallel and bidirectional connections between the two maps intertwine the two modalities, reproducing the similar qualitative features of the mirror neurons system to simulate the missing modality as a virtual perception. This is achieved by the detection of particular visual cues to which the network has learnt to be sensitive to.

Observation

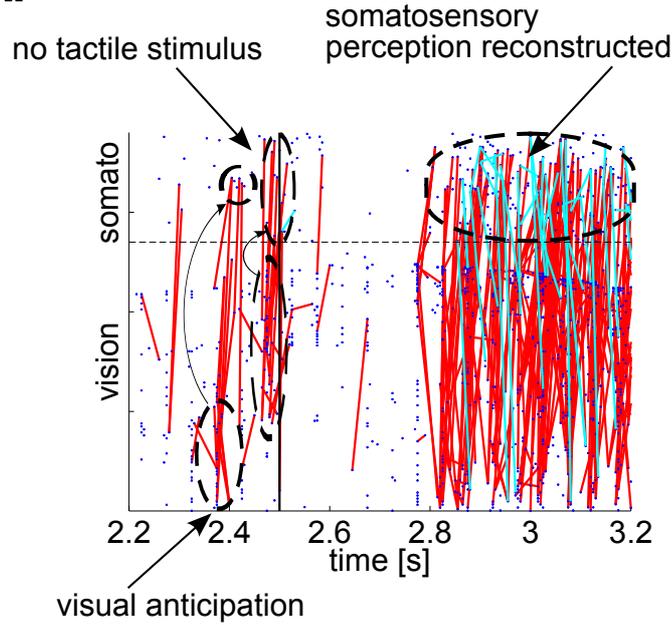


Figure 10. Reconstruction of the tactile modality from the observed action of grasping at the time-to-contact. The network anticipates the tactile stimulation at the precise time to contact. During handling at $t > 2.8 \text{ sec.}$, the visual patterns permit to simulate and to reconstruct the missing tactile perception. Links from the tactile to the visual map in cyan show that perception is an active process inside the system emerging from the mirroring between the two maps, whether physical (stimuli-based) or virtual (not stimuli-based).

2.3. Contingency perception and agency index at the neural level

The parietal cortex has been found to subserve agency perception and body-ownership, which are respectively the senses that I am the cause or author of the movement and that I conform the spatial extent of my physical body [Jeannerod, 2007, Schwabe and Blanke, 2007]. It has been hypothesized that comparator models in the parietal cortex, such as coincidence detectors, integrate efferent information (motor) with afferent ones (proprioception) during action contexts to represent coherent experiences of the body [Tsakiris et al., 2007]. We propose that the synchronization mechanism of STDP, which is responsible to pro-actively detect and anticipate contingency among a large neural population, can serve as a biologically plausible mechanism of the compliance in the parietal networks supporting these functions. A possible mechanism of agency at the neural level in the parietal lobe can be the computing of the predictive power of STDP neural pairs with respect to afferent signals. The calculation of its accuracy level using a score function can be then a quantitative measure of agency in sensorimotor networks, like the F-measure introduced in information retrieval theory [van Rijsbergen, 1979].

Fig. 11 explains the basic mechanism of contingency detection and predictive anticipation in a pair of neurons #1 and #2. Contingency detection means that the activation of neuron #2 matches with the reception of an external input stimulus #2 *and* neuron #1's

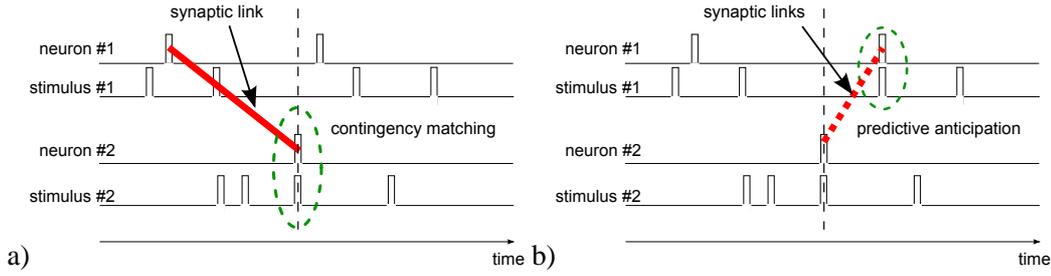


Figure 11. Contingency detection and predictive anticipation. The sense of agency arises from the matching between afferent (proprioception) and efferent information (motor prediction). In our model, it corresponds to the synchronization between the pre-synaptic neuron #1 and the incoming input stimulus #2 that activate in the same time the neuron #2. To fire contingently with the input, the pre-synaptic neuron #1 must trigger in advance.

