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How ageing shapes body and space representations: A comparison study between healthy young and older adults

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ABSTRACT

To efficiently interact with the external world, the brain needs to represent the size of the involved body parts - body representations (BR) - and the space around the body in which the interactions with the environment take place - peripersonal space representation (PPS). BR and PPS are both highly flexible, being updated by the continuous flow of sensorimotor signals between the brain and the body, as observed for example after tool-use or immobilization. The progressive decline of sensorimotor abilities typically described in ageing could thus influence BR and PPS representations in the older adults. To explore this hypothesis, we compared BR and PPS in healthy young and older participants. By focusing on the upper limb, we adapted tasks previously used to evaluate BR and PPS plasticity, i.e., the body-landmarks localization task and audio-tactile interaction task, together with a new task targeting explicit BR (avatar adjustment task, AAT). Results show significantly higher distortions in the older rather than young participants in the perceived metric characteristic of the upper limbs. We found significant modifications in the implicit BR of the global shape (length and width) of both upper limbs, together with an underestimation in the arm length. Similar effects were also observed in the AAT task. Finally, both young and older adults showed equivalent multisensory facilitation in the space close to the hand, suggesting an intact PPS representation. Together, these findings demonstrated significant alterations of implicit and explicit BR in the older participants, probably associated with a

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less efficient contribution of bodily information typically subjected to age-related decline, whereas the comparable PPS representation in both groups could be supported by preserved multisensory abilities in older participants. These results provide novel empirical insight on how multiple representations of the body in space, subserving actions and perception, are shaped by the normal course of life.

1. Introduction

We directly interact with the external world via our physical body; to do so, our brain needs an internal representation of the dimension of the body parts involved in those interactions (i.e., body representations, BR) (e.g., de Vignemont, 2010; Longo, Azañón, & Haggard, 2010; Schwoebel & Coslett, 2005), as well of the space where those interactions occur, i.e., a representation of the space immediately surrounding our body, called peripersonal space (PPS) (Rizzolatti, Fadiga, Fogassi, & Gallese, 1997; Serino, 2019). Several behavioral, neurophysiological and imaging studies have described these representations in young, healthy individuals (for recent reviews Bufacchi & Iannetti, 2018; Cléry & Ben Hamed, 2018; Noel, Blanke, & Serino, 2018; Riva, 2018; Serino, 2019; Serino et al., 2015). Regarding the size and the shape of the different body parts, authors have suggested that an implicit model of the metric proprieties of the body is stored in the brain (Longo & Haggard, 2010, 2012b) and it is updated through on-line peripheral signals, such as sensorimotor, proprioceptive and kinesthetic inputs coming from the skin, the muscles and the joints as well as visual bodily information (de Vignemont, 2010; Longo et al., 2010; Medina & Coslett, 2010; Serino & Haggard, 2010). Concerning the PPS, single neuron data in non-human primates (e.g., Cléry, Guipponi, Wardak, & Ben Hamed, 2015; Graziano & Cooke, 2006) as well as neuropsychological (e.g., Pavani, Ládavas, & Driver, 2003), neuroimaging (e.g., Grivaz, Blanke, & Serino, 2017; Makin, Holmes, & Ehrsson, 2008) and behavioral (see for a review Serino, 2019) studies in humans indicate that the representation of the PPS is coded by the special interaction between somatosensory signals coming from a specific body part (e.g., face, hand and trunk (Serino et al., 2015)) and external visual or acoustic stimuli presented close, but not far from that specific body part.

Furthermore, studies also indicate that both BR and PPS are built and continuously updated by signals from different sensory modalities (Dijkerman & Lenggenhager, 2018; Kandula, Van der Stoep, Hofman, & Dijkerman, 2017; Maravita, Spence, & Driver, 2003; Salomon et al., 2017), implying that BR and PPS are not fixed, but plastically modified through the continuous flow of sensorimotor information arising from the interactions with the environment.

A paradigmatic example of the plasticity of BR and PPS is the use of the tools allowing to reach objects located in the far space (e.g., Maravita & Iriki, 2004; Martel, Cardinali, Roy, & Farnè, 2016; Miller et al., 2018). Studies in non-human primates, patients and healthy participants have demonstrated that short or long experiences with tools (Bassolino, Serino, Ubaldi, & Làdavas, 2010; Biggio, Bisio, Avanzino, Ruggeri, & Bove, 2017; Maravita & Iriki, 2004; Serino, Bassolino, Farnè, & Làdavas, 2007) affect PPS representation, for instance by increasing multisensory interactions between stimuli on the body and in the far space (see for a review Maravita & Iriki, 2004). Similarly, plasticity of BR after tool-use has been reported both in terms of kinematic changes and modifications of the perceived limb dimensions (Canzoneri et al., 2013; Cardinali et al., 2009, 2011; Garbarini et al., 2015; Romano, Uberti, Caggiano, Cocchini, & Maravita, 2018; Sposito, Bolognini, Vallar, & Maravita, 2012). Moreover, BR and PPS are also modifiable by reduced use of the upper limb as during immobilization in healthy participants (Bassolino, Finisguerra, Canzoneri, Serino, & Pozzo, 2014; Toussaint, Wamain, Bidet-Ildei, & Coello, 2018).

The plastic properties of BR and PPS, driven by sensorimotor experiences, also suggest that these representations could be modified and updated during the entire life span (Bremner, 2017; Lewkowicz & Ghazanfar, 2009). For instance, considering the important changes in body size in children (Bremner, Holmes, & Spence, 2008), BR and PPS representation have to evolve across the development in childhood. Similarly, it is possible to suppose that BR and PPS could be affected in older adults by the functional decline of primary sensory inputs and/or motor function during normal ageing. For instance, functional, physiological and anatomical changes in the hand have been reported in the older adults, such as a reduction of the muscles mass and strength ("sarcopenia of old age"), together with a decrease of sensitivity and motor performance (Carmeli, Patish, & Coleman, 2003). Moreover, it has been shown that tactile and auditory thresholds are significantly increased in older compared to young adults, probably due to a decrease in density or distributions and degeneration of the dedicated receptors (Liu & Yan, 2007; Wickremaratchi & Llewelyn, 2006). Similarly, several findings suggest that proprioception (Adamo & Brown, 2007; Goble, Coxon, Wenderoth, Van Impe, & Swinnen, 2009; Shaffer & Harrison, 2007) and vision (Owsley, 2011) are vulnerable to ageing.

