

Short-term upper-limb immobilization alters peripersonal space representation

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Abstract

Peripersonal space is a multisensory interface between the environment and the body subserving motor interactions with the physical and social world. Although changing body properties has been shown to alter the functional processing of space, little is known about the effect of short-term limb immobilization specifically on the motor representation of peripersonal space. In the present study, we investigated the effect of a right upper-limb immobilization for a duration of 24 hours on a reachability judgment task and a brightness judgment task. Analyses of perceptual thresholds revealed a reduction of peripersonal space representation after the immobilization period, which was not observed when there was no immobilization (control group). In contrast, no variation appeared in the brightness judgment task, suggesting no presence of specific visual perception or decisional deficits in the limb immobilization group. Considered together, the results confirm the crucial role of the motor system in the representation of peripersonal space. They also highlight the plasticity of the motor system resulting in a rapid change of its activity following limb immobilization, with a concomitant effect on motor-related perceptual and cognitive processes.

Introduction

The specific effect of the motor system on visual perception as a function of the location of objects in space has led to the conception of external space not as a continuum but rather as a series of nested functional regions defined by potentialities of action (Previc, 1998). Accordingly, the brain dissociates the region in the environment where objects are accessible *hic et nunc* (namely the peripersonal space) from the region in space where the body must be transported to reach distant objects (namely the extrapersonal space). Dominant theoretical frameworks emphasize that the peripersonal space is a dynamic representation of the environment where object coding specifically involves a multisensory (Graziano and Gandhi, 2000; Rizzolatti, Scandolara, Matelli, Gentilucci, 1981) and body-part centred frame of reference in relation to the motor system (Coello and Iachini, 2016; Di Pellegrino and Ládavas, 2015; Cléry, Guipponi, Wardak, Ben Hamed, 2015). In line with this view, modifying arm length in the body schema through tool-use (Bourgeois, Farnè, Coello, 2014), or biasing the spatial outcome of a manual reaching action (Bourgeois and Coello, 2012) were found to modify the representation of the peripersonal space. The fact that the presence of threatening stimuli also modifies the representation of peripersonal space (Coello, Bourgeois, Iachini, 2012) has led to the view that peripersonal space similarly represents a safety buffer zone protecting body integrity by prompting defensive/avoidance motor actions (De Vignemont and Iannetti, 2015; Di Pellegrino and Ladavas, 2015; Graziano and Cooke, 2006; Ruggiero, Frassinetti, Coello, Rapuano, di Cola, Iachini, 2017). Accordingly, peripersonal space underlies two functions: the guidance of non-defensive behaviours in relation to neutral, nonthreatening objects; and the guidance of defensive behaviours in relation to threatening or potentially harmful stimuli (De Vignemont and Iannetti, 2015; Coello, 2018; Hunley and Lourenco, 2018).

In agreement with previous statements, neural alteration of the motor system was found to produce alteration of the representation of peripersonal space. This is indeed what stroke patients with brain damage in motor-related regions suggested, by showing not only specific deficits in the control of motor actions, but also in their representation of peripersonal space (Bartolo, Carlier, Hassaini, Martin, Coello, 2014; Bartolo, Rossetti, Revol, Urquizar, Pisella, Coello, 2018). Another way of altering the normal functioning of the motor system is to prevent people to move by constraining their limb degree of freedom for a predefined duration. Neuroimaging studies have effectively shown that finger or arm immobilization by means of a cast or a rigid splint for a short time ranging from 10 hours to 4 days can decrease activity in the contralateral motor cortex (Avanzino, Bassolino, Pozzo, Bove, 2011; Facchini, Romani, Tinazzi, Aglioti, 2002; Huber, Ghilardi, Massimini, Ferrarelli, Riedner, et al., 2006). In the same vein, behavioural studies highlighted the negative impact of sensorimotor

restriction on the sensorimotor and cognitive control of action. Overall, the immobilization-induced effects associated with the decrease of input/output signal processing were reflected in the less accurate aiming (Huber et al. 2006), alteration of inter-joint coordination (Moisello, Bove, Huber, Abbruzzese, Battaglia et al., 2008) and movement kinematics (Bassolino, Bove, Jacono, Fadiga, Pozzo, 2012), as well as by slowdown of motor simulation processes (Meugnot, Almecija, Toussaint, 2014; Meugnot and Toussaint, 2015; Toussaint and Meugnot, 2013).

Assuming that restricting upper-limb movements for even a short period of time alters cortical excitability of the motor regions dedicated to limb control (Avanzino et al., 2011; Facchini et al., 2002; Huber et al., 2006), and that idiosyncratic representation of peripersonal space relies on the sensorimotor system (Coello and Iachini, 2016), one may expect those individuals prevented to use their arm to show a specific alteration of the representation of their peripersonal space leaving visual perception as a whole unaffected. Previous findings by Bassolino and collaborators (2015), who examined the effect of sensorimotor deprivation on the multisensorial representation of peripersonal space, reported a shrinkage of that space following a period of several hours of arm immobilization. Using an audio–tactile interaction task before and after a short period of arm immobilization, they indeed found that the space where multisensory processing occurred, based on response time variations, contracted for the non-used arm but not for the other arm. However, in this study peripersonal space representation was derived from multisensory processing of approaching and receding auditory stimuli, thereby emphasizing the defensive function of peripersonal space (Cléry et al., 2015; De Vignemont and Iannetti, 2015; Coello, 2018; Hunley and Lorenzo, 2018). In the present experiment, we specifically examined the effect of movement restriction (i.e. 24 hours of arm immobilization) on the motor representation of peripersonal space. For that, we used a reachability judgment task thought to imply the motor system in the coding of visual objects in relation to peripersonal space (Bartolo et al., 2014; Coello, Bartolo, Amiri, Houdayer, Derambure, 2008). Our hypothesis was that if the motor function of peripersonal space was affected by movement restriction, then immobilizing the upper-limb for 24 hours would affect the perception of object's reachability, but would leave unchanged the perception of other object visual attributes assessed by means of a brightness judgement task.