activity potential (i.e., contingency matching), see Fig. 11 a). Predictive anticipation means that each firing neuron pro-actively triggers other neurons based on the learnt synaptic links they acquired, activating therefore contingency detectors for future signals, see Fig. 11 b). We can compute the agency index at current time t in a neural population as the number of correctly predicted stimuli divided by the number of all returned predictions done at time t either correct or false (the “precision”) and the number of correctly predicted stimuli divided by the number of predictions that should have been returned (the “recall”):

$$\begin{aligned}
 precision &= \frac{nb_correctly_predicted}{nb_predicted} \\
 recall &= \frac{nb_correctly_predicted}{size_current_input} \\
 agency_idx &= \frac{2 \cdot precision \cdot recall}{(precision + recall)}
 \end{aligned}$$

where the *size_current_input* corresponds to the current dimensionality of the incoming signals. We normalize the agency index such that the lowest values (e.g., $agency_idx = 0$) correspond to complete mismatch between sensory inputs and motor predictions (no agency) whereas the highest ones correspond to perfect contingency prediction (maximum level of agency).

We propose to study how agency arises in visuo-motor networks embedded in a head-like robot with cameras, see Fig. 12. The details of the experimental setup is done in [Pitti et al., 2009b]. As in the previous experiment, a global network composed of neurons from different modalities is initialized with random connections. This time, motor neurons replace the somatosensory neurons and control the cameras angles in the ocular and pan axis. They represent 2×256 of the excitatory neurons within the network and the motor value is read at as a rate code in the motor population. The visual neurons represent 2×4900 neurons receiving the pixels output from the two cameras and transformed in log-polar coordinates. In addition, inhibitory inter-neurons were added representing 20% of the population of excitatory neurons to stabilize the system. Each neuron is allocated with 30 synaptic links connected randomly to other neurons with random lengths and delays below 20 *ms*.

There, the network is fully constrained by sensorimotor activity and hebbian learning. During enaction, the sensorimotor maps integrate their dynamics and learn simple perceptuo-motor patterns between the current motors state (eyes and neck orientation) and the visual scene. In Figure 12 on the right, we superimpose the synaptic links between neurons on the neural dynamics. The lines in cyan correspond to the links activated by the neurons in the vision map and the red lines correspond to the links activated by the neurons in the motor maps. The signals on the top correspond to their respective firing rate.

These links constitute contingency detectors which can serve to compute the network's agency level. The correctness of the predictions ensures the integrity in sensori-motor networks. Fig. 13 a) displays the agency index computed from the synaptic links and the input patterns from Fig. 12 with the agency index formula given previously. This graph reveals that the agency level is not static but dynamic and can rapidly switch within seconds. Its values are on average above 0.15, which corresponds to the system's agency reference level. It indicates a certain confidence level of the predictions on the sensorimotor inputs when the device moves: its actions afford its agency. Since the "signature" of live enaction corresponds to a certain agency index, it follows that perturbing contingency can affect also the system's agency level like during visual illusions with mirrors or with feedback delays.

To expose the incidence of temporal delays on our system, we delay the visual information with respect to the proprioceptive information, see Fig. 13 b). The delays in the sensorimotor networks mismatch the synaptic links and decrease the level of agency index. Its level falls down below 0.1 revealing discrepancy between the system dynamics and the inputs. Although agency changes, it cannot be accounted as a discrete 0 or 1 mental state.

