A Neural Network Model of Peri-Hand Space Representation and Its Plastic Properties Related to Tool Use

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Abstract—In the present study, we investigated the neural basis of peri-hand space representation and its plastic modifications related to tool-use by means of a neural network model. The model includes two networks (one per hemisphere/hand); each network includes two unimodal areas (visual and tactile, respectively) linked via synapses to a third downstream bimodal (visual-tactile) area. The two hemispheres interact via inhibitory synapses. The model assumes that synapses linking unimodal to bimodal neurons can be reinforced by a Hebbian rule during tool-use training; this reinforcement is also under the influence of spatial attentive mechanisms. To assess the effects of tool-use training, we simulated the visual-tactile interaction both in a healthy and a pathological subject with left tactile extinction, before and after the training. Results show that the integrative visual-tactile peri-hand area, limited around the hand before the training, is modified by tool-use to include new sectors of space, thanks to the sprouting of new visual synapses. The new size and shape of peri-hand area is determined by the attentive mechanisms active during tool-use training, which highlight only specific portions of the visual space functionally relevant to the use of the tool. The model may be of value to analyze the neural mechanisms responsible for representing and plastically shaping peripersonal space, and for the interpretation of psychophysical data on neurological patients with spatial perceptual deficits.

I. INTRODUCTION

OUR ability to interact successfully with objects in the environment crucially depends on an adequate representation of objects location in space with respect to our own body and especially our hands. Studies on animals and humans suggest that the brain constructs separate representation of peripersonal space (the space immediately surrounding our body, where objects can be reached and grasped), and extrapersonal space (located beyond the reach of our limbs) [1].

Electrophysiological recordings in monkeys have revealed the existence of neurons in the parietal and premotor cortices and putamen, that are activated by tactile stimuli on a specific body part (e.g., the face or a hand) and visual stimuli near the same body part [2], [3]. The visual response is stronger for visual stimuli close to the cutaneous receptive field (RF) and decreases at farther distances. The visual RF remains anchored to the tactile RF, when the body part is moved in space. Because of these functional properties, such bimodal neurons were postulated to form an interconnected visual-tactile system coding peripersonal space in body-centered coordinates.

The most compelling evidence for a similar visuotactile coding of peripersonal space in humans comes from studies on right brain damaged (RBD) patients affected by cross-modal extinction [4]. These patients are able to detect left or right stimuli when presented in isolation (unilateral stimulation), but show unawareness of contralesional (left) tactile stimuli when an ipsilesional (right) visual stimulus is presented simultaneously (bilateral stimulation). Crucially, tactile extinction is much severe when the visual stimulus is delivered close (≈ 5 cm) to the ipsilesional (right) hand, whereas left tactile perception significantly ameliorates when the same visual stimulus is presented away (≈ 30 cm) from the right hand [4]-[6]. The presence of extinction only in bilateral stimulation is suggestive of a competition between the representations of the two hemispaces [6]; the near-far modulation of cross-modal extinction suggests that the two representations are tuned to the space close to the body. This evidence has been considered the behavioral hallmark of an integrated visual-tactile representation of peri-hand space in humans, similar to that achieved by bimodal neurons in monkeys.

The use of manual tools expands the accessible space, enabling to act on objects located in the far space, where they are not directly reachable by hands. Consequently, the relation between our body and the external objects is modified while using a tool. Several recent works have investigated the effects of tool use on space perception, starting from the pioneering results obtained by Iriki *et al.* in macaques trained to use a rake to retrieve distant food [7]. In these monkeys, after few minutes of tool use, visual RF of intraparietal visuotactile neurons, originally limited to the space around the hand, expanded along the axis of the tool, up to include the far space where the tool had been used. Behavioral evidence for a similar re-mapping of far space as near space are reported by studies on normal humans and RBD patients [8]. For example, in RBD patients, left tactile extinction induced by a visual stimulus presented at a distal end of a rake was more severe immediately after the tool was used to retrieve distant objects than before its use [9], [10].

The growing body of studies about tool-use dependent modulation of peripersonal space has raised a number of crucial questions that still remain open. Among them: Which are the neurophysiological correlates of peripersonal space plasticity? How do the boundaries of the visuotactile peripersonal space modify? How can behavioral results be related to the properties of individual neurons? Moreover, spatial attentive mechanisms, activated by the functional use of a tool, may have an important role in producing peripersonal space re-sizing. Hence, which is the influence of these attentive mechanisms on the neural circuit subserving peripersonal space representation and its plasticity?