Together, previous data show that sensory and motor functions implied in BR and PPS are prone to ageing-related changes, thus suggesting possible distortions in BR and PPS in older adults (Costello & Bloesch, 2017). Accordingly, few studies explored BR and associated subjective experiences in older adults (see for reviews Costello & Bloesch, 2017; Kuehn et al., 2018), by investigating age-related changes in the sense of body ownership and agency after typical experimental manipulations such as the rubber hand illusion (Graham, Martin-Iverson, Holmes, & Waters, 2014; Kállai et al., 2017; Marotta, Zampini, Tinazzi, & Fiorio, 2018; Palomo et al., 2018; Zeller & Hullin, 2018). However, whether BR and PPS are affected by healthy ageing is still a matter of debate. To investigate this topic, in the present study, we compared BR and PPS of the upper limbs in healthy young and older adults. First, to evaluate BR, we used an adaptation of an implicit task, the body-landmarks localization task (BL task), already used in the literature to capture the perceived dimensions of one's own upper limbs (e.g., Longo, 2018) and its plasticity (Bassolino et al., 2014; Canzoneri et al., 2013). Authors showed typical distortions at BL task in young participants, that supposedly reflect distortions of cortical somatosensory processing, which however are not so extreme as the somatosensory homunculus because they are mitigated by the contribution of peripheral signals (Longo et al., 2010). Considering the decline of somatosensory processing in ageing (see above), we can hypothesize higher distortions in older adults rather than young participants at the BL task, because of a possible reduced role of afferents bodily signals in updating the stored, distorted model of body parts' metrics.

Second, metric characteristics of body parts have been assessed also with explicit tasks, asking participants to indicate the perceived dimension of their own body parts by modifying the size of a visual model, such as a line (see the line length task, Longo & Haggard, 2012b) or an image of specific body parts (see template matching task, Longo & Haggard, 2012b) or of the whole body (see Body Image task, Fuentes, Longo, & Haggard, 2013, or Frontal Body Evocation task, Raimo et al., 2019 or the Body Image Revealer, Zamariola, Cardini, Mian, Serino, & Tsakiris, 2017). In line with this, to explore also a form of explicit perception of body metrics in older adults, we introduced a new task, assessing the explicit estimation of one's own upper limbs dimensions by asking participants to adjust the width and the length of the upper limbs of a realistic human avatar presented on a screen (avatar adjustment task, AAT, see paragraph 2.2.2 for details). According to previous studies, explicit tasks employing a visual model would benefit of additional visual inputs that, at least in young participants, contribute to reducing typical distortions in body metrics perception with respect to the BL task (Longo & Haggard, 2012b). Thus, through the AAT we would assess if predicted distortions in older adults would be present also at an explicit level and even when the task implies a combination of information from one's own body and a visual model of another body. If older adults prioritize visual information over somatosensory ones (Costello & Bloesch, 2017), we would expect absent or less severe distortions at the AAT.

Third, to study the PPS representation, we used an adaptation of the audio-tactile interaction task previously employed in young participants to capture multisensory properties of PPS representation's plasticity after tool-use (Canzoneri et al., 2013; Serino, 2019; Serino et al., 2015) and after a reduced use of the upper limb during immobilization (Bassolino et al., 2014). In principle, ageing is characterized by a general reduction of activity, including the activity of the upper limbs, so that one might hypothesize a contraction of PPS representation in older adults. On the other hand, previous studies have demonstrated efficient multisensory mechanisms, compensating for the decline in unisensory signals, in healthy ageing (e.g., Kuehn et al., 2018), thus suggesting an unaltered PPS representation in older adults. These two alternative hypotheses have been tested.

Given that side-specific effects in BR and PPS representation could be present even in young participants (see for instance Hach & Schütz-Bosbach, 2010; Hobeika, Viaud-Delmon, & Taffou, 2018) and considering that hand dominance seems changed in older adults with a reduced difference in the performance between the two hands (Kalisch, Wilimzig, Kleibel, Tegenthoff, & Dinse, 2006), we administered all the three tasks on both upper limbs, to exploratory assess if different effects on the right or left side emerge.

2. Methods

2.1. Participants

Considering that, so far, no previous studies on the BL task or the audio-tactile interaction, nor the new AAT task have been conducted in older adults, and considering that existing data in young participants on the BL task or the audio-tactile interactions task are typically based on a within-subjects repeated measure design (e.g., a pre-post difference), and not on a group difference, no data are available allowing a proper sample size estimation. However, concerning BR, an estimation is possible by using data on plastic effects at the BL task induced by the tool-use in young participants (Canzoneri et al., 2013). A priori power analysis based on these data suggested that a sample of 21 subjects is required to detect modifications in perceived dimensions of upper-limbs (Cohen's dz $= .843$, α error probability $= .05$, and power (1-β error probability) $= .95$, GPower version 3.1). Similarly, concerning the audio-tactile interaction task, considering previous data on healthy participants (Serino et al., 2015), a sample of 23 subjects is required to detect differences in reaction time to tactile stimuli associated with near or far external stimuli (see below for a description of the task) (partial eta square $= .44$; α error probability $= .05$, power (1-β error probability) $= .95$, GPower version 3.1).

Given these indications, we decided to recruit few more participants than the calculated sample size to prevent any reduction in statistical power due to limitations linked to the accuracy in performing the task in older adults (e.g., tactile perception for the audio-tactile interaction) or potential technical problems during the recording.

A group of 30 young participants and a group of 58 older participants were recruited in total for the study. Two participants from the older group were excluded because they did not match the inclusion criterion related to the health status (one reported polyneuropathies and the other suffered from major depression). To avoid fatigue that could have affected the performances, older participants were divided into two groups: the first group of 29 participants undergoing the BL task and the AAT in two separate randomized sessions performed on the same day, and the second group of 27 participants performing the audio-tactile interaction task (but only 23 subjects were finally included in the analysis, see paragraph 2.3 for explanations). Young participants performed the three tasks in different sessions on the same day. In this group, one participant for the BL task and another one for the audio-tactile interaction task could not perform these tasks, after the AAT task, so that at the BL and audio-tactile interaction task the total number of subjects is 29, instead of 30 as at the AAT. The order among the tasks (i.e., the BL task and the AAT in older adults and the 3 tasks in young participants) was randomized among participants in both groups. Information related to age, gender, and education in the groups of participants performing each task is shown in Table 1.