Method

Participants

Forty right-handed French speaking students (29 women, 11 men, 18-24 years old, mean age = 21.3 years) were recruited in the University of Poitiers. Right hand dominance was estimated using the Edinburgh Inventory Scale (Oldfield 1991). The participants were separated randomly into 2 groups of 20 participants: a control group (14 women, 6 men, 18-24 years old, mean age = 22 years) and an immobilized group (15 women, 5 men, 18-24 years old, mean age = 20.5 years). In a survey, each participant indicated that he/she was healthy, had normal or corrected-to-normal vision and had no history of motor or neurological disorders. The study has been approved by the ethics committee for research in science of physical and sports activities and has therefore been performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki and its later amendments. All participants gave their informed consent prior to their inclusion in the study and received course credits (for the control group) or money (for the immobilized group, €25) for their participation. Before testing, participants were naïve about the aims of the experiment.

Material and procedure

All participants were administered two experimental tasks: a reachability judgment task and a brightness discrimination task. Both tasks were identical to those proposed in the study of Bartolo and collaborators (2014). Stimuli consisted in the presentation of a picture created with a 3D graphic software (Blender 3D modeler under GNU General Public License) and represented a virtual scene with a mug (height: 7.5 cm, diameter: 4.2 cm) lying on a table (See Figure 1). The geometry of the visual scene was computed with advantage point at eye level 43 cm above the horizontal surface. The virtual surface on which the objects were presented was a 2m × 8m rectangular surface made with a homogenous texture. On the surface, a black dot was displayed 5 cm from the nearest side of the table on the sagittal axis. Participants (all right-handed) were instructed to imagine having their right index finger on the black dot while performing the perceptual task. The surface of the table was generated with a linear texture extracted from a picture of a piece of wood, which produced a realistic rendering using a ray-tracing algorithm with shadow calculation, but with no information about absolute distance (Shirley and Morley, 2008). Due to the geometry of the virtual scene, the distance of the visible object could be estimated mainly on the basis of the relative size and perspective cues.

In the reachability judgment task, participants were required to estimate as fast as possible if the mug displayed was reachable or unreachable with their right-hand. The brightness of the mug (considering the average value between red, green, and blue channels using the 0 to 255RGB levels scale) was 66.33 during the

entire task. The mug was placed in perspective at different distances with respect to the starting location (from 30 to 175 cm by step of 5 cm), providing thus 30 possible distances for the mug.

In the brightness discrimination task, participants were instructed to indicate as fast as possible whether the presented mug had a bright or dark brightness. The mug used in this task was identical to this one used in the reachability judgment task but it was placed consistently at 50 cm from the starting location. Here, the brightness of the mug (estimated through 0 to 255 RGB levels scale) varied along the task between bright (103.09) and dark (29.26), by step of 2.546, providing thus 30 levels of brightness for the mug.

For both tasks, the stimuli were presented on a 15'' CRT computer screen that was placed on a horizontal table at a viewing distance of 50 cm. The experiment was run using E-prime programme (Psychology Software Tools, Inc. www.pstnet.com). Each task offered two possible answers for the participants (reachable/unreachable for the reachability judgment task and bright/dark for the brightness discrimination task). In both cases, responses were provided verbally. For each trial, the experimenter registered directly the nature of the response whereas verbal responses times were collected using a microphone connected with SR-BOX of E-prime software.

In each task, each trial started with the presentation of a picture with one of the stimuli. This picture stayed visible until the participant's response was provided, within a time window of maximum 4 seconds followed by another 2 seconds of black screen. The other stimuli were presented randomly according to the same temporal sequence. After 30 trials (1 block), participants could have a break of 2 minutes if they asked for. Each task contained 4 blocks where each possible distance or brightness was presented randomly. In total, participants performed 120 trials in each task, which lasted about 10–12 min leading to a total duration of about 20-24 minutes (2 tasks \times 10–12 min).