Here, we proposed a neural network model of visual-tactile coding of peripersonal space, to investigate the plastic modifications of peri-hand space following tool-use and to provide possible answers to the previous questions. Training with a tool has been reproduced by including a Hebbian learning rule, according to which synapses are reinforced in presence of the simultaneous activation of the pre-synaptic and post-synaptic neurons. In order to simulate alternative hypotheses on peri-hand space resizing, we considered two different conditions of training, related to tool-mediated task and attention, which differently modify the boundaries of visual-tactile integrative area. Then, the effects of these alternative modifications of peri-hand space have been tested by simulating the responses to visual-tactile stimulations both before and after tool-use training, in a healthy subject and a RBD patient with left tactile extinction.

II. METHOD

A. General model structure

The model include two networks, one per hemisphere, each composed of three areas of neurons (Fig. 1).

The two upstream regions are unimodal, tactile and visual respectively. They are defined with reference to the hand of a hypothetical subject: neurons in the tactile area respond to tactile stimuli on the hand; neurons in the visual area respond to visual stimuli on the hand and around it (both in the near and far space). Each element of the unimodal areas has its own receptive field (RF) through which receives stimulation by an external input. The neurons in the same unimodal area interact via lateral synapses with a Mexican hat disposition (a central excitatory area surrounded by an inhibitory annulus).

The third downstream region is multimodal, devoted to visual-tactile integration. It includes: i) A multimodal excitatory neuron which receives feedforward synapses from the unisensory neurons, and sends back feedback synapses. Moreover, it projects long-range connections towards the other hemisphere. ii) A multimodal inhibitory interneuron, which realizes inter-hemispheric interaction. It receives visual-tactile information from the multimodal excitatory neuron in the other hemisphere and sends inhibitory synapses to the unimodal neurons within the same hemisphere. Inclusion of these connections implements a competitive

mechanism in case of the simultaneous activation of the right and left hand representations.

All neurons in the network are normally in a silent state and can be activated if stimulated by a sufficiently high input. The activity of each neuron is described through a sigmoidal relationship and a first order dynamics.
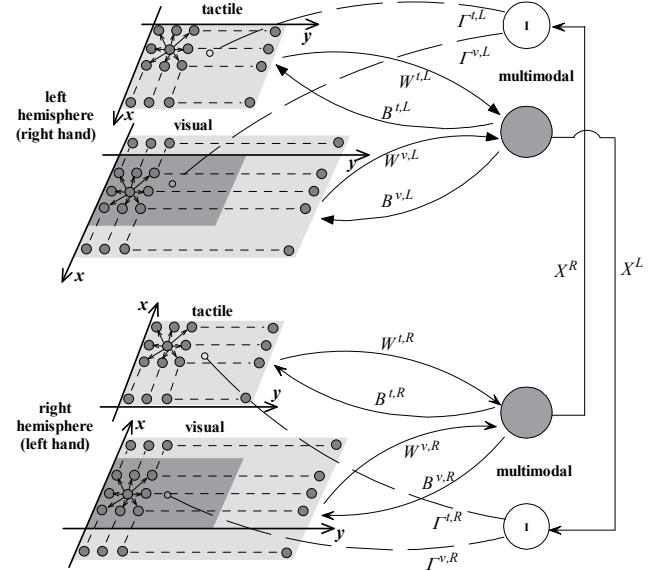

Fig. 1. Schematic diagram describing the general structure of the model. Each dark circle represents an excitatory neuron. The two hemispheres interact via inhibitory interneurons (open circles with symbols I).

B. Mathematical description

Since the overall network has a symmetrical structure, only the equations for one hemisphere (the left one) will be presented. We will use: the superscripts t, v, and m to denote quantities referring to tactile, visual and multimodal excitatory neurons; the superscript g to indicate quantities referring to inhibitory interneurons; the superscripts L and R for the left and right hemisphere; the subscritps ij or hk to represent the spatial position of single neurons.