All the participants were right-handed as confirmed by the Flinders Handedness Survey (Nicholls, Thomas, Loetscher, & Grimshaw, 2013), had a normal or corrected-to-normal vision, hearing and touch, no psychiatric or neurological deficits, no pain or sensorimotor pathologies in the upper limbs or fractures in the previous 12 months. Participants in the older group did not show any cognitive impairment as assessed by the Montreal Cognitive Assessment (MOCA) (all equivalent scores $\geq$ 2) (Conti, Bonazzi, Laiacona, Masina, & Coralli, 2015).

Participants were all naïve to the purpose of the study and participated after giving informed consent. The study was conducted with the approval of the local ethics committee (Commission Cantonale Valaisanne d'Ethique Médicale, CCVEM 017/14).

2.2. *The experimental tasks*

2.2.1. *Implicit body representation task: the body-landmarks localization task (BL task)*

To assess the implicit perceived dimension of the upper limbs, we adapted the body-landmarks localization task (BL) (Bassolino et al., 2014; Canzoneri et al., 2013; Longo, 2018). The BL task can be considered implicit because participants had to indicate only the locations of some anatomical landmarks, while not providing explicit judgments about width or length of the body parts, that are then reconstructed a posteriori during the data analysis (e.g., Fuentes et al., 2013; Longo, 2015). Precisely, participants were instructed to verbally indicate when a moving marker reached the felt position of one of five possible non-visible anatomical landmarks that were: the tip of the index finger, the tip of the annular finger, the internal part of the wrist (the radius styloid), the external part of the wrist (the ulnar styloid) and the elbow joint (the olecranon).

Participants were seated on a chair with the forearm (left or right, depending on the condition) resting palm down on a table, aligned with the shoulder and positioned 20 cm far from the body midline and 10 cm far from the border of the table. To avoid movements and to standardize the position, the participants' forearm was fixated to the table for the entire duration of the experiment while the hand was resting on a computer mouse. Before starting the experiment, while participants were blindfolded, we recorded the actual position of the five anatomical landmarks. Afterward, subjects removed the eyeshades to perform the task. During the task, to prevent participants from viewing their arm, we positioned a wooden table (80 cm $\times$ 80 cm) above the arm, and we put an additional cloth to impede the view of the shoulders. During each trial, the experimenter showed on her body the target landmark to judge. Then, the experimenter manually moved a marker attached to a wooden stick over the surface of the table, along the longitudinal axis of the forearm. Participants were instructed to say "Stop" when the marker was perceived just above the felt position of the target anatomical landmark. At that signal, the experimenter stopped the movement, leaving the marker where indicated. Importantly, participants were allowed to further adjust the position of the marker by asking the experimenter to move it backward, forward or laterally and, following the final confirmation, the marker's location was recorded.

The task comprised five blocks in which we recorded the five landmarks, randomized between blocks (i.e., one landmark per block), for a total of five repetitions for each landmark (see Fig. 1). Data were collected for both left and right upper limb in randomized order among participants.

We used retro-reflective markers (1 cm of diameter) recorded using an optical motion capture system (OptiTrack V120: TRIO; Motive 1.7.5 Final 64-bit, 2015) and a custom-made script in Matlab (R2018a). Data analysis was performed using a custom-made script written in Matlab.

2.2.2. *Explicit body representation task: the avatar adjustment task (AAT)*

Here, we propose a novel procedure to explicitly assess the perceived dimension of the participants' upper limbs with respect to a visual model. During the experiment, participants were seated in front of a monitor (52 $\times$ 32 cm) with a white cloth covering their shoulders, arms and hands. A distorted body model on an avatar matching the participant's characteristics of age and gender was showed in diagonal view (see Fig. 2). In each trial, participants were instructed to modify the

Table 1 – Demographic information.

TASK	GROUP	AGE (years)	EDUCATION (years)	GENDER (female)
BL	Young (n = 29)	25.24 ± 3.31 (20–33)	14.93 ± 2.98 (9–20)	21
	Older adults (n = 29)	71.76 ± 7.81 (53–86)	12.62 ± 3.62 (6–18)	24
AAT	Young (n = 30)	25.48 ± 3.34 (20–33)	14.74 ± 2.98 (9–20)	21
	Older adults (n = 29)	71.52 ± 8.07 (53–86)	12.45 ± 3.47 (6–18)	24
PPS	Young (n = 29)	25.31 ± 3.34 (20–33)	14.72 ± 3.03 (9–20)	19
	Older adults (n = 23)	73.48 ± 8.20 (61–91)	12.30 ± 4.22 (3–23)	18

For each task, it is indicated the number of participants included in the two groups (young and older adults) with the related average age and education (mean values ± standard deviation and the range in brackets) as well as the gender distribution (number of female participants).

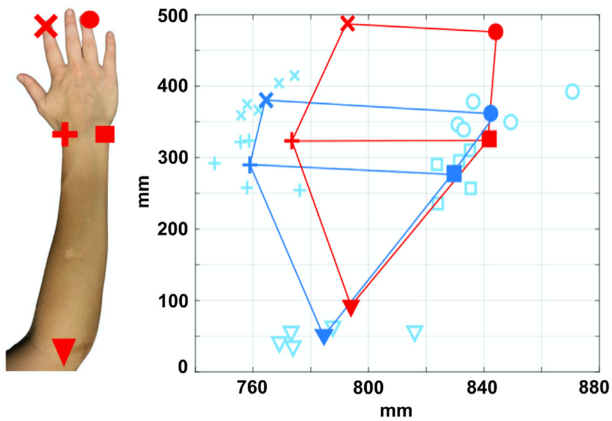

Fig. 1 – The body-landmarks localization task. Panel A shows the five anatomical landmarks that were recorded during the task: the tip of the index finger (multiplication sign), the tip of the annular finger (dot), the internal part of the wrist (the radius styloid, plus), the external part of the wrist (the ulnar styloid, square) and the elbow joint (the olecranon, triangle). Panel B shows the reconstruction of the actual positions of the anatomical landmarks, recorded at the beginning of the experiment (in red) as well as the reconstruction of the perceived position recorded for each landmark on every single trial (five repetitions for each landmark, light blue) and averaged among repetitions (dark blue) in one simulated subject (the horizontal displacement is depicted on the x, mm, while the vertical ones on the y, mm).