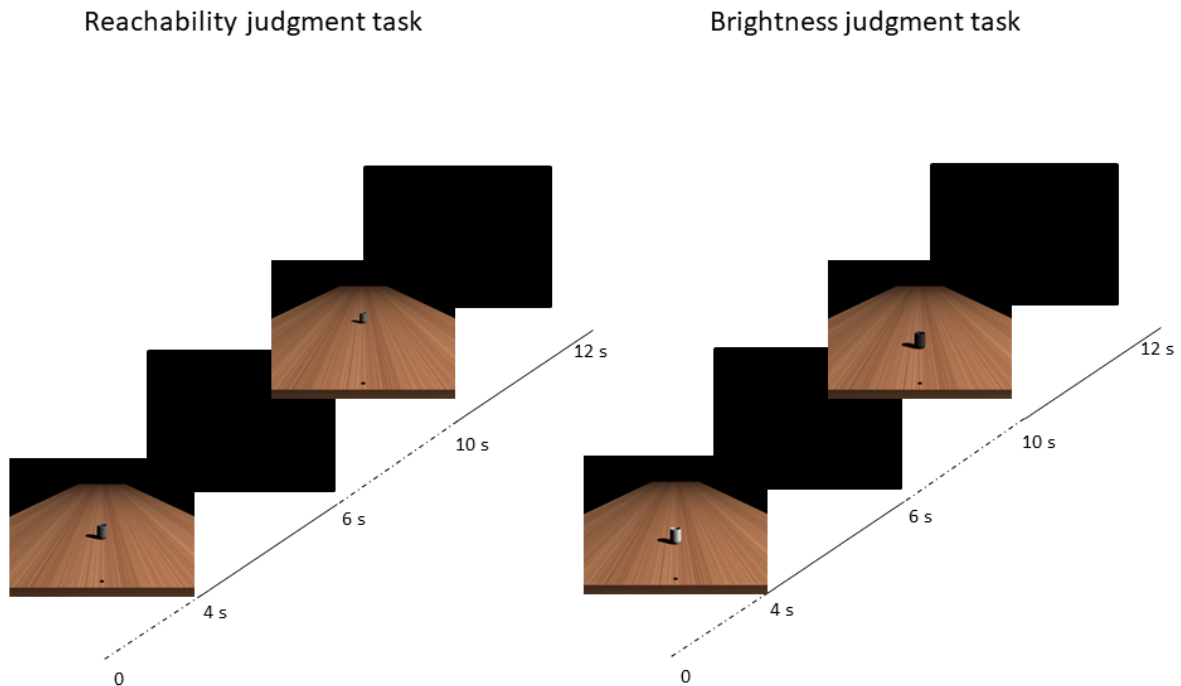


Fig. 1. Examples of two trials in the reachability judgment task (on the left) and the brightness judgment task (on the right).

To assess the role of short-term upper-limb immobilization on the perception of peripersonal space, both the control and immobilized groups performed the reachability judgment and the brightness discrimination tasks in two experimental sessions with a 24-hr interval between sessions (session 1 and session 2). In our design, the brightness discrimination task served as a control task to evaluate whether the participants showed specific modifications in the perception of peripersonal space or general modifications concerning visual perception. Therefore, and also because the immobilization-induced effects can be masked when participants perform a non sensorimotor task first (Toussaint and Meugnot, 2013), the reachability task was made before the brightness discrimination task in both sessions. It is worth noting that the brightness discrimination task contained a region of ambiguity according to the decision to make (transition area between bright and dark decision), as it is the case for the reachability judgment task (transition area between reachable and unreachable stimuli; Coello et al. 2008). Therefore, the two tasks had similar difficulties in relation to the decision process.

For the immobilized group, we used a rigid splint (model DONJOY "Comfort Digit"; DJO, Surrey, UK) to prevent the right wrist and fingers movements and an immobilization vest (model DONJOY "Immo Axmed") to restrain movement from the right shoulder, arm, and forearm. The participants were instructed to remove the immobilization vest for the night, but to never remove the splint during the 24 hours immobilization period. To ensure that participants followed the instructions to keep their right hand at rest as much as possible during immobilization, we monitored the physical activity of both hands through wrist actimeters, which provided continuous record of hands activity (i.e., changes in position and acceleration) during 24 hours, expressed as the number of counts per minute. Therefore, fewer counts per minutes for the immobilized hand should confirm compliance with the immobilization procedure. On average 578 counts/min were recorded for the immobilized right hand and 2822 counts/min for the non-immobilized left hand (see also Toussaint and Meugnot, 2013, for a similar procedure). The ANOVA performed on the actimeters values confirmed that the level of activity was higher for the left hand than for the right hand [$F(1,19)=468.88$, $p<.0001$, $\eta^2p=.96$].

Data analyses

In the reachability judgment task and the brightness discrimination task, the transition between one type of response (reachable-bright) to the other (unreachable-dark) was computed using a maximum likelihood fit procedure based on the second-order derivatives (quasi-newton method) to obtain the logit regression model that best fitted the reachable (bright) / unreachable (dark) responses of the participants, using the equation:

$$y = e^{(\alpha+\beta X)} / (1 + e^{(\alpha+\beta X)})$$

in which y was the participant's response, X corresponded to the distance, $(-\alpha/\beta)$ was the critical value of X at which the transition from one type of response (reachable-bright) to the other type of response (unreachable-dark) occurred, thus expressing the perceived maximum reachable distance or the brightness perceived mid-way between brightness and darkness. Note that quality of the fitting was measured for each participant thanks to R-squared. We excluded data from one participant because R-squared estimate was below than 3 SD from the mean R-squared. After exclusion, the mean R-squared computed for the reachability judgment task was to 0.752 (SD = 0.124) before limb immobilization and 0.797 (SD = 0.102) after. For the brightness judgment task, the mean R-squared computed was to 0.730 (SD = 0.110) before limb immobilization and 0.744 (SD = 0.131) after. ANOVA performed for each task on the R-squared values did not reveal any effect of session.