1) Organization of the unimodal and multimodal areas: The unimodal areas are composed by $N^s x M^s$ neurons (s = t, v), with $N^t = 20$, $M^t = 40$; $N^v = 30$, $M^v = 200$. In both areas, the RFs of neurons are arranged at a distance of 0.5 cm along both the x and y directions. Hence, the tactile area covers a space of 10 cm x 20 cm, representing the surface of one hand in an extremely simplified form, while the visual area covers a space of 15 cm x 100 cm, representing the visual space on the hand and around it (extending by 2.5 cm on each side and 80 cm ahead). The RF of unisensory neurons is described with a Gaussian function.

We assumed that the synapses from and to tactile neurons have a uniform distribution over the entire tactile area (i.e., their value is independent from the position of neurons in the area). On the contrary, the synapses from and to the visual area have a Gaussian distribution, with synaptic strength decreasing with the distance from the central point of the hand ($x_0 = 5$ cm, $y_0 = 10$ cm). Hence, in agreement with

physiological data [2], a single multimodal neuron covers the entire visual-tactile peri-hand space, with a uniform tactile RF and a Gaussian visual RF that includes the visual space on the hand and close to it (about 5 cm around the hand).

2) The activity of the unisensory neurons: The total input received by a generic neuron ij in the unisensory areas is the sum of four different contributions.

a) The contribution due to the external stimulus (say $\varphi_{ij}(t)$). This is computed as the inner product of the stimulus and the receptive field. The external stimulus may be punctual, and activate only a small bubble of neurons, or more extended and activate a wider region of neurons.

b) The contribution due to the lateral synapses linking the neuron with the other elements in the same area (say $\lambda_{ij}(t)$). This is defined as:

$$\lambda_{ij}^{s,L}(t) = \sum_{h=1}^{N^S}\sum_{k=1}^{M^S} \Lambda_{ij,hk}^{s,L} \cdot z_{hk}^{s,L}(t), \quad s = t, v \tag{1}$$

$z_{hk}^{s,L}(t)$ represents the activity of the hk neuron in the area s ($s = t, v$) of the left hemisphere. $\Lambda_{ij,hk}^{s,L}$ indicates the strength of the synaptic connection from the pre-synaptic neuron at the position hk to the post-synaptic neuron at the position ij. These synapses are arranged according to a "Mexican hat".

c) The contribution due to the feedback excitatory projections from the multimodal neuron (say $\beta_{ij}(t)$). This is:

$$\beta_{ij}^{s,L}(t) = B_{ij}^{s,L} \cdot z^{m,L}(t), \quad s = t, v \tag{2}$$

where $z^{m,L}(t)$ represents the activity of the multimodal neuron in the left hemisphere and $B_{ij}^{s,L}$ indicate the strength of the synaptic connection from the multimodal neuron to the unimodal neuron at the position ij. Synaptic strengths are computed as follows:

$$B_{ij}^{t,L}(t) = B_0^{t,L}, \quad \forall i, j \tag{3}$$

$$B_{ij}^{v,L}(t) = B_0^{v,L} \cdot \exp\left(-\frac{\left(x_i^{v,L} - x_0\right)^2}{2 \cdot \left(\sigma_x^{v,L}\right)^2} - \frac{\left(y_j^{v,L} - y_0\right)^2}{2 \cdot \left(\sigma_y^{v,L}\right)^2} \right) \tag{4}$$

where $x_i^{v,L}$ and $y_j^{v,L}$ represent the centre of the RF of the visual neuron ij, x_0 and y_0 are the coordinates of the central point of the hand. Parameters $B_0^{v,L}$, $\sigma_x^{v,L}$ and $\sigma_y^{v,L}$ set the amplitude and extension of the synapses.

d) The contribution due to the synapses from the inhibitory interneuron (say $\gamma_{ij}(t)$). This term is defined as:

$$\gamma_{ij}^{s,L}(t) = \Gamma_{ij}^{s,L} \cdot z^{g,L}(t) \quad s = t, v \tag{5}$$

$z^{g,L}(t)$ is the activity of the inhibitory interneuron and $\Gamma_{ij}^{s,L}$ is the synaptic weight from the interneuron to neuron ij in the

unimodal area s ($s = t, v$). These synapses are computed according to equations similar to (3) and (4), with different amplitude values.

Hence, the total input for the unisensory neuron ij is:

$$u_{ij}^{s,L}(t) = \varphi_{ij}^{s,L}(t) + \lambda_{ij}^{s,L}(t) + \beta_{ij}^{s,L}(t) + \gamma_{ij}^{s,L}(t) \tag{6}$$

Then, neuron activity ($z_{ij}^{s,L}(t)$) is computed from its input via a first order dynamics and a static sigmoidal relationship.