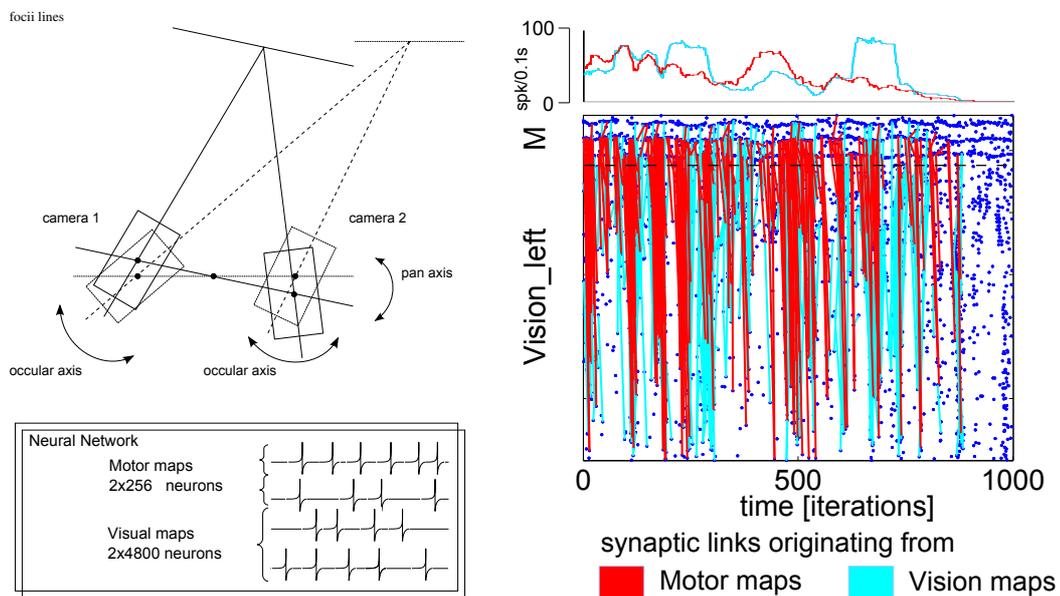


Figure 12. Visuo-motor integration in sensorimotor networks embedded in a head-like robot (left). The superimposed lines on the neural dynamics represent the most robust anatomical synaptic links between pre-synaptic and post-synaptic neurons between the vision and motor maps.

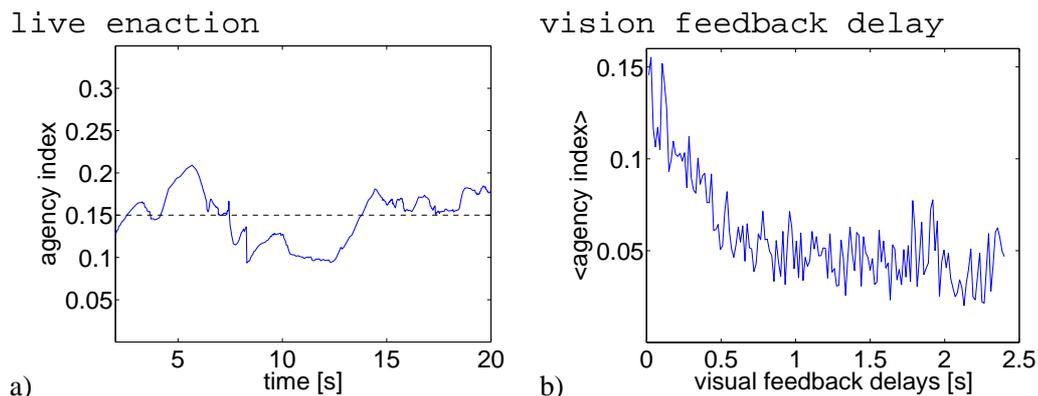
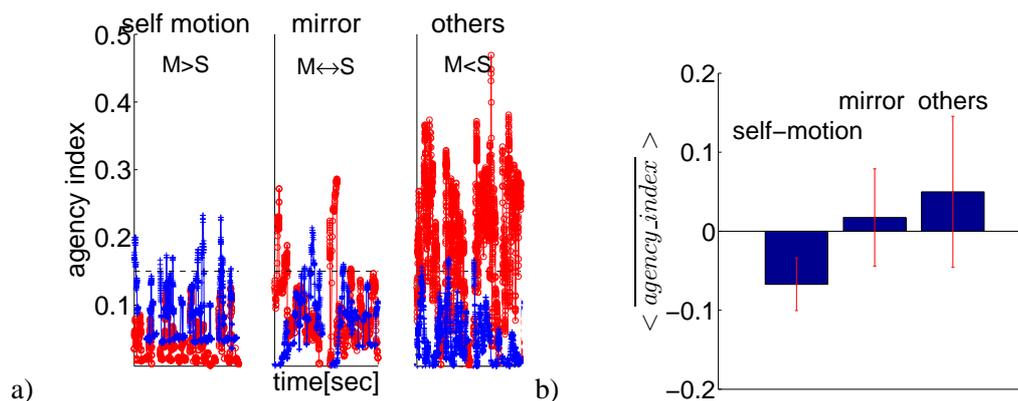


Figure 13. Agency index during enaction. The agency index between is calculated as the distance between the visuo-motor input patterns and their prediction by the neural maps. The system's action produces the change of its own degree of agency. Its averaged value represents the reference level for coherent sensorimotor information. Agency index for different interval range delays between proprioceptive and visual feedbacks. Each value correspond to the temporal delay of visual feedback. Delays decrease the agency index and a drastic fall occurs around 500 ms indicating sensorimotor mismatching (functional visuo-motor discrepancy).

