Neuropsychologia 48 (2010) 812–830

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Neural bases of peri-hand space plasticity through tool-use: Insights from a combined computational–experimental approach

Elisa Magosso[a,**], Mauro Ursino[a], Giuseppe di Pellegrino[b,c], Elisabetta Làdavas[b,c], Andrea Serino[b,c,*]

[a] Department of Electronics, Computer Science and Systems, University of Bologna, Bologna, Italy
[b] Department of Psychology, University of Bologna, Bologna, Italy
[c] Centro studi e ricerche in Neuroscienze Cognitive, Cesena, Italy

ARTICLE INFO

Article history:
Received 19 April 2009
Received in revised form
24 September 2009
Accepted 29 September 2009
Available online 14 October 2009

Keywords:
Neural network modelling
Body representation
Space representation
Multisensory integration
Cross-modal extinction
Attention
Hebbian plasticity
Sense of body

ABSTRACT

Visual peripersonal space (i.e., the space immediately surrounding the body) is represented by multimodal neurons integrating tactile stimuli applied on a body part with visual stimuli delivered near the same body part, e.g., the hand. Tool use may modify the boundaries of the peri-hand area, where vision and touch are integrated. The neural mechanisms underlying such plasticity have not been yet identified. To this aim, neural network modelling may be integrated with experimental research. In the present work, we pursued two main objectives: (i) using an artificial neural network to postulate some physiological mechanisms for peri-hand space plasticity in order to account for in-vivo data; (ii) validating model predictions with an ad-hoc behavioural experiment on an extinction patient.

The model assumes that the modification of peri-hand space arises from a Hebbian growing of visual synapses converging into the multimodal area, which extends the visual receptive field (RF) of the peripersonal bimodal neurons. Under this hypothesis, the model is able to interpret and explain controversial results in the current literature, showing how different tool-use tasks during the learning phase result in different re-sizing effects of the peri-hand space. Importantly, the model also implies that, after tool-use, a far visual stimulus acts as a near one, independently of whether the tool is present or absent in the subject's hand. This prediction has been validated by an in-vivo experiment on a right brain-damaged patient suffering from visual–tactile extinction. This study demonstrates how neural network modelling may integrate with experimental studies, by generating new predictions and suggesting novel experiments to investigate cognitive processes.

1. Introduction

1.1. Peripersonal space representation and its plastic properties

The brain constructs multiple and functionally segregated spatial representations of the external world, that are called into play according to different tasks (Colby, 1998; Gross & Graziano, 1995). The origin of different space representations is the subject's body: distinct sectors of space can be defined as a function of the distance from the body. It is possible to distinguish a *personal space*, corresponding to the body surface, *a peripersonal space*, the space closely surrounding body parts and an *extrapersonal space*, the space outside the hand-reaching distance (Beschin & Robertson, 1997; Previc, 1998; Rizzolatti, Fadiga, Fogassi, & Gallese, 1997). In such space taxonomy, peripersonal space representation is particularly important, because within its limits the body can directly interact with the external world. The focus of the present paper is on peripersonal space representation.

Different spatial representations are supported by quite distinct neural networks. Animals and humans studies converge in showing that peripersonal space is represented by a specialized brain system within the frontal and parietal lobe (Làdavas, 2002; Maravita, Spence, & Driver, 2003). Neurophysiological research in monkeys has revealed the existence of subpopulations of neurons, within a network of cerebral structures (including the putamen, parietal and premotor areas), that have a tactile receptive field (RF) centred on a specific body-part (hand, face, arm, shoulder, etc.) and a visual RF roughly matching the location of the tactile RF, and extending only few centimetres outward from the skin (Duhamel, Colby, & Goldberg, 1998; Fogassi et al., 1996; Graziano, Hu, & Gross, 1997; Rizzolatti, Luppino, & Matelli, 1998). These neurons – called bimodal neurons – respond to incoming stimuli of either modal-

* Corresponding author at: Dipartimento di Psicologia, viale Berti-Pichat 5, I-40123 Bologna, Italy. Tel.: +39 0547 338951; fax: +39 0547 338952.
** Corresponding author at: Dipartimento di Elettronica, Informatica e Sistemistica, Viale Risorgimento 2, I-40136 Bologna, Italy. Tel.: +39 051 2093943; fax: +39 051 2093073.
E-mail addresses: elisa.magosso@unibo.it (E. Magosso), andrea.serino@unibo.it (A. Serino).

0028-3932/$ – see front matter © 2009 Elsevier Ltd. All rights reserved.
doi:10.1016/j.neuropsychologia.2009.09.037

ity, the strength of the visual response decreasing as the distance between the visual events and the cutaneous RF increases. The visual RF remains anchored to the tactile RF when the body part is moved in space, and its location does not change when the eyes move. These response properties suggest that bimodal neurons operate by integrating multisensory cues in body part-centered coordinates, specifically for the space near the body.

In humans, considerable insight into peripersonal, and in particular peri-hand, space representation has been provided by neuropsychological studies in right brain-damaged (RBD) patients, suffering from cross-modal extinction, a clinical sign whereby an ipsilesional (right) visual stimulus interferes with the detection of a simultaneous contralesional (left) tactile stimulus. Crucially, tactile perception on the contralesional hand is modulated by the distance between the visual stimulus and the ipsilesional hand: left tactile extinction is more severe when visual stimuli are presented near the hand (~5 cm from the right hand) compared to when they are presented in the far space (~35 cm from the right hand) (di Pellegrino, Làdavas, & Farnè, 1997; Làdavas, di Pellegrino, Farnè, & Zeloni, 1998; Ladavas & Farnè, 2004). Moreover, in a case study in which the patient's hands were crossed, a visual stimulus near the right hand (now in the left hemispace) still induced significant extinction of tactile stimuli on the left hand (in the right hemispace), suggesting that visual–tactile interaction responsible for extinction operates in a reference system anchored to the hand (di Pellegrino et al., 1997). These results have been taken as a behavioural evidence of the existence of a multisensory integrative system in humans, operating in the near space and in a body part-centred reference frame, similar to that achieved by bimodal neurons in monkeys.

A recent fMRI study in healthy participants (Makin, Holmes, & Zohary, 2007) has identified regions (in the posterior parietal and premotor cortex) selectively responding to a tactile stimulation on the hand and to a visual stimulus approaching the hand (see also Bremmer et al., 2001; Sereno & Huang, 2006 for neural basis of the peripersonal space around the head).

Peripersonal space representations in humans, as in monkeys, have basically a motor function: spatial locations of multisensory stimuli are encoded in relationship to body parts to generate appropriate motor responses (goal-directed, defensive or avoidance movements) (Graziano & Cooke, 2006; Ladavas & Farnè, 2004; Legrand, Brozzoli, Rossetti, & Farné, 2007; Rizzolatti et al., 1998). Normally, such action space is delimited by the physical length of body effectors. Tools can be used as physical extensions of the body, enabling to reach and interact with distant objects. This leads to the intuitive idea that tool use may modify the boundaries of the peri-hand area, where vision and touch are integrated. Such intuition is supported by in-vivo studies.

In a pioneering study on monkeys (Iriki, Tanaka, & Iwamura, 1996), Iriki and colleagues observed that, after the animal had repeatedly used a tool to retrieve distant food pellets, the visual RF of intraparietal bimodal neurons was elongated to include the entire length of the tool, whereas originally it was limited to the space around the hand. A possible neural mechanism underlying this phenomenon has been suggested by recent neurophysiological findings: tool-use training may promote the emergence of novel projections from high-order visual-related areas to bimodal regions in the intraparietal sulcus (Hihara et al., 2006; Ishibashi et al., 2002).

Spatial redistribution of visual–tactile integration has been observed also in humans following tool use. In extinction patients, a visual stimulus located at the end of a right hand-held tool induced more severe left tactile extinction immediately after the tool use than before (Farnè & Làdavas, 2000; Maravita, Husain, Clarke, & Driver, 2001). A remapping of far space into near space by active tool-use has been demonstrated also in healthy subjects, using the cross-modal congruency task (Holmes, Calvert, & Spence, 2004; Maravita, Spence, Kennett, & Driver, 2002) and in neglect patients using the line bisection task (Berti & Frassinetti, 2000; Neppi-Mòdona et al., 2007; Pegna et al., 2001).

In the last years, much research has been performed at a behavioural level in healthy subjects and RBD patients, in order to identify the functional and spatial characteristics of peri-hand space plasticity (Bonifazi, Farnè, Rinaldesi, & Làdavas, 2007; Farnè, Iriki, & Làdavas, 2005; Farnè, Serino, & Làdavas, 2007; Holmes et al., 2004; Holmes, Sanabria, Calvert, & Spence, 2007; Maravita et al., 2002). However, interpretation of behavioural results into a coherent theory and identification of underlying neural mechanisms are extremely difficult, because of dissimilarity between experimental paradigms and sometimes discrepancy among observed results and interpretative accounts. Neural network modelling may contribute to gain a deeper insight into the neural and functional mechanisms of peripersonal space representation and its plasticity: mathematical models may favor integration of the current neurophysiological and behavioural knowledge into a coherent synthesis, and may help interpretation of the variability of the results reported in the literature. Furthermore, new experiments may be suggested on the basis of model predictions, to test the different hypotheses.

Recently, we have developed a neural network model that mimics the visual–tactile representation of peripersonal space around the left hand and the right hand: the model identifies plausible neural structures and connections, and is able to account for several psychophysical and behavioural results both in healthy subjects and in extinction patients (Magosso et al., 2009).

The aim of the present work is to use a modified version of the model to investigate the neural mechanisms underlying plasticity of the peri-hand space representation. In particular, the model will be used: (i) to hypothesize some physiological mechanisms for synapses plasticity in the model, and to assess whether these mechanisms can account for dynamic changes in peri-hand space representation after tool use; (ii) to simulate the consequence of a brain damage (as in the case of extinction patients) on perceptual awareness, before and after synapses training; (iii) to bring together controversial results in the literature on the peri-hand space reconfiguration within a single theoretical framework; (iv) to test the model hypothesis on synapses plasticity with an ad-hoc behavioural experiment on an RBD patient.

1.2. A neural network model for peri-hand space representation: Qualitative description

The model is an updated version of the previous one (Magosso et al., 2009) with just few changes that simplify the network structure and facilitate simulation and analysis of peri-hand space plasticity. In this section, the model is described in a qualitative way; a quantitative description with all equations can be found in Appendix A.

The model is made of two networks, one per hemisphere, each referred to the contralateral hand of an hypothetical subject (Fig. 1). The two networks are reciprocally interconnected.

Each network embodies three areas of neurons, which communicate via synaptic connections. The two upstream areas are two-dimensional matrices of unimodal neurons: neurons in one area respond to tactile stimuli on the contralateral hand (*tactile area*); neurons in the other area respond to visual stimulation on the same hand and around it (*visual area*). Each neuron has its own receptive field, reproduced by means of a Gaussian function, through which it receives external stimulation. In both areas, the RFs are in hand-centred coordinates, and are arranged at a distance of 0.5 cm along both the x and y directions; hence, within each area, proximal neurons respond to stimuli coming from proximal positions of the hand and space. The tactile area maps a surface of 10 cm × 20 cm, roughly representing the surface of the hand. The