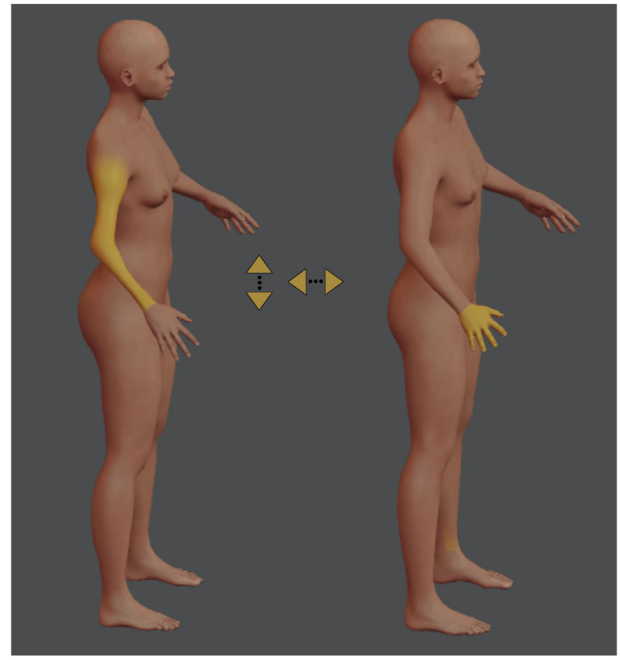

Fig. 2 – The avatar adjustment task. The figure shows an example of the avatar used in the avatar adjustment task (AAT). At the beginning of the experiment, the avatar's dimensions were set to match the anatomical characteristics in terms of age and gender of each participant. During the task, the participant guided the experimenter who operated on a keyboard to adjust the avatar's body parts (hand or arm) dimensions (in yellow) by making them longer or shorter (length), fatter or narrower (width), to resemble his/her body parts.

dimensions (i.e., the width or the length) of the observed avatar's hands or arms to resemble their occluded body parts. To do so, they had to verbally guide the experimenter who operated on a keyboard to adjust the avatar's body parts dimensions, making them longer or shorter, fatter or narrower. The starting dimension of the body model was extremely enlarged in one-half of the trials and extremely shrunk in the other half. Divided into two blocks, we recorded four trials for each dimension (width and length, two trials with each starting position) and each body parts (arm and hand), for both left and right side, for a total of 32 trials (16 for each block). The order of the trials was randomized for the starting position (extremely enlarged and extremely shrunk), the dimensions (width and length), the body parts (arm and hand), and the side (left and right upper limb).

The avatars were designed by using an open-source tool capable of producing realistic virtual humans (Make Human, http://www.makehumancommunity.org/). To limit the possibility that the similarity between the depictured body and individual characteristics would differently impact the two groups, at the beginning of the session, the avatar was modified to match the gender and the age of the participant, based on the anatomical characteristics available in a database collecting information about the physical appearance of the general population at specific age and gender (Bastioni, Re, & Misra, 2008). The avatar was seen from a third-person perspective, in line with previous works where participants were asked to compare their body dimensions with a visual model (e.g., line length task or template matching task, Longo & Haggard, 2012b; Body Image task, BIT, Fuentes et al., 2013 or Frontal Body Evocation task, Raimo et al., 2019).

The software developed for the task was written in Phyton programming language (http://www.makehumancommunity.org/frontpage/makehuman_110_has_been_released.html/).

2.2.3. *Peripersonal space task (PPS)*

We adopted the audio-tactile interaction task previously used elsewhere (Bassolino et al., 2014; Canzoneri et al., 2013; Canzoneri, Magosso, & Serino, 2012; Serino et al., 2015) to evaluate PPS representation around the left and right hand. Participants were blindfolded and seated in a comfortable position with their arm (left or right, depending on the condition) resting on a table. The acoustic stimuli consisted of a dynamic broadband noise looming toward the participants' hand. Two loudspeakers generated the sound: one was positioned near the participant's hand (0 cm), and the other one placed 100 cm distant from the near speaker (i.e., far from the participants' hand). To give the impression of approaching to the subject's body, the sound was manipulated in intensity (Canzoneri et al., 2012). For the tactile stimulation, we used a single vibrotactile device that was placed on the dorsum of participant's hand (Precision MicroDrives shaftless vibration motors, model 312–101, 3 V, 60 mA, 9000 rpm, 150 Hz, 5 g). Tactile stimulation lasted 100 msec. Acoustic and tactile stimuli were delivered in a controlled manner using an inhouse software (ExpyVR; https://c4science.ch/w/expyvr-wiki/installation/), also used to store the data.

Participants were informed that during the task, they would feel a single tactile vibration and hear a sound coming from the speakers. They were asked to answer as fast as possible to the tactile stimulation by pressing a foot pedal with their right foot and to ignore the non-informative looming sound. The crucial manipulation of this task consists on the fact that the tactile stimulus was randomly presented at one out of three temporal delays (D3, D2 and D1, randomized among trials) from sound onset, i.e., when the sound was perceived at one out of three possible distances from the body (D3/far = .3 sec; D2/medium = 1.5 sec; D1/near = 2.7 sec). The correspondence between the temporal interval from the sound onset and the spatial distance between the sound and the touch location matched linearly and negatively (Serino et al., 2015). Similarly, also unimodal trials (only tactile) were administered at three different delays (randomized among trials), corresponding to the equivalent timing of the farthest, medium and the nearest distance of sound. According to previous works (Serino et al., 2015, 2018), unimodal trials were considered as a baseline and were used to normalize audio-tactile trials. The rationale of this task is based on the fact that a multisensory facilitation effect in bimodal versus unimodal trials is expected on tactile RTs due to sounds presented close, i.e., within the PPS, but not far from the body. Such multisensory effects have been used as a proxy of PPS representations (Noel, Pfeiffer, Blanke, & Serino, 2015; Serino et al., 2015). In total, the trials consisted of 20 bimodal trials for each temporal delays (20 × 3), in which participants heard a sound and at a given moment in time they received the tactile stimulation; 10 unimodal trials for each temporal delays (10 × 3), in which the tactile stimulation was delivered in the absence of auditory stimulation. In addition, 20 catch trials with only auditory stimuli were included to control for automatic motor response. The order of the trials was randomized by taking into account the trial types (unimodal tactile, bimodal audio-tactile, and auditory catch trials). During each trial, the sound lasted 3 sec and participants had 2 sec, starting from the moment in which the tactile stimulus was delivered, to answer to the stimulation. The interstimulus intervals were randomized between .5, .75 and 1 sec. Data were collected for both left and right upper limb in randomized order among participants.