Other perceptual experiences, like scrutinizing a mirror or interacting with others, are special cases of sensorimotor interaction which involves double synchronization between afferent (sensor) and efferent information (motor). In the case of self-perception in front of a mirror, both internal and external dynamics are perturbing each other and conflict. Interacting with others, on the other hand, triggers more information exchange from the external to the internal dynamics, which rises then the agency level. In a sense, oneself agency level can leverage itself by interacting with others. Hence, rather than strict self-other distinction, the agency index measures the fuzziness of the dynamical limit of the bonding that can emerge between oneself and others. The first condition for developing the self in relation to others (c.f., social resonance [Nadel et al., 2005, Hiraki, 2006, Decety and Sommerville, 2003, Decety and Chaminade, 2003]).

All in all, Fig. 14 a) summarizes the agency indices for the three studied cases but this time by separating the quantities relative to afferent to efferent information ($S \rightarrow M$, red circles) and to efferent to afferent information ($M \rightarrow S$, blue crosses). Their amount and ratio vary depending on the type of perceptual experiences. During interaction with others, the visuomotor circuits are entrained by external signals ($S > M$) which differs from the case of self-motion where it is the motor events that guide the visuomotor circuits ($M > S$). The case of mirror is interesting, since motor events and sensory events are conflicting from each other since the two are affected at the same time by the dynamics of the other ($M \leftrightarrow S$). Beside, Fig. 14 b) resumes the relative mean scores of the three agency indices after being averaged and zero-centered. It shows that once the embedded network learns the visuomotor associations during self-motion, it becomes then more sensitive to the external inputs and to perturbations. It follows that visual external inputs can easily entrain or conflict with the visuomotor circuits and drive agency.



agency measure from

○ sensor to motor + motor to sensor

Figure 14. (a) Summary of the agency indices of the three cases studied separating the relative quantity from afferent to efferent information ($S \rightarrow M$, red circles) and from efferent to afferent information ($M \rightarrow S$, blue crosses). (b) Mean scores of agency in the three situation studied after being averaged and centered (in blue). The red vertical lines indicate their variance.

We suggest then a sensorimotor account of social engagement in line with [Nadel et al., 2005, Prince and Hollich, 2005], based on STDP contingency detection at the neural level (c.f. [Keysers and Perrett, 2004]). In a developmental viewpoint, the spike-timing dependent plasticity might provide the sufficient neural basis for babies to sense contingency, what [Watson, 1994] hypothesized to be the premises for future body representation, self-perception and the discrimination between self and others, the conditions for developing social capabilities [Rochat, 1998, Rochat, 2003, Nadel et al., 2005, Hiraki, 2006, Shimada and Hiraki, 2006]. In this line, we hypothesize that the present neural architecture might support some principles for cognitive development and social competences necessary for communication by means of gesture and language [Falck-Ytter et al., 2006].

2.4. Construction of the peripersonal space from body-places associations

Shared networks are not only employed for interacting physically within the environment, they are also a window to higher cognitive skills for interacting socially with others and for perceiving oneself agency [Decety and Sommerville, 2003, Decety and Chaminade, 2003]. They achieve to perform dynamically self-other contagion or discrimination through the temporal extent of sensorimotor activity. This dynamical mechanism is considered to occur also for representing the spatial extent of the body in the parietal lobes [Tsakiris et al., 2007, Schwabe and Blanke, 2007, Shimada et al., 2005]; i.e., the location of the body parts and of the nearby objects, the body image. As for agency perception where contingency detection notifies in real-time the sensorimotor activity, we propose that the same comparator

model at the neural level informs about the spatial extent of the body *if* sensorimotor synchrony (mis)matches. Sensorimotor contingency gives rise to perceptual effects of spatial expansion of the body image as it occurs during the famous experiment of the rubber-hand illusion or during tool-use when (fake) synchrony is sustained in sensorimotor signals [Botvinick and Cohen, 1998, Murata and Ishida, 2007, Shimada et al., 2009].

Interestingly, 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]. We propose to model how such binding between the body dynamics and the external spatial cues emerges in shared neural networks.

We note that 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 premotor lobes during handling and reaching as well as during sucking and gazing [Futagi et al., 1998, Del Giudice et al., 2008]. Indeed, the hippocampus is known to play an important role for processing the allocentric spatial information [O'Keefe and Burgess, 2005] and some developmental studies attribute the spatial improvements of infants to the maturation of the hippocampal system and its surrounding cortex [Nelson et al., 2006]. These observations may 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], see Fig. 15.

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]. Theta phase coding forms associations between continuous states and continuous actions with the use of oscillations for encoding temporal intervals, 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., 2008], we suggest that this later mechanism provides the ground for contingency detection and learning of ones 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. The details of the experiments are presented in [Pitti et al., 2010] but the idea is that 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. Then, the visual cells finish to merge the neighbouring cells from each others and to refine their locations into the map, see Fig. 15.