Response times were also analysed, but differentiating response times for the 5 most reachable (bright) and 5 most unreachable (dark) stimuli, as well as for the 5 stimuli at the boundary of reachable space or at the

threshold between bright and dark brightness (corresponding hereafter to the Distance and Brightness factors). Data above or below 2.5 SD from the mean response time in all condition were discarded for the statistical analysis (less than 3% of the data for Brightness judgment and Reachability judgment tasks). For the judgment performance, statistical analysis was performed in the two tasks using a Group (immobilized, control) x Session (session 1, session 2) ANOVA, with repeated measures on the last factor. Concerning response time, statistical analysis was performed using a Group (immobilized, control) x Session (session 1, session 2) x Space (peripersonal, boundary, extrapersonal) ANOVA in the reachability judgment task, and using a Group (immobilized, control) x Session (session 1, session 2) x Brightness (bright, boundary, dark) ANOVA in the brightness judgment task, with repeated measures on the two last factors. Local comparisons were performed using the post-hoc Bonferroni test with threshold corrections to account for multiple comparisons and measures of effect size were performed using generalized eta squared (Olejnik and Algina, 2003).

Results

Reachability judgment task

Estimation of maximum reachable distance

A Group (control, immobilized) x Session (session 1, session 2) ANOVA on reachability judgments revealed a significant effect of Session ($F_{1,37} = 5.85$; $p = 0.021$; $\eta^2 = 0.14$), and a significant Session x Group interaction ($F_{1,37} = 4.71$, $p = 0.036$; $\eta^2 = 0.11$). Post-hoc comparisons revealed a reduction of perceived maximum reachable distance in session 2 compared to session 1, but only for the group with an immobilized limb. As depicted in Figure 2, perceived maximum reachable distance space decreased from 104.3 cm (SD = 3.5) before limb immobilization to 96.2 cm (SD = 4.1) after limb immobilization ($p = 0.013$), while perceived maximum reachable distance stayed unchanged between sessions in the control group (106.8 cm [SD = 3.3 cm] and 106.4 cm [SD = 3.4 cm] for session 1 and 2 respectively).

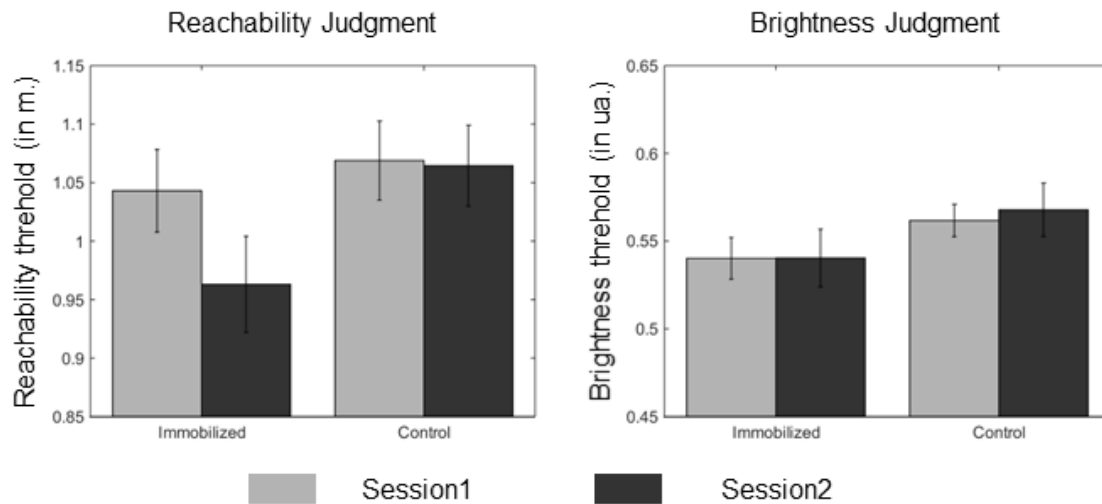


Fig. 2. Evolution of the reachability threshold (left) and brightness (right) as a function of experimental session and Group. Error bars represent standard error.

Response Time

A Group (control, immobilized) x Session (session 1, session 2) x Space (reachable, boundary, unreachable) ANOVA did not revealed any effect of the Group ($F_{1,37} = 0.13$; $p = 0.72$; $\eta^2 = 0.004$) on response time. However, a significant effect of Session ($F_{1,37} = 33.96$, $p < 0.0001$, $\eta^2 = 0.48$), with shorter response time in session 2 than in session 1, and a significant effect of Space ($F_{2,74} = 239.75$, $p < 0.0001$, $\eta^2 = 0.87$) were observed on the response time. Post hoc comparisons revealed an increase of response time for stimuli at the boundary of reachability in comparison to reachable and unreachable stimuli (+162.92 ms and +115.14 ms respectively, both $p < 0.001$). Moreover, response time for reachable stimuli was shorter than for unreachable ones (-47.77 ms, $p < 0.001$). We also found a significant Group x Session interaction ($F_{1,37} = 6.17$, $p < 0.02$, $\eta^2 = 0.14$, see Figure 3). In fact, we observed that response time was shorter during the second session in comparison to the first one but only for the immobilized group (-65.86 ms, $p < 0.001$), not for the control group (-26.50 ms, $p = 0.12$). Note however that post hoc comparisons did not revealed significant differences in session 1 and in session 2 between both groups.