3) The activity of the multimodal neurons: The multimodal excitatory neuron receives input from neurons in the two unisensory areas via feedforward synapses:

$$u^{m,L}(t) = \sum_{h=1}^{N^t}\sum_{k=1}^{M^t} W_{hk}^{t,L} \cdot z_{hk}^{t,L}(t) + \sum_{h=1}^{N^v}\sum_{k=1}^{M^v} W_{hk}^{v,L} \cdot z_{hk}^{v,L}(t) \tag{7}$$

where $z_{hk}^{s,L}(t)$ represents the activity of the neuron hk in the unimodal (tactile or visual) area, and $W_{hk}^{s,L}$ denotes the synapses from the unisensory neuron hk to the multimodal neuron. These synapses are computed as follows:

$$W_{hk}^{t,L}(t) = W_0^{t,L}, \quad \forall h, k \tag{8}$$

$$W_{hk}^{v,L}(t) = W_0^{v,L} \cdot \exp\left(-\frac{\left(x_j^{v,L} - x_0\right)^2}{2 \cdot \left(\sigma_x^{v,L}\right)^2} - \frac{\left(y_j^{v,L} - y_0\right)^2}{2 \cdot \left(\sigma_y^{v,L}\right)^2} \right) \tag{9}$$

where the meaning of the symbols is the same as (3) and (4).

Then, the activity of the multisensory neuron ($z^{m,L}(t)$) is obtained from its input through a first order dynamics and a static sigmoidal relationship.

The multimodal inhibitory interneuron in the left hemisphere receives its input ($u^{g,L}(t)$) from the multimodal excitatory neuron in the right hemisphere. Accordingly

$$u^{g,L}(t) = X^R \cdot z^{m,R}(t - D) \tag{10}$$

$z^{m,R}(t)$ is the activity of the multimodal neuron in the right hemisphere and D is a pure delay (representing the inter-hemispheric transit time). X^R is the strength of the cross-connection from the right to the left hemisphere. Finally, the activity of the interneuron ($z^{g,L}(t)$) is obtained from its input via a first order dynamics and a static sigmoidal function.

Basal values for all model parameters, representing a normal healthy subject, have been assigned on the basis of physiological and behavioral studies. The RBD patient with left tactile extinction has been simulated by reducing the strength of all the synapses originating from the tactile neurons in the right hemisphere (both lateral and feedforward synapses). This modification may reflect a loss of neurons in the right tactile area consequent to the lesion.
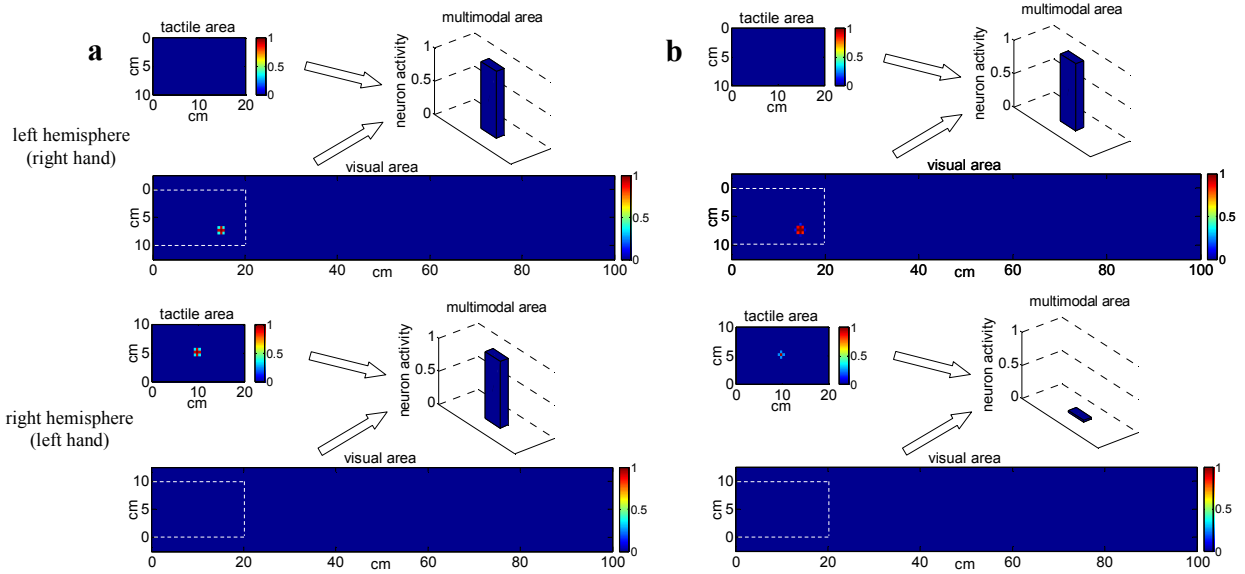
Fig. 2. Network activity in response to a visual stimulus on the right hand and a tactile stimulus on the left hand, in the healthy subject (panel a) and in the RBD patient (panel b). In the latter case, left tactile extinction occurs. The dashed line in the visual area delimits the visual space on the hand.

C. Model Plasticity

The model has been used to simulate tool-use experiments, in which the subject uses a long tool to connect his right hand with far space. To reproduce tool use, we considered a tactile stimulus, corresponding to the part of the hand stimulated while holding the tool, and a visual stimulus, representing the portion of the visual space where the tool is functionally used, selected by attentive mechanisms. During the application of these inputs, synapses linking the unimodal areas to the multimodal area in the left hemisphere ($W_{hk}^{s,L}$) are subject to Hebbian plasticity, according to the equation :

$$W_{hk}^{s,L}(t+T_S) = W_{hk}^{s,L}(t) + \varepsilon \cdot z_{hk}^{s,L}(t) \cdot z^{m,L}(t) \qquad (11)$$

T_S is the sampling time, and ε is the learning rate.

III. RESULTS

Fig. 2 shows the network activity in response to a tactile stimulus on the left hand and a simultaneous visual stimulus on the right hand, both in the normal (Fig. 2a) and RBD (Fig. 2b) subject, in basal conditions (i.e., before tool use). In the normal subject (Fig. 2a), each stimulus produces a significant activation in the related unisensory area, and triggers the corresponding multimodal neurons, leading to a competition between the two simultaneous representations (via the inhibitory interneurons). In this case, the competition is unbiased and both multimodal neurons are activated at the same level (the two hand representations coexist). In the RBD subject (Fig. 2b), right hemisphere activation is impaired, and the ipsilesional (right) hand representation is advantaged in the competition. The final outcome is a weaker activity in the right tactile area, unable to activate the

multimodal neuron, which remains completely silent (only the right hand representation survives).

Then, the model was used to reproduce the results of learning experiments, in which a subject uses a long tool in his right hand to interact with far space. We imagined a tool extending from the hand to the position $x = 5$ cm, $y = 50$ cm (tip). Two distinct conditions of training (A and B) were simulated, which differ as to the applied visual input. We hypothesize that different visual stimuli may be ascribed to spatial attentive mechanisms that select different portions of visual space, depending on the specific tool-use task. In condition A, we applied a right visual stimulus which covered a wide portion of space, being centred at the tip in the far space, and extending several centimetres along the y axis both before and after that position. This visual stimulation during the learning phase might correspond to a tool-use task requiring subject's visual attention to be spread all along the tool axis for several centimetres before and beyond the functional tip. For example, such a kind of attention may be involved when the subject uses a rake to reach objects in the far space and retrieve them near the body. In condition B, we considered a right visual stimulus strictly concentrated within a limited portion of the far space around the tip. This could represent a tool-mediated task in which subject's attention is focused on the functional tip of the tool, e.g., when the tool is used to touch a far point with the tip. In both conditions, the right visual stimulus was paired with a right tactile stimulus mimicking the parts of the hand stimulated while wielding the tool. Fig. 3a shows visual synapses before tool-use. Fig. 3b shows the modification of the visual synapses after the training A: new synapses were formed all along the extended visual space highlighted during the training. Fig. 3c shows the modification of the visual synapses after the training B: new synapses originate from the localized visual region active during the training.
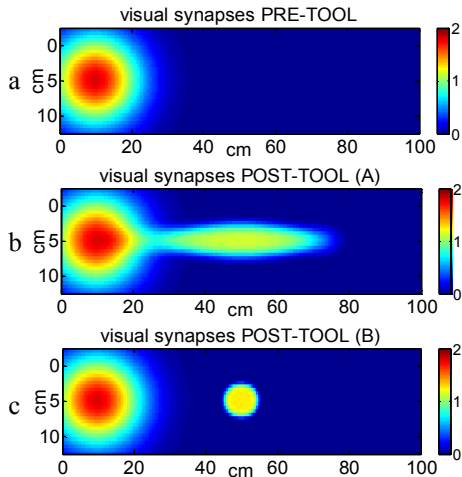
Fig. 3. Modification of the visual synapses after tool-use training in two different conditions (A and B) of spatial visual attention.
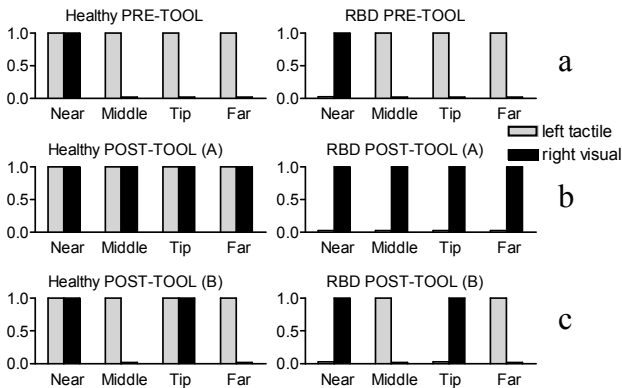

Fig. 4. Activity of the multimodal neurons in the two hemispheres, in response to a left hand tactile stimulus and a simultaneous right-side visual stimulus, in the healthy and RBD subject, before and after the two trainings.

To assess the effects of the previous learning experiments on visual-tactile interaction, we simulated the response to bilateral stimulation (as in Fig. 2) both in the healthy and RBD subject, before and after the two training conditions, with the right visual stimulus located at four different positions: Near (on the hand); Middle (x= 5 cm, y = 32 cm); Tip (x = 5 cm, y = 50 cm), Far (beyond the tip, x= 5 cm, y = 70 cm). Results are reported in Fig. 4. The histograms show the multimodal neuron activity in the left and right hemisphere. Because of the pattern of the original visual synapses, the multimodal neuron responds only to the near visual stimulus before training, and left tactile extinction in the patient occurs only for this stimulus position (Fig. 4a). After the training in condition A, right visual stimulus located in any of the four positions activates the multimodal neuron in the left hemisphere: in the healthy subject, the two stimuli coexist in any position, whereas in the RBD subject, left tactile extinction occurs for all four stimulus positions (Fig. 4b). After the training in condition B (Fig. 4c), the multimodal neuron in the left hemisphere is activated only by a right visual stimulus located on the hand or at the tip of the tool. In the RBD subject, the left tactile stimulus is extinguished by a right visual stimulus at these two positions.

IV. DISCUSSION

The present work has several important implications, both at theoretical and clinical level.

First, it provides an original model of visual-tactile integration in specialized areas of the cortex, implicated in peripersonal space representation, as documented by a great amount of neurophysiological, and behavioural studies [2]-[5], [7]. The representation of peri-hand space is simulated by a network of three interconnected neural areas (two unimodal converging into one multimodal), with suitable patterns of synaptic connections. Furthermore, the model assumes that stimuli in the two sides of space interact via a competitive mechanism, in agreement with the theory that simultaneous events (both in the same and different modalities) compete for representation in the brain [6]. It is worth noting that the model does not aspire to reflect the neurophysiology and neuroanatomy of the real system in details, but rather to identify a plausible structure of the network and the functional links between its different parts, able to provide a possible interpretation of psychophysical and behavioral results. In particular, a single neuron in the model, should not be considered as an individual cell, but rather as a pool of cells, with RFs approximately in the same spatial position. By adopting the previous structure, the model can reproduce response properties of neurons representing peripersonal space in normal conditions (see Fig. 2a and Fig. 4a left panel) and it allows interpretation of behavioural results in terms of neural responses, assuming that the conscious perception of an event in the peri-hand space is signalled by the activation of the multimodal area.

As a consequence, the model may be of value to identify possible alterations of the neural circuitry at the basis of deficits in spatial awareness, such as extinction. Studies on cross-modal extinction have provided considerable insights into the multimodal spatial representations in humans [4]; moreover this phenomenon is widely exploited to investigate the spatial properties of peri-hand space resizing following tool-use [9], [10]. Left tactile extinction has been reproduced by reducing the synapses from right tactile neurons, to reflect a loss of neurons consequent to the right brain lesion. The predicted results (Fig. 2b) are consistent with fMRI and ERP studies [11] showing that extinguished left touches are accompanied by a residual activation of the somatosensory cortex (that may correspond to the tactile unimodal area in the model) without any activation of multimodal areas in the right parietal cortex (bimodal neuron in the model).

An important property of peripersonal space representation, that can be proficiently investigated with the model, is its plastic alteration related to tool-use experiences.

Dynamic resizing of visual-tactile peri-hand space following tool use has been reproduced by assuming a Hebbian plasticity of the feedforward synapses converging into bimodal neurons. Indeed, recent studies on monkeys [12] show the formation of new synapses from visually-related areas to the intraparietal bimodal area, induced by

tool-use. Moreover, the model emphasizes the importance of attentive mechanisms in determining the spatial features of peri-hand space resizing. A key role of attentive mechanisms is supported by neurophysiological and behavioural data [7], [10]: they show that expansion of the peri-hand space occurs only in case of active tool uses, involving attention, and not in case of passive exposure to a hand-held tool.

The model reproduces two different alterations of the boundaries of the visual-tactile peri-hand area, related to two different conditions of tool-use [10], [13].

The first condition (A) considered a wide visual input, centred on the tip and spreading longitudinally. We assumed this condition as representative of tool-use tasks requiring visual attention to cover a broad portion of visual space along the tool axis, before and beyond the tip. The model predicts a genuine extension of the visual-tactile integrative area, to include the elongated visual space highlighted during tool training (Fig. 3b), with consequent extinction of left tactile stimulus in the patient for any visual stimulus located in this space (Fig. 4b). These model predictions are in agreement with results by Farnè *et al.* [9], [10] obtained on RBD patients that used a tool with the right hand to retrieve distant objects. In these studies, after 5 min of tool use, left tactile extinction produced by visual stimuli located at the middle and distal location along the tool (in the model, Middle and Tip stimuli) was as severe as that obtained by a visual stimulation near the ipsilesional hand (Near stimulus in the model). Moreover, strong extinction was also caused by a visual stimulus located several centimeters beyond the tip of the tool [9] (Far stimulus in the model).

In the second condition (B), we applied a visual stimulus confined within a restricted portion of the far space. We supposed this condition as representative of tool-mediated tasks requiring a visual attention closely localized around the tip of the tool. The model predicts the formation of a novel integrative visual-tactile area around the tip of the tool, the original area near the hand remaining unchanged (Fig. 3c). Accordingly, in the patient the right visual stimulus interferes with left tactile stimulus only if it is placed near the hand or near the distal edge of the tool (Fig. 4c). These model results are consistent with findings reported by Holmes *et al.* in normal participants [13]. During tool-use tasks, the authors assessed the effects of visual-tactile interference at different locations along the hand-held tool, finding a significant effect only at the handle and at the tip of the tool.

As suggested by the model, the discrepancy between results by Farnè *et al.* and by Holmes *et al.* may be related to spatial attentive mechanisms, which select a different sector of visual space, more or less localized, depending on the specific nature of the tool-mediated task. Indeed, in the study by Holmes *et al.* [13] the subjects were asked to push a button with the tip of the tool; this task presumably requires visual attention to be strictly focused around the button, where the tool is functionally used. Conversely, in the studies by Farnè *et al.* [9], [10] the patients had to reach and retrieve distant objects with a rake. Retrieving objects may highlight a wider portion of space functionally relevant to the task, including the area where the distant objects are located and the space between the tip of the tool and the hand, along which the objects are dragged towards the body subject.

V. CONCLUSIONS

The present study proposes a plausible scenario of the neural circuitry at the basis of peripersonal space representation. The model does not aspire to reproduce in details how the real system works, but rather to identify the functional links between its different parts. The model may be of value to investigate the alterations of the neural mechanisms associated to particular conditions such as neurological deficits or tool-use experiences. In particular, the model can help solving the discrepancy between in vivo-data, integrating them into a unique framework, and may suggest new experiments to validate the proposed mechanisms. In perspective, it may be also used to identify and plane rehabilitation procedures for neurological patients.

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