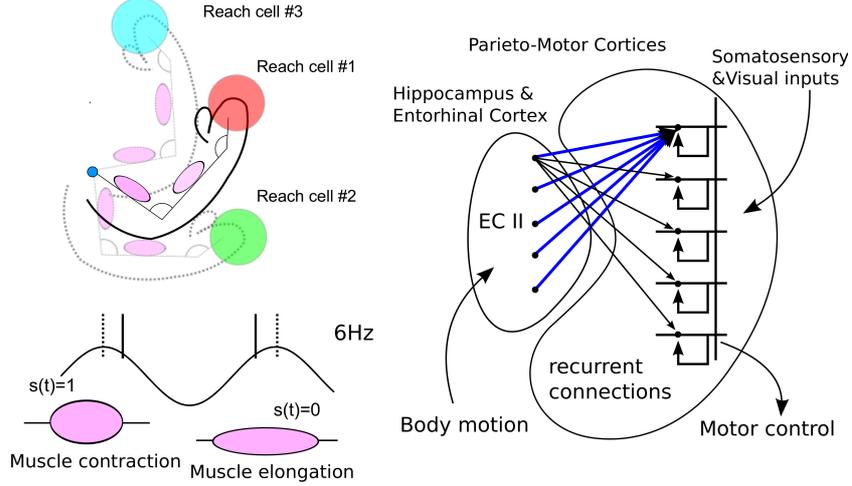


Figure 15. Proposed framework of the parieto-hippocampal body/space transformation. ECII retranscribes the amplitude's variations of the body signals into a temporal code and the cortical layer learns the associated “postural cells” that it binds recurrently with signals from other modalities to merge “reach cells” via Hebbian learning.

More concretely, the construction of reach places within the parieto-hippocampal system is done in two steps: (1) the enthorinal system transforms the input signals (e.g., the body posture) into a temporal code, (2) the parietal circuits stores this temporal code as a topological memory, see Fig. 17. On the one hand, the ECII layer composed of individual cells, generates a phase code. On the other hand, the parietal system, which differs from the ECII layer by the recurrent connections it has between its units, encodes the reach cells from the current temporal code of the body posture. The recurrent connections between the parietal reach cells are reinforced via a Hebbian-like learning rule such that the grounous postural cells (and the afferent reaching location) are more likely to wire.

The ECII layer is composed of individual cells that generate the phase code via a phase modulation of an external signal [Hasselmo et al., 2009]. individual entorhinal cells are composed of a soma and a dendrite cell which provide respectively the baseline frequency f_S and the carrier signal f_D . In our experiments, the soma has the frequency $f_S = 6.42Hz$ and the dendrites frequency $f_D = f_S + s(t)B$, where B is a constant. There, the speed signal $s(t)$ of an external input modulates the frequency of the dendrite and therefore its phase ϕ_D whereas the baseline phase of the soma ϕ_S increases constantly at each time step:

$$\begin{cases} \Delta \phi_D = 2\pi f_D(t)\Delta t, \\ \Delta \phi_S = 2\pi f_S\Delta t \end{cases} \quad (5)$$

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:

$$g^{ECII}(t) = \Theta_D[\cos(\phi_D) + \cos(\phi_S)] \quad (6)$$

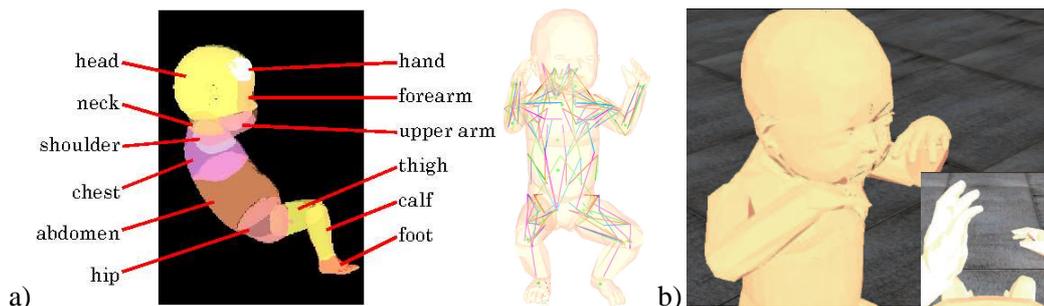


Figure 16. Overview of the infant model. (a) Body part name of the infant model with 198 muscles. In this paper, we control only the left and right arms (the hand, the forearm, the upper arm and the shoulder) which are constituted each by 37 muscles and 4 joint angles. (b) eye view and third person view of the infant model.

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. The amplitude variation of the muscle –e.g., its contraction or its elongation– can be translated as a temporal code in advance or in retard to the baseline frequency in the soma, see Fig. 15 and Fig. 17. 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.

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 [Kuniyoshi and Sangawa, 2006, Kinjo et al., 2008], see Fig. 16. We constrain nonetheless our study to the body signals coming from the arms' muscles spindles, the joint angles from the shoulder-elbow-wrist system (37 degrees of freedom for each arm) and the eye's vision cells. Section 2.5. explains how the entorhinal cells transform the muscle limbs signals into a temporal code and how the parietal neurons encode this temporal code and other signals into a spatial body image using hebbian learning. Section 2.6. explains how spatial locations can then be reached from motor commands.

2.5. Calibrating the body image, encoding motor coordination

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; see also Fig. 17. The relative advance or retard in phase to the baseline theta rhythm retranscribes the correct length of the spindles –thus, the actual arm's posture– which can then be learnt as a spatial code by the parietal system. These temporal relations, which represent a postural code, can then be learnt by the parietal system as a spatial code.

During sensory-motor exploration, central pattern generators self-organize the motion behavior of the infant's arms (c.f., [Kinjo et al., 2008]). Over time, the muscles are contracting their dynamics to preferred configurations of the motor commands. As novel locations are reached, novel temporal codes emerge in ECII. We plot in Fig. 17 different temporal

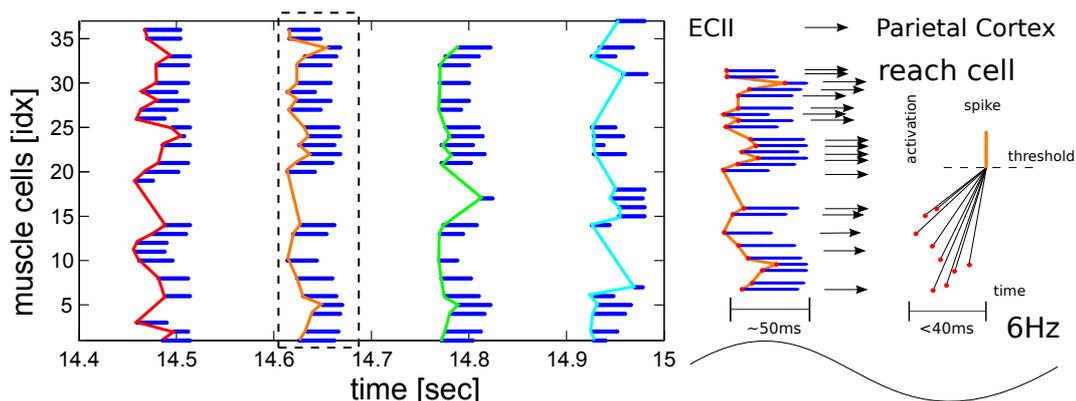


Figure 17. Parieto-hippocampal interface for coding spatial memory. The parietal system receives the temporal codes from the ECII layer (left), which trigger its associated “reach cells” above a certain threshold and every theta cycles (right). The recurrent links between the reach cells reinforced via the asymmetric Hebbian learning create a map.

codes marked with different color codes. The occurrence of one specific temporal pattern in the ECII dynamics, computed by a distance measure and filtered above a certain threshold, triggers its corresponding reaching cell in the parietal map. If the ECII temporal code corresponds to a new posture, then the new postural cell is added to the parietal map.

We display in Fig. 18 a) the raster plot of the parietal reach cells (top) that retranscribes the trajectory in space of the left hand and of the left arm (bottom). In the right, we superimposed with different colors the spatial area of four reach cells. One can see that each cell fills out one specific region in space that sometimes overlaps with other regions: cell 1 in green fills the region on the top whereas cell 6 in cyan fills the region on the bottom. The proprioceptive information taken from the body limbs and translated into a temporal code by the entorhinal cells can serve then to create a spatial map in the parietal circuit.

The relationship between the reach cells can be learnt via hebbian learning and STDP of the link transitions –see Section 1.1.. Here, the hebbian learning can provide the statistical relations and topological distance between the cells. The statistical relations between the reach cells 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: the figure in Fig. 18 b) is a reconstructed graph extracted from the weight matrix of the learnt link transition between the reach cells. In comparison with the map in Fig. 18 a), the graph shows that cell 1 region in green is effectively close to cell 4 in yellow, and that cell 1 is more distant from cell 10 in red and cell 6 in cyan. The weight matrix can transcribe then a spatial relation between the reach from the weights: a strong synaptic weight retranscribes a close distance to the reaching cell (the reachable region from that cell) whereas a weak synaptic weight will retranscribe a weak spatial relation and a far distance to the cell (an unreachable region from that cell). This topological graph constructed from proprioceptive information can be refined with other modalities like vision or somatosensory sensation. This can serve to the construction of a multimodal body image useful for a reaching task based on visual cues.

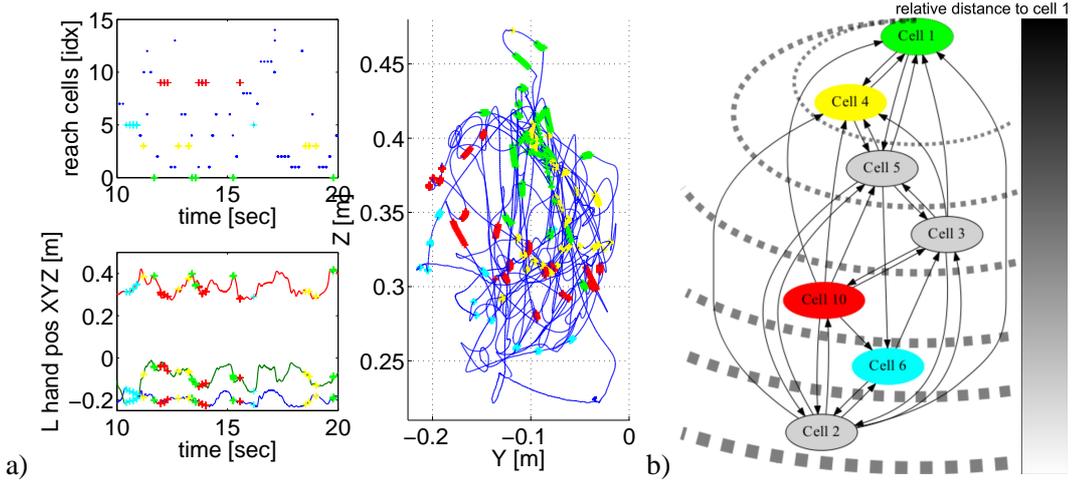


Figure 18. Reach Cells. In a), raster plot of the reach cells relative to the spatial trajectory of the left hand. The superimposed colours indicate when the reach cells are firing in the upperleft raster plot and to which spatial regions they correspond to when the hand is moving around. In b), sub-graph reconstructed from the weights matrix between the cells.

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

As explained in the previous paragraph, 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, see Fig. 19 a). During hand regard, for example, the vision cells can reinforce their links with the contingent reach cells. The reach cells, which are not-yet wired, can then be binded from the vision information; e.g., those which are close in the peripersonal space but distant in the postural space.

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. 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:

$$\begin{cases} H_{i,j} &= \phi_D^i(t) - 2\pi f_S \eta_{i,j} - \phi_D^j(t), \\ \Delta\phi_D^j &= \Delta\phi_S + w_{i,j} H_{i,j}. \end{cases} \quad (7)$$

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:

$$x_j(t) = \frac{\phi_D^j(t) - \phi_S(t)}{2\pi B} \quad (8)$$

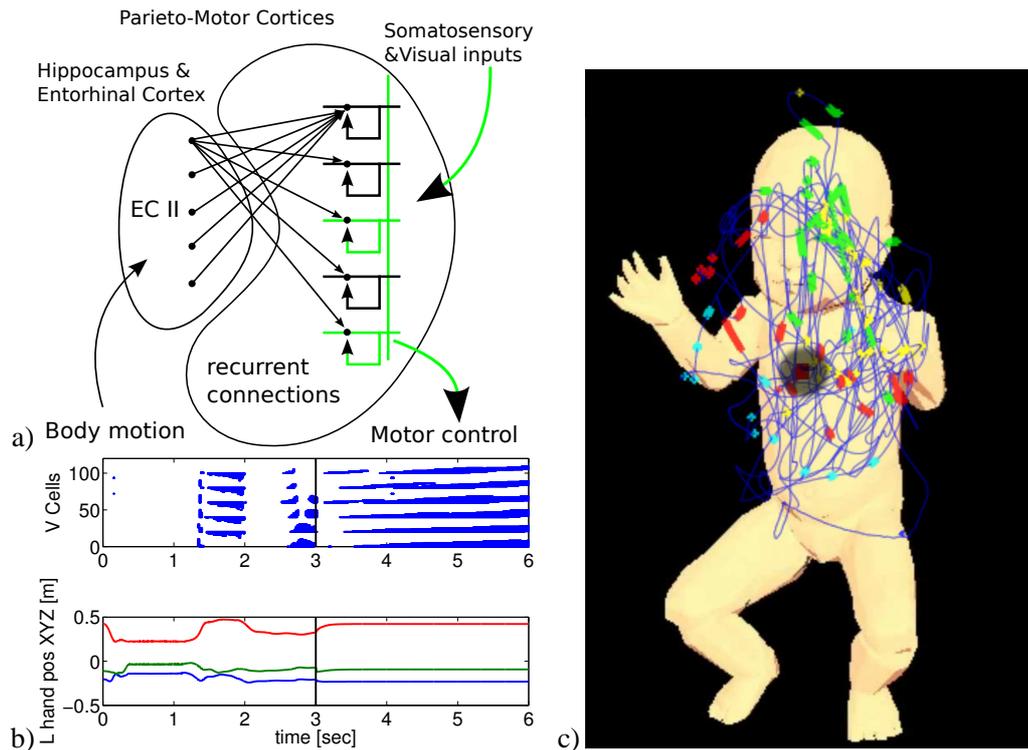


Figure 19. Activation of one selected reach cell from visual inputs at $t = 3.0 \text{ sec}$ and retrieval of the arms joint angles and hand position. In a), schematic mechanism of reafferentation. In b), time series of the visual inputs and of the hand position. In c), the superimposed hand location trajectory on the baby simulation.

It follows that the stimulation of the vision cells located in the left-side of the vision field triggers the associated reach cells, see Fig. 19 b). 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. 19 c).

All in all, we suggest that the mechanism of phase precession in the para-hippocampal cells could be essential for sensory-motor transformation and the construction of the spatial representation of the body in the parieto-motor circuits. The hippocampus dynamics could shape then the parieto-motor cortices that include the mirror neurons system, as it has been suggested recently [Del Giudice et al., 2008], and the visual receptive fields, which remap dynamically the frames of reference of the peripersonal space: the reachable space around the body. Furthermore, the ability to perceive the spatial boundaries of *oneself* body parts can serve to experience how the self relates to others physically and socially. The body image can serve to identify agency and inter-subjectivity and other cognitive skills like social engagement and imitation, which require the imitator to solve the correspondence problem by mapping visual information into his own body space.

CONCLUSION

This section closes the chapter dedicated to neural networks models of the mirror neurons system for motor and social development. Although the neural mechanisms underlying their organization are still in debate, as well as their primary functions, mirror neurons furnish an appealing explanation how social skills could emerge from the neural extent of the body physics, to recognize others actions and others intentions, to perceive oneself and others agency, to represent the personal space.

In line with the few proponents that support the learning hypothesis [Keysers and Perrett, 2004, Heyes, 2010], we propose that these skills may be learnt from multimodal experiences (vision and somatosensation in Section 2.1.) and sensorimotor experiences (vision and motor systems in Section 2.3. and 2.4.) during early development and that the MNS organization may emerge from a mostly unstructured network of learning spiking neurons. We have shown that the idea of hebbian learning and of spike-time dependent plasticity, that has been proposed over 6 years ago, actually works, and leads to the emergence of somatosensory-visual and visuo-motor connections that resemble those that visuo-motor mirror neurons have. The learnt networks present the properties of complex systems to be organized sparsely and hierarchically and to rely on specific units, efficiently connected, that rule out the overall neural activity. These neurons function like hub connectors that fuse unimodal signals into multimodal information.

The primary role attributed to sensorimotor networks, to transform sensory signals into motor commands, can serve then to construct the body image, to represent actions and to identify self-produced body signals (i.e., agency). Learning to combine the various kinds of body signals can serve to intrust the position of the body limbs, to authentify oneself actions and to transform the whole-body activity into spatial coordinates. Besides, the intertwining between perception and action may permit to anticipate and predict associations within and across modalities even in the case of missing modalities as it occurs when we interact with others. These properties may serve to simulate others actions from the basis of our own sensorimotor system, and work as a window to social abilities [Gallese, 2005, Meltzoff, 2007].

For instance, we showed that the learnt neural associations from live enaction between tactile and visual patterns can serve to reconstruct one missing modality from partial information, like during the observation of someone else actions. The level of synchrony in sensorimotor networks can serve then to quantify the agent's agency. Meanwhile, interacting with other agents can modulate the level of sensorimotor integration, which can be interpreted then as authentifying others agency. A failure in this mechanism may cause troubles in agency perception and social development.

Finally, the ability to perceive the spatial boundaries of *oneself* body parts can serve also to delimit the social boundaries with others for self-perception, self-other differentiation 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 his own body space.

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