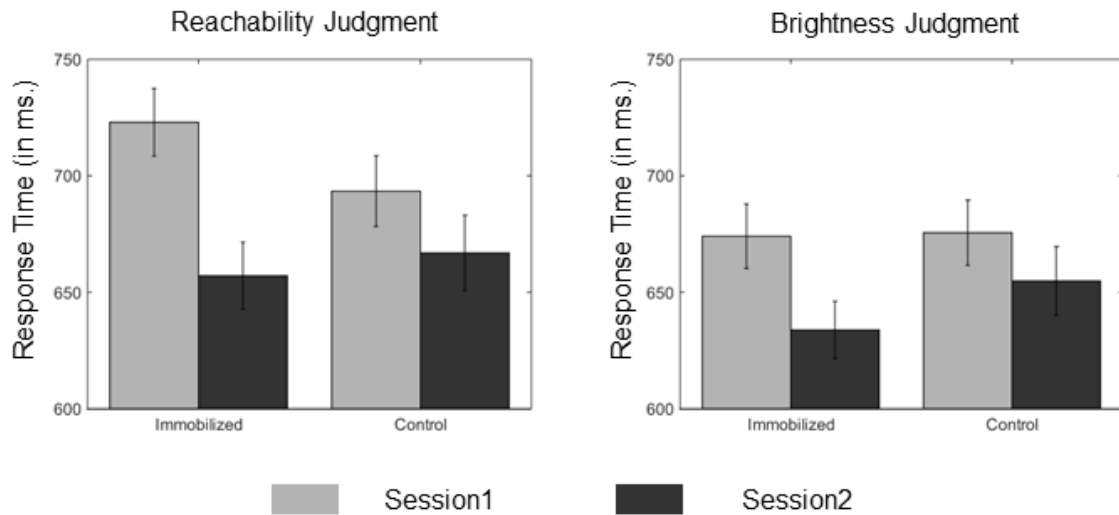


Fig. 3. Evolution of response time for the reachability judgment (left) and brightness judgment task (right) as a function of experimental session and Group. Error bars represent standard error.

Brightness judgment task

Boundary of bright-dark discrimination

A Group (control, immobilized) x Session (session 1, session 2) ANOVA did not show any significant main effect of Group ($F_{1,37} = 2.08$; $p = 0.15$; $\eta^2 = 0.05$, see Figure 2) or Session ($F_{1,37} = 0.13$; $p = 0.71$; $\eta^2 = 0.003$) on brightness judgments. The Group x Session interaction was also not significant ($F_{1,37} = 0.12$; $p = 0.73$; $\eta^2 = 0.003$).

Response time

A Group (control, immobilized) x Session (session 1, session 2) x Brightness (bright, boundary, dark) ANOVA showed no effect of Group ($F_{1,37} = 0.17$; $p = 0.68$; $\eta^2 = 0.005$) on response time. However, a significant effect of Session ($F_{1,37} = 16.03$, $p < 0.001$, $\eta^2 = 0.30$) and a significant effect of Brightness ($F_{2,74} = 129.15$, $p < 0.001$, $\eta^2 = 0.78$) were observed, but the factors did not interacted (see Figure 3). We found that response time was shorter in session 2 than in session 1 (-30.21ms). Moreover, while no difference was observed in response time for bright and dark stimuli ($p = 0.10$), post hoc comparisons revealed an increase of response time for stimuli at the boundary in comparison to bright and dark stimuli (+99.40 ms and +112.26 ms respectively, both $p < 0.001$).

Discussion

The aim of the present study was to examine the effects of short-term upper-limb immobilization on the motor representation of the peripersonal space. For this purpose, immobilized and control (i.e. without immobilization) participants performed a reachability judgment task and a brightness judgment task in two experimental sessions with a 24-hr interval, corresponding to the duration of sensorimotor restriction in the immobilized group. In agreement with previous literature, it is surmised that reachability judgments implied processing motor-related properties of visual objects and depend on how peripersonal space is represented (Coello and Iachini, 2016; Grade, Pesenti, Edwards, 2015; Patané, Farnè, Frassinetti, 2017; Valdés-Conroy, Román, Hinojosa, Shorkey, 2012). The brightness judgment task served as control task, as focusing essentially on the visual attributes of objects. The main outcome of the present study was that the maximum distance at which objects are perceived as reachable was altered by the upper-limb immobilization, suggesting shrinking of the motor representation of peripersonal space after the period of immobilization. No variation of reachability judgments was observed across sessions in the control group, which was not submitted to the limb immobilization. Moreover, no immobilization-induced effect appeared when judging the brightness of objects.