Unimodal sound localization task. In order to demonstrate that participants actually perceived the looming sound in the three different locations (far, medium and near) at the three possible delays (D3, D2 and D1) in both groups, all participants from older adults group (N = 23) and a subgroup from the young group (N = 23) underwent a sound localization task, following a procedure already used in previous works with young participants (e.g., Canzoneri et al., 2012; Finisguerra, Canzoneri, Serino, Pozzo, & Bassolino, 2014). During the task, participants were seated in a chair with the eyes closed and with their arm resting on a table in front of them. While listening to the looming sound, participants received a tactile stimulation on the right hand at one of the three temporal delays in a randomized order. After each trial, participants opened the eyes and were instructed to verbally report at which distance was the sound when they perceived the tactile stimulation. To answer, they referred to a meter positioned on the table with visible digits ranging from 0 cm to 100 cm. This task was always done after having performed the audio-tactile interaction task on both sides.

2.3. *Data analysis*

2.3.1. *Body-landmarks localization task*

To calculate the width and length of the two body parts (hand and arm), we considered the position (real and perceived) of the five landmarks (see Fig. 1). The hand length was calculated as the mean of the distance (considering both horizontal and vertical coordinates) between the markers on the fingers and the wrist. More precisely, it was calculated as the mean value between two distances, i.e., the distances between the tip of the index and annular finger and the internal and external part of the wrist, respectively. The arm length was obtained calculating the mean between the markers on the wrist and the elbow. Specifically, it was computed as the mean between two distances, i.e., the distances between the internal and external parts of the wrist and the elbow. The hand width was calculated as the distance between the tip of the index and annular fingers, while the arm width was obtained calculating the distance between the internal and external parts of the wrist. Then, for each participant, we calculated an index of the bias in the perceived dimension with respect to the actual one (estimated dimension, e.g., Peviani & Bottini, 2018), as the ratio between the perceived and the real size for each body parts (arm length, arm width, hand length, hand width). In this way, values below 1 represent an underestimation of the perceived dimension with respect to the real one, and values above 1 indicate an overestimation. Moreover, similarly to previous studies (Longo et al., 2010), we calculated a global index of the perceived shape of the arm and the hand. In the present work, we calculated for each subject the ratio between the estimated dimension (i.e., the ratio between the perceived and the real size) on the width and the length, for both the arm and hand (from here on, Normalized Shape Index). In this case, values higher than 1 indicate a higher estimated dimension for the width with respect to the length of the body segment.

2.3.2. *Avatar adjustment task*

Data analysis was performed on the estimated length and width of the arm and hand expressed as a percentage of overestimation or underestimation with respect to the average (i.e., unbiased) size of the body model (i.e., the size corresponding to the reference population of equal age and gender provided by the software) (Bastioni et al., 2008, see Fig. 2). Similarly to the BL task, values above 1 indicated an overestimation and values below 1 indicated an underestimation with respect to the average size of the reference population (=1). We calculated the mean of the data collected in all trials for each dimension and body parts (arm length, arm width, hand length, hand width). Finally, as in the BL task, we calculated the Normalized Shape Index as a general index of the perceived shape of the arm and the hand, by dividing the estimated dimension between the width and the length. As defined above, values higher than 1 indicate higher values on the width with respect to the length. Namely, participants showed a higher estimated dimension for the width than for the length.

2.3.3. *Peripersonal space task*

Before proceeding with the analysis of interest based on RTs, we had to ensure that the accuracy was comparable in the two groups. Thus, we calculated a general index of accuracy considering the percentage of correct trials participants answered to, with respect to the total of the administered tactile trials. Note that the PPS task has been designed to assess speeded RTs to easy-to-detect tactile stimuli, to avoid the confounding effect of speed-accuracy trade-off or post-perceptual metacognitive decision processes. Thus, it is important that accuracy from participants involved in the RTs analysis demonstrated a sufficiently high accuracy. Based on this index, we decide to exclude 4 participants from the older group (original sample: $N = 27$, sample included in the analysis: $N = 23$) because they had an accuracy level below 60%. Once these subjects were excluded, the accuracy of the remaining 23 older adults finally included in the analysis was 97.8%, while the accuracy in younger participants was 99.2%, with no difference between the two groups (Wilcoxon rank sum test: $W = 1156$, $p = .09$).

2.3.4. *Data analysis was performed on RTs*

We expect that, when the acoustic stimulus reach and exceed the boundaries of the hand-PPS, sounds interact in a multisensory way with tactile processing, resulting in faster RTs to tactile stimuli delivered to the hand, compared to unimodal tactile stimulation (Canzoneri et al., 2012; Serino et al., 2015, 2018). For each subject, we first calculate the mean RT to tactile stimuli for every temporal delay both for unimodal and bimodal trials. We removed from the analysis all the trials exceeding 2 standard deviations from the mean RT (outlier trials). We considered the mean RT to tactile stimulus in the audio-tactile conditions for each distance (bimodal raw data). Then, we also identified, on the individual basis, the baseline unimodal condition, which is the fastest mean RT among the unimodal tactile conditions, and we subtracted this value from the mean RT to tactile stimulus in the audio-tactile conditions for each distance (bimodal baseline-corrected data). By using bimodal baseline-corrected data, we show a facilitation effect on tactile RTs due to auditory stimulation with respect to the fastest unimodal tactile RT. Accordingly, negative values (below the baseline, that by definition is zero) indicate a multisensory facilitation effect (Serino et al., 2015).

2.4. *Statistics*

To compare performances between the young and older groups, we ran the main statistical analysis using Linear Mixed Effect Models (LMM) with the software R Studio (R Core Team, 2017, http://www.R-project.org/). The use of LMM is justified by a model selection based on Akaike's Information Criterion (AIC) and Bayesian information criterion (BIC), always showing better parameters for LMM rather than ANOVA. In all the analyses, we considered participants as random effect. Additional random effects were added based on a model selection with AIC and BIC values. In all the analyses, the normality of residuals of the selected model was checked by using the Shapiro–Wilk test. If the residuals were not normally distributed, we transformed the data in their log. For fixed effects, *p*-values were obtained by likelihood ratio tests and degrees of freedom were approximated by using the Satterthwaite method.

In the BL and AAT tasks, for the main analysis run on the estimated dimension, we considered as fixed effects the body parts dimensions (4 levels: arm length, arm width, hand length, and hand width), the side (2 levels: left and right) and the group (2 levels: young and older adults). For the Normalized Shape Index, we considered as fixed effects the group, the side and the body parts (2 levels: arm, hand). Additionally, to test possible relations between the results at the two tasks in the groups, we performed correlations (Pearson or Spearman correlations, depending on results of the Shapiro–Wilk normality test) between some indexes of interests, i.e., parameters that revealed significant differences between the two groups, at the BL task and the AAT. Bonferroni corrections were applied based on the number of parameters considered.

In the PPS task, for the task on sound localization, we considered as fixed effects the temporal delays (3 levels: D3, D2, and D1) and the group (2 levels: young and older adults), while for the main analyses on RTs to the unimodal tactile stimuli and on RTs to the bimodal audio-tactile stimuli (raw and baseline-corrected data), we considered as fixed effects the hand (2 levels: left and right), the temporal delays (3 levels) and the group (2 levels). After a significant triple interaction, further analyses were applied to explore the interaction. Otherwise, the Tukey post hoc test was used to check for multiple comparisons. In addition, linear fittings were performed on the responses obtained at the unimodal auditory localization task using a custom-made script written in Matlab. The estimated individual slopes were compared between the two groups with the appropriate statistical tests (i.e., two sample *t*-test or Wilcoxon rank sum test depending on results of the Shapiro–Wilk normality test).

Finally, to account for a possible effect of age within each group, we performed correlations (Pearson or Spearman correlations, depending on results of the Shapiro–Wilk normality test) between indexes of interests at the three tasks (i.e., parameters that revealed significant differences between the two groups) and age. Bonferroni corrections were applied by taking into account the number of parameters of interests considered for each task.

3. Results

3.1. *Body-landmarks localization task*

The residuals of the model were not normally distributed (Shapiro–Wilk normality test: $W = .925$, $p < .001$), so the data were log-transformed for the analysis. The model ($R^2 = .86$) on the estimated dimension (i.e., ratio between the perceived and the real size) revealed a significant interaction between the body parts and the group ($F(3, 58) = 6.51$; $p = .001$), regardless of the side (body parts X side X group: $F(3, 232) = .318$; $p = .812$). Tukey post hoc comparisons revealed an underestimation of the arm length in the older participants that was significantly different from the young participants ($p < .001$). No differences emerged in the comparison between the two groups in the arm width (p = .141), hand length (p = .246) and hand width (p = .732) (see Fig. 3 A/C).

We then ran a model on the Normalized Shape Index (the ratio between the normalized width and the length) for the arm and the hand. The residuals of the model were not normally distributed (Shapiro–Wilk normality test: W = .838, $p < .001$), so the data were log-transformed for the analysis. The model ($R^2 = .86$) revealed a main effect of body parts (F (1, 58) = 74.78; $p < .01$) with a higher bias for the hand with respect to the arm, independently from the side and group (side X group X body parts: (F (1,116) = .323; p = .571)). Crucially, also the main effect of the group emerged (F (1, 44.64) = 12.58; p = .001), with a higher bias in the older compared to the young participants, without any significant difference in the two body parts (group X body parts: F (1, 58) = 2.506; p = .119) or side (group X side: F (1,116) = .271; p = .604) (see Fig. 3 B/D).

Taken together, these data indicate that older participants perceived their arms as shorter than the actual size and than the younger participants (Fig. 4), a bias that seemed common between the two sides (left or right arm). Moreover, we found a distortion in the global shape of the arms, indicating a higher bias on the overall aspect ratio between the estimated width (slightly underestimated) and length of the arm (clearly underestimated) in the older with respect to the young group. This higher distortion of the global shape of the arm in older rather than in young seems true also for the hand given that no significant effects between body parts (hand, arm)

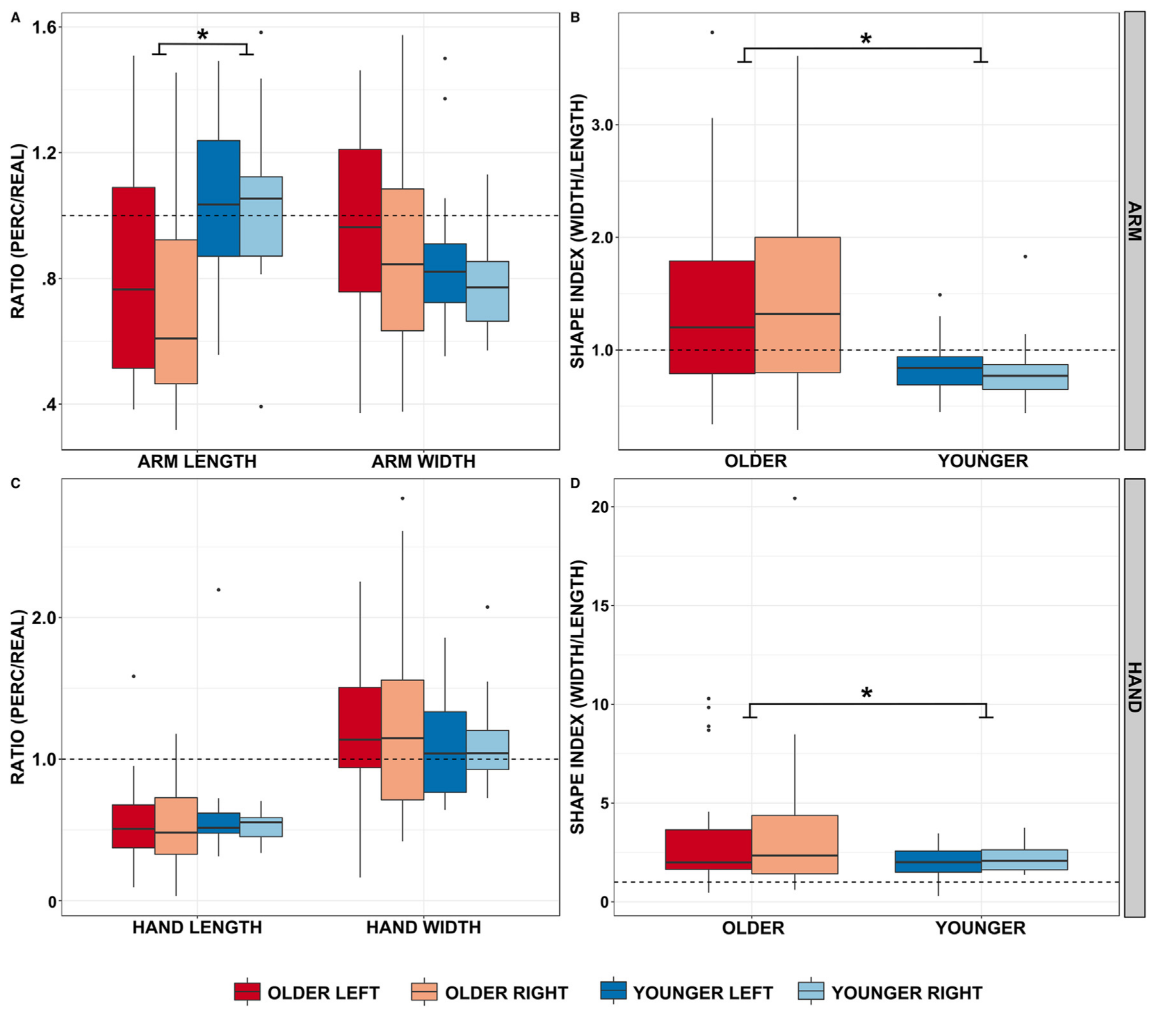

Fig. 3 – Distortions in implicit body representation in healthy ageing. The panels on the left represent the estimated width and length (i.e., ratio between the perceived and the real size) of the arm (A) and hand (C). Values below 1 (thin dashed line) indicate an underestimation of the perceived dimension with respect to the real one, while values above 1 indicate an overestimation. The panels on the right (B and D) show the Normalized Shape Index of the arms (above) and the hands (below), respectively, expressed as the ratio between the estimated width and length. Values higher than 1 indicate a higher estimated dimension on the width with respect to the length. In all panels, black brackets with asterisks above the boxes indicate a significant main effect between the groups. Data are represented through boxes indicating the first (lower hinges) and third quartiles (upper hinges), with internal lines for the median, whiskers for the largest (upper) and the smallest (lower) value ≥ 1.5 * the inter-quartile range, and black points for data beyond the end of the whiskers.

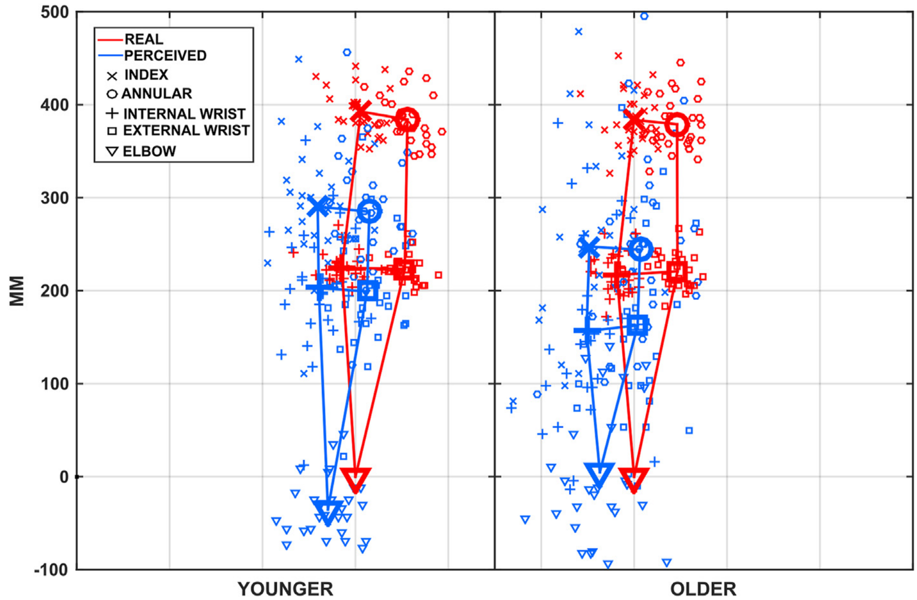

Fig. 4 – Older participants show greater distortions in implicit body representation. The figure presents the localization of the real (red) and of the averaged perceived (blue) position of every anatomical landmark on the right upper limb for each participant. The five landmarks are represented with 5 different symbols (see the legend and Fig. 1). The symbols in bold indicate the group average position.

emerged, although the analysis on the estimated dimension of the length or width did not differ between the two groups for the hand.

3.2. *Avatar adjustment task*

The residuals of the model were normally distributed (Shapiro–Wilk normality test: W = .997, p = .425). The model (R^2 = .79) on the estimated length and width of the arm and the hand revealed a significant triple interaction between body parts, side, and group (F (3, 295) = 6.491; p < .001). To further explore this interaction, we ran separated analyses for each body part (arm and hand) and dimension (width and length) (see Fig. 5).

ARM LENGTH. Older participants underestimate the length of their left arm with respect to their right arm (p < .001) and to the young participants' left arm (p = .002) (model: R^2 = .80; interaction: F (1, 59) = 13.62; p < .001). No difference between sides was present in the young group (p = .155) (Fig. 5 A).

ARM WIDTH. No difference between the two groups emerged (model: R^2 = .87; group: F (1,59) = 2.021; p = .16; group X side: F (1,59) = .398; p = .531), while a main effect of the side (F (1,59) = 39.21; p < .001) was found indicating that the arm width of the left side is overestimated with respect to the right side (p < .001) in older and young participants (Fig. 5 A).

HAND LENGTH. The model (R^2 = .79) on the hand length revealed a main effect of the side (F (1,59) = 18.16; p < .001) and a main effect of group (F (1,59) = 15.66; p < .001). Besides a similar difference in the two groups between the left and right hand (i.e., a higher underestimation for the right than the left hand), a greater underestimation appeared in older adults than in young, on both sides (side x group: F (1,59) = 1.765; p = .189) (Fig. 5C).

HAND WIDTH. A side-related distortion emerged in the young group, with a higher underestimation of the width for the right hand with respect to the left hand (p < .001), not present in the older group in which the perceived width of the two hands was comparable (p = .379) (model: R^2 = .66; interaction: F (1,59) = 26.13; p < .001) (Fig. 5C).

NORMALIZED SHAPE INDEX. The residuals of the model were normally distributed (Shapiro–Wilk normality test: W = .994, p = .505). We first considered the Normalized Shape Index of the arm and the hand together. The model (R^2 = .92) revealed a significant triple interaction between the body parts, side and group (F (1,59) = 34.1; p < .001). To further explore this interaction, we ran separated analyses for each body part (see Fig. 5 B). The model (R^2 = .81) on the shape index for the arm showed a significant interaction between side and group (F (1,59) = 4.717; p = .034). Post hoc comparison revealed that both older and young participants have a higher distortion in the overall aspect ratio between width and length for their left arm with respect to the right arm (all p < .01). Crucially, older participants' left arm was more distorted then the homologous of the young group (p < .001), while this was not the case for the right arm between the two groups (p = .202) (Fig. 5 B). The model (R^2 = .63) on the Normalized Shape Index for the hand revealed a significant interaction between side and group (F (1,59) = 10.99; p = .002). Post hoc comparison showed that young participants show a bigger bias for the left than the right hand (p = .004), similarly to the arm, while the two sides are similarly perceived in older adults (p = .082). Comparing the two groups, the right hand seems more biased in the older than in the young group (p < .001), while this was not the case for the left (p = .933) (Fig. 5 D).

Taken together, these data show a distortion in the length (underestimation) and the global shape of the arm in the older

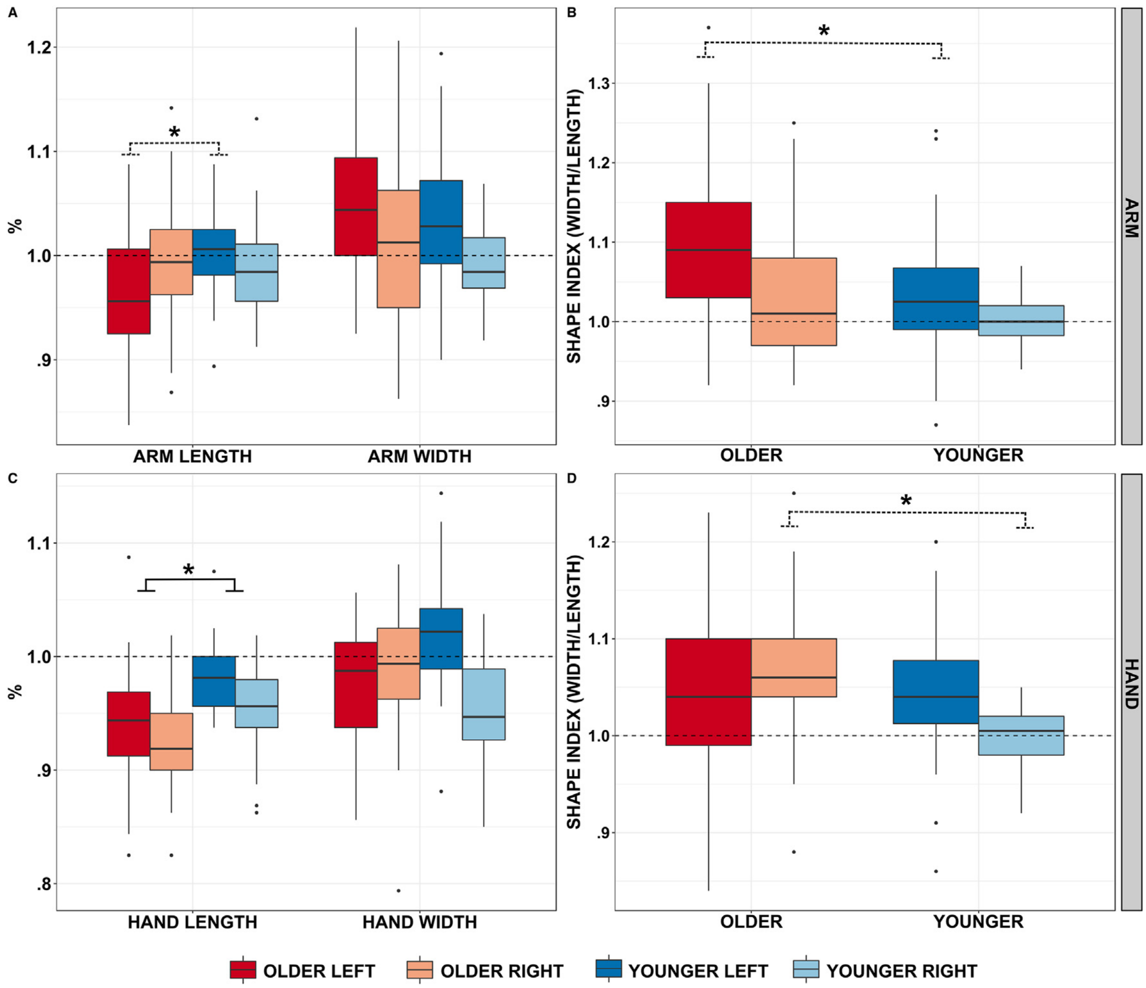

Fig. 5 – Distortions in the explicit body representation in healthy ageing. The panels on the left, represent the estimated dimensions of the arms (A) and the hands (C), expressed as a percentage of overestimation (above 1) or underestimation (below 1) with respect to the average size of the body model (1, thin dashed line) at the avatar adjustment task. The panels on the right show the Normalized Shape Index of the arms (B) and the hands (D), calculated by dividing the ratio between the width and the length. Values higher than 1 indicates higher values on the width with respect to the length. Asterisks highