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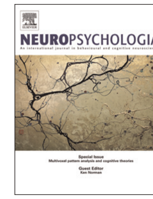

Dissociating effect of upper limb non-use and overuse on space and body representations

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ABSTRACT

Accurate and updated representations of the space where the body acts, i.e. the peripersonal space (PPS), and the location and dimension of body parts (body representation, BR) are essential to perform actions. Because both PPS and BR are involved in motor execution and display the same plastic proprieties after the use of a tool to reach far objects, it has been suggested that they overlap in a unique representation of the body in a space devoted to action. Here we determined whether manipulating actions in space, without modifying body metrics, i.e. through immobilization, induces a dissociation of the plastic properties of PPS and BR. In 39 healthy subjects we evaluated PPS and BR for the non-used right limb and the overused left limb before and after 10 h of right arm immobilization. We observed that non-use reduces PPS representation around the immobilized arm, without affecting the metric representation (i.e. perceived length) of that limb. In contrast, overuse modulates the metric representation of the free arm, leaving PPS unchanged around that limb. These results suggest that the plasticity in PPS and BR depends on different mechanisms; while PPS representation is shaped as a function of the dimension of the acting space, metric characteristics of BR are forged on a complex interplay between visual and sensorimotor information related to the body. This behavioral dissociation between PPS and BR defines a new scenario for the role of action in shaping space and body representations.

1. Introduction

To properly reach an object positioned in front of the body, the brain needs to represent both size and location of the involved body parts and the space lying in between. Neuroscientists have studied such body and space representations for many years. On one side, since no direct sensory signals inform the brain of the metrics of different body parts (Longo and Haggard, 2010), a body representation (BR) is generated from the integration of the somatosensory, proprioceptive and kinesthetic signals coming from skin, joints and muscles with visual information (De Vignemont, 2010; Medina and Coslett, 2010; Serino and Haggard, 2010). On the other side, the representation of the action space has been studied in monkeys (e.g. Rizzolatti et al., 1997) and humans (Farnè and Làdavas, 2000; Holmes et al., 2007; Serino et al., 2007) through the interaction between somatosensory information and visual or acoustic inputs, specifically when these occur within a limited area around the body, the peripersonal space (PPS). The encoding of the spatial position of external stimuli in a body-centered frame of reference facilitates the “possibility to act in space,” in terms of approaching (Rizzolatti et al., 1997) and defensive responses (Graziano and Cooke, 2006). BR and PPS refer, by definition, to different sectors of the space: the former would be limited to the body, whereas the latter includes the space surrounding the body itself (e.g. Cardinali et al., 2009a). However, previous reports have highlighted that PPS and BR jointly support efficient motor behaviors (e.g. Gallese and Sinigaglia, 2010) and show similar plastic effects. For instance, they both extend after tool-use (Bassolino et al., 2010; Canzoneri et al., 2013a; Cardinali et al., 2009b; Farnè and Làdavas, 2000; Holmes et al., 2007; Iriki et al., 1996; Maravita

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and Iriki, 2004; Maravita et al., 2002; Serino et al., 2007; Sposito et al., 2012) and rather at present there is no empirical evidence to support the dissociable effects on BR and PPS. Here, we investigated the hypothesis of a potential dissociation between BR and PPS, by manipulating "the possibility of acting in space" without modifying the body structure. For this purpose, right arm movements were limited for 10 h through immobilization (Bassolino et al., 2012) in a total of 39 healthy right-handed participants. Given that it has been shown that the non-use of one arm is systematically associated with a compensatory overuse of the free limb (Avanzino et al., 2011), in this study we then evaluated the PPS representation and the perceived length of both arms before and after immobilization. If PPS and BR rely on dissociable plastic mechanisms, upper limb non-use and overuse would differently impact on PPS representation and on the perceived arm length. Alternatively, analog effects of immobilization on PPS and BR would indicate a complete overlap in plastic effects of the two representations.

2. Materials and methods

2.1. Subjects

The study included a total of 39 healthy subjects (20 males, 19 females; age: 24.63 ± 3.09 years; range: 20–30 years). The participants were randomly assigned to 3 groups: Experiment 1, Experiment 3 and Experiment 3 (Exp. 1, Exp. 2 and Exp. 3), each composed of 13 subjects matched for age and gender, as described in the section below "Task Selection". All the participants were right-handed, as determined using the Edinburgh Handedness Inventory (Oldfield, 1971). All of them had normal or corrected-to-normal vision and hearing, with no previous history of sensory or orthopedic problems for the upper limbs. The subjects, naive to the purpose of the study, provided written informed consent and received an attendance fee at the end of the experiment. The study protocol was approved by the local ethics committee (ASL-3, "Azienda Sanitaria Locale", Genoa) and was performed in accordance with the Declaration of Helsinki.

2.2. Immobilization

The experiments were conducted for 2 consecutive days (the first day as baseline: PRE-test; the second one after immobilization: POST-test). The participants were tested around 6 p.m. During both days, subjects spent 10 working hours in the laboratory under experimenter's visual control, performing daily life activities (i.e. reading or working at the computer). Particularly, the participants did not use any type of tool to act in the far space, such as a computer mouse (Bassolino et al., 2010). On the second day, subjects were required not to use their right arm from the morning (8 a.m.) to the evening (6 p.m.). A soft painless bandage was wrapped around the subjects' hand and forearm, and a cotton support was applied to limit the arm movement and to keep the elbow joint at 90° flexion (Avanzino et al., 2011; Bassolino et al., 2012). During immobilization, the participants performed the same activities of the first day using only the left free limb. During the two testing days, the left arm activity was monitored using an accelerometer set up in a multisensory actigraph (InnerView Professional, SenseWear PRO Armband), recording the cumulative amount of time spent (in minutes) during physical activity under a level of energy expenditure set to the typical level of deskwork activity (Ainsworth et al., 2000).

At the end of the immobilization period, the experimenter removed the bandage, and the subjects were instructed not to use the right arm until the end of the entire experimental session. The overused and constrained arms were evaluated in a counterbalanced order.

2.3. Task selection

The exact number and functions of different body representations are currently a matter of discussion (see Kammers et al., 2009). Thus, on account of this on-going debate, here we deliberately decided to adopt the more neutral and generic term of body representation (BR), being well aware of the possibility to include in this definition rather different levels of body-related information processing in the brain. In particular, we refer to the metric features of BR. Accordingly, to assess a multisensory, high-level, mental representation of the body, processing several sensory cues to represent the size and position of body parts, we used two different tasks previously employed to demonstrate plastic effects induced by tool-use on body metric, that are the tactile distance perception task and body-landmarks localization task (Canzoneri et al., 2013a). Likewise, also for PPS examination, we applied the same task previously employed after tool-use, namely the audio–tactile interaction (Canzoneri et al., 2012; 2013a).

In this way, to test for a possible dissociation between BR and PPS, we recurred to the same tasks previously used to show similar dynamic effects on these bodily and spatial representations (Canzoneri et al., 2013a).

A between-subjects design was chosen to avoid the effects of carry-over and fatigue after 10 h of immobilization. Three experiments were performed in different groups of subjects to measure the effects of non-use and overuse on BR and PPS representations for both arms. Specifically, we evaluated BR in Exp. 1 (Group 1), using the tactile distance perception task (Canzoneri et al., 2013a) and in Exp. 2 (Group 2) through the body-landmarks localization task (Canzoneri et al., 2013a). Moreover, in Exp. 2 a visual representation of the whole body was also assessed using the Daurat-Hmeljiak test (Daurat-Hmeljiak et al., 1978). Finally, in Exp. 3 (Group 3), we examined PPS by using the audio–tactile interaction task (Canzoneri et al., 2012, 2013a).

2.4. Task description

2.4.1. Body representation (Experiments 1 and 2)

In Exp. 1, to assess the representation of the metric properties of the arm after non-use/overuse, we adopted *the tactile distance perception task* (Canzoneri et al., 2013a). Two pairs of tactile stimuli were administered, one on the forehead (as a reference body part) and the other on the forearm (the target body part). To set the spatial distance between stimuli, we initially measured the two-point discrimination threshold (2pdt) on the forearm. The 2pdt was defined as the shorter distance between two touches at which subjects clearly detect two different stimuli. The 2pdt was determined for each arm in the two testing days (before and after immobilization) using a Staircase method before the beginning of the experiment. Blindfolded subjects were tactilely stimulated with tappers (diameter 5 mm) mounted on a calliper while they were lying down with the arms resting in a prone position. Either double or single posts were randomly administered. Only double posts were used to compute the staircase. The starting double post separation was 40 mm, clearly above the 2pdt. The separation was progressively reduced by 50% after each set of three successive correct responses. In case of errors by the subjects, the separation was subsequently increased to midpoint of the current (erroneous) trial and the immediately preceding (correct) trial. This procedure was terminated at the shortest separation at which two distinct posts were clearly perceived. We subsequently confirmed this 2pdt determination applying five double posts at this separation randomly intermixed with five single posts. If the subjects scored

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