The sensitivity of the boundary of the peripersonal space to the individuals' sensorimotor abilities have been previously reported in the literature. Although different measures were used to probe the representation of peripersonal space (audio or visuo-tactile integration, line bisection, spatial alignment effect, reachability judgments), all results converged towards the finding that modifying the possibilities of interacting manually with the environment alters the representation of the peripersonal space. In audio-tactile interaction paradigms, that emphasize the defensive component of peripersonal space, the plasticity of the sensory peripersonal space has been highlighted following short-term tool use training (Canzoneri, Ubaldi, Rastelli, Finisquerra, Bassolino, Serino, 2013) and short-term upper-limb movement restriction (Bassolino et al., 2015). Interestingly, it has been shown that tool-use changed the body metric representation and extended the representation of the peripersonal space (Cardinali, Brozzoli, Urquizar, Salemme, Roy, Farnè, 2011; Cardinali, Jacobs, Brozzoli, Frassinetti, Roy, Farnè, 2012). On the contrary, limb immobilization reduced the peripersonal space representation although no change in body metric representation was observed (Bassolino et al., 2015). Likewise, in reachability judgment paradigms that emphasize the motor component of peripersonal space, modifying arm length through tool-use was found to alter the representation of peripersonal space due to the functional extension of action capabilities.

The present experiment extends this knowledge by showing that limb non-use influences reachability judgments and suggested a reduction of peripersonal space representation. This confirms that judging whether an object is reachable or not required the contribution of the sensorimotor system (Bartolo et al., 2014; Coello et al., 2008; Wamain et al., 2016), which could be altered as a consequence of action deprivation, even in healthy participants. This also shows that the representation of peripersonal space can be updated very quickly, a period of 24 hours of sensorimotor deprivation being sufficient to affect the reachability judgments.

Response time analyses in the reachability judgment task revealed that objects near the body (i.e., in the peripersonal space) are recognized faster as reachable than distant objects as unreachable (i.e., in the extrapersonal space), and objects at the boundary of peripersonal space led to the highest response time. Considering brightness judgments, the longest response time appeared for stimuli located at the brightness-darkness boundary, but no differences were observed for objects clearly bright or dark objects. These results confirmed previous experiment (Bartolo et al., 2014; Coello et al., 2008). In both tasks, the incertitude for stimuli at the threshold of reachability/brightness was at the origin of the longer time required to provide the response. With regard to the shorter response time in the reachability judgment task for reachable objects, this effect could be interpreted as resulting from the motor coding of object in peripersonal space, which was found to facilitate visual processing (Costantini et al., 2010). A possible interpretation is also that, assuming that the participants look at the centre of the screen while waiting for the forthcoming stimulus, objects in peripersonal space projected predominantly on the upper retina (lower visual field) whereas objects in extrapersonal space projected predominantly on the lower retina (upper visual field). Lower and upper visual field differences have been observed across various tasks (Christman and Niebauer, 1997), with a lower visual field bias emerging in many instances. Anatomical disparity in the superior–inferior retinal axis (Curcio and Allen, 1990) leads to a lower visual field advantage for attentional resolution (Handy, Grafton, Shroff, Ketay, Gazzaniga, 2003), motion segmentation (Lakha and Humphreys, 2005) and the control of goal-directed actions (Danckert and Goodale, 2001). This difference in the processing of information in the upper and lower visual fields represents thus a potential explanation for the differences in the time required to process object in the peripersonal and extrapersonal space. Another possible interpretation for this effect is that taking the decision of unreachability might require more time than taking the decision of reachability. Previous studies indeed highlighted that, in 2-alternative forced choice paradigms, time to respond “yes” is usually shorter than time to respond “no” (Brouillet, Heurley, Martin, Brouillet, 2010) and implies different processing (Coltheart, Rastle, Perry, Ziegler,

Langdon, 2001; Grainger and Jacobs, 1996). The fact that reachable responses were still faster than unreachable responses after the immobilization period suggests that this difference in response time cannot unambiguously be related to the contribution of the motor system to the perceptual decision for reachable stimuli (Coello and Bonnotte, 2013). Further experiments would be required to disentangle these different interpretations.

To sum up, the present study provided new evidence for the plasticity of the peripersonal space representation which was quickly updated in the presence of upper-limb perturbation. Twenty four hours of upper-limb immobilization was sufficient to affect the accuracy of reachability judgments thought to depend on the motor representation of peripersonal space. As a whole, these findings provide new evidence for the crucial requirement of a neurologically intact sensorimotor system in the representation of the peripersonal space.

Ethical standards

The study has been approved by the ethics committee for research in science of physical and sports activities and has therefore been performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki and its later amendments.

All participants gave their informed consent prior to their inclusion in the study. Details that might disclose the identity of the participants have been omitted.

Conflict of interest

The authors declare that no conflict of interest exists. Moreover, they have full control of all primary data and they agree to allow the journal to review their data if requested.

References

- Avanzino, L., Bassolino, M., Pozzo, T., Bove, M. (2011). Use-dependent hemispheric balance. *Journal of Neuroscience*, 31, 3423-3428. doi:10.1523/JNEUROSCI.4893-10.2011.
- Bartolo, A., Carlier, M., Hassaini, S., Martin, Y., Coello, Y. (2014). The perception of peripersonal space in right and left brain damage hemiplegic patients. *Frontiers in Human Neuroscience*, 8, 3. doi: 10.3389/fnhum.2014.00003.
- Bartolo, A., Rossetti, Y., Revol, P., Urquizar, C., Pisella, L., Coello, Y. (2018). Reachability judgement in optic ataxia: Effect of peripheral vision on hand and target perception in depth. *Cortex*, 98, 102-113. doi: 10.1016/j.cortex.2017.05.013.
- Bassolino, M., Bove, M., Jacono, M., Fadiga, L., Pozzo, T. (2012). Functional effect of short-term immobilization: kinematic changes and recovery on reaching-to-grasp. *Neuroscience*, 215, 127-134. doi:10.1016/j.neuroscience.2012.04.019.
- Bassolino, M., Finisguerra, A., Canzoneri, E., Serino, A., Pozzo, T. (2015). Dissociating effect of upper limb non-use and overuse on space and body representations. *Neuropsychologia*, 20, 385-392. doi: 10.1016/j.neuropsychologia/2014.11.028.
- Bourgeois, J., Coello, Y. (2012). Effect of visuomotor calibration and uncertainty on the perception of peripersonal space. *Attention, Perception & Psychophysics*, 74(6), 1268-1283. doi: 10.3758/s13414-012-0316-x.
- Bourgeois, J., Farné, A., Coello, Y. (2014). Costs and benefits of tool-use on the perception of reachable space. *Acta Psychologica*, 148, 91-95. doi: 10.1016/j.actpsy.2014.01.008.
- Brouillet, T., Heurley, L., Martin, S., Brouillet, D. (2010). The embodied cognition theory and the motor component of "yes" and "no" verbal responses. *Acta Psychologica*, 134, 310-317. doi: 10.1016/j.actpsy.2010.03.003.
- Canzoneri, E., Ubaldi, S., Rastelli, V., Finisguerra, A., Bassolino, M., Serino, A. (2013). Tool-use reshapes the boundaries of body and peripersonal space representations. *Experimental Brain Research*, 228(1), 25-42. doi: 10.1007/s00221-013-3532-2.
- Cardinali, L., Brozzoli, C., Urquizar, C., Salemme, R., Roy, A.C., Farné, A. (2011). When action is not enough: tool-use reveals tactile-dependent access to body schema. *Neuropsychologia*, 49, 3750-3757. doi: 10.1016/j.neuropsychologia.2011.09.033.

- Cardinali, L., Jacobs, S., Brozzoli, C., Frassinetti, F., Roy, A.C., Farnè, A. (2012). Grab an object with a tool and change your body: tool-use-dependent changes of body representation for action. *Experimental Brain Research*, 218, 259-271. doi: 10.1007/s00221-012-3028-5.
- Christman, S.D., Niebauer, C.L. (1997). The relation between left-right and upper-lower visual field differences. In S. Christman (Ed.), *Cerebral asymmetries in sensory and perceptual processing* (pp.263-298). Amsterdam: Elsevier.
- Cléry, J., Guipponi, O., Wardak, C., Ben Hamed, S. (2015). Neuronal bases of peripersonal and extrapersonal spaces, their plasticity and their dynamics: knowns and unknowns. *Neuropsychologia*, 70, 313-326. doi: 10.1016/j.neuropsychologia.2014.10.022.
- Coello, Y. (2018). Action space representation in social contexts. In Shigemasa, K., Kuwano, S., Sato, T., Matsuzawa, T. (Eds.), *Diversity in harmony - Insights from psychology*. Proceedings of the 31st International Congress of Psychology. doi:10.1002/9781119362081.ch12.
- Coello, Y., Bartolo, A., Amiri, B., Houdayer, E., Derambure, P. (2008). Perceiving what is reachable depends on motor representations: A study using transcranial magnetic stimulation. *Plos One*, 3(8), e2862. doi: 10.1371/journal.pone.0002862.
- Coello, Y., Bonnotte, I. (2013). The mutual roles of action representations and spatial deictics in French language. *Quarterly Journal of Experimental Psychology*, 66(11), 2187-2203. doi: 10.1080/17470218.2013.775596.
- Coello, Y., Bourgeois, J., Iachini, T. (2012). Embodied perception of reachable space: how do we manage threatening objects ? *Cognitive Processing*, 13, S131-S135. doi: 10.1007/s10339-012-0470z.
- Coello, Y., Iachini, T. (2016). Embodied perception of objects and people in space: towards a unified theoretical framework. In Y. Coello, M. Fischer (Eds.), *Foundations of embodied cognition* (pp. 198-219). New York, Psychology Press.
- Coltheart, M., Rastle, K., Perry, C., Ziegler, J., Langdon, R. (2001). DRC: A Dual Route Cascaded model of visual word recognition and reading aloud. *Psychological Review*, 108, 204-256. doi: [10.1037/0033-295X.108.1.204](https://doi.org/10.1037/0033-295X.108.1.204)
- Costantini, M., Ambrosini, E., Tieri, G., Sinigaglia, C., Comitteri, G. (2010). Where does an object trigger an action? An investigation about affordances in space. *Experimental Brain Research*, 207(1-2), 95-103. doi: 10.1007/s00221-010-2435-8.

- Curcio, C.A., Allen, K.A. (1990). Topography and ganglion cells in the human retina. *Journal of Comparative Neurology*, 300, 5-25.
- Danckert, J., Goodale, M.A. (2001). Superior performance for visually guided pointing in the lower visual field. *Experimental Brain Research*, 137, 303–308.
- Di Pellegrino, G., Làdavas, E. (2015). Peripersonal space in the brain. *Neuropsychologia*, 66, 126-133. doi: 10.1016/j.neuropsychologia.2014.11.011.
- De Vignemont, F., Iannetti, G. D. (2015). How many peripersonal spaces? *Neuropsychologia*, 70, 327–334. doi: 10.1016/j.neuropsychologia.2014.11.018
- Facchini, S., Romani, M., Tinazzi, M., Aglioti, S. M. (2002). Time-related changes of excitability of the human motor system contingent upon immobilization of the ring and little fingers. *Clinical Neurophysiology*, 113, 367-75.
- Grade, S., Pesenti, M., Edwards, M.G. (2015). Evidence for the embodiment of space perception: concurrent hand but not arm action moderates reachability and egocentric distance perception. *Frontiers in Psychology*, 6, 862. doi: 10.3389/fpsyg.2015.00862.
- Grainger, J., Jacobs, A.M. (1996). Orthographic processing in visual word recognition: A multiple readout model. *Psychological Review*, 103, 518-565.
- Graziano, M.S., Gandhi, S. (2000). Location of the polysensory zone in the precentral gyrus of anesthetized monkeys. *Experimental Brain Research*, 135(2), 259-266.
- Handy, T.C., Grafton, S.T., Shroff, N.M., Ketay, S., Gazzaniga, M.S. (2003). Graspable objects grab attention when the potential for action is recognized. *Nature Neurosciences*, 6, 421–427. doi: [10.1038/nn1031](https://doi.org/10.1038/nn1031).
- Huber, R., Ghilardi, M.F., Massimini, M., Ferrarelli, F., Riedner, B.A., Peterson, M.J., Tononi, G. (2006). Arm immobilization causes cortical plastic changes and locally decreases sleep slow wave activity. *Nature Neuroscience*, 9, 1169-1176. doi:10.1038/nn1758.
- Hunley, S.B., Lourenco, S.F. (2018). What is peripersonal space? An examination of unresolved empirical issues and emerging findings. *Wiley Interdisciplinary Reviews (Cognitive Science)*, e1472. doi: 10.1002/wcs.1472.
- Lakha, L., Humphreys, G. (2005). Lower visual field advantage for motion segmentation during high competition for selection. *Spatial Vision*, 18, 447-460.

- Meugnot, A., Almecija, Y., Toussaint, L. (2014). The embodied nature of motor imagery processes highlighted by short-term limb immobilization. *Experimental Psychology*, 61, 180-186. doi:10.1027/1618-3169/a000237.
- Moisello, C., Bove, M., Huber, R., Abbruzzese, G., Battaglia, F., Tononi, G., Ghilardi, M. F. (2008). Short-term limb immobilization affects motor performance. *Journal of Motor Behavior*, 40, 165-176. doi:10.3200/JMBR.40.2.165-176.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia* 9, 97–113.
- Olejnik, S., Algina, J. (2003). Generalized eta and omega squared statistics : measures of effect size for some common research designs, 8(4), 434–447. doi: [10.1037/1082-989X.8.4.434](https://doi.org/10.1037/1082-989X.8.4.434).
- Patané, I., Farnè, A., Frassinetti, F. (2017). Cooperative tool-use reveals peripersonal and interpersonal spaces are dissociable. *Cognition*, 166, 13-22. doi: [10.1016/j.cognition.2017.04.013](https://doi.org/10.1016/j.cognition.2017.04.013)
- Previc, F.H. (1998). The neuropsychology of 3-D space. *Psychological Bulletin*, 124(2), 123-164.
- Rizzolatti, G., Scandolara, C., Matelli, M., Gentilucci, M. (1981). Afferent properties of periarculate neurons in macaque monkeys. II. Visual responses. *Behavioral Brain Research*, 2(2), 147-163.
- Ruggiero, G., Frassinetti, F., Coello, Y., Rapuano, M., di Cola, A.S., Iachini, T. (2017). The effect of facial expressions on peripersonal and interpersonal spaces. *Psychological Research*, 81(6), 1232-1240. doi: 10.1007/s00426-016-0806-x.
- Shirley, P., Morley, K. (2008). *Realistic Ray Tracing*. Natick: A.K. Peters.
- Toussaint, L., Meugnot, A. (2013). Short-term limb immobilization affects cognitive motor processes. *Journal of Experimental Psychology: Learning, Memory and Cognition*, 39, 623-632. doi:10.1037/a0028942.
- Valdés-Conroy, B., Román, F.J., Hinojosa, J.A., Shorkey, S.P. (2012). So far so good: emotion in the peripersonal/extrapersonal space. *PLoS One*, 7(11), e49162. doi: 10.1371/journal.pone.0049162.
- Wamain, Y., Gabrielli, F., Coello, Y. (2016). EEG μ rhythm in virtual reality reveals that motor coding of visual objects in peripersonal space is task dependent. *Cortex*, 74, 20-30. doi: 10.1016/j.cortex.2015.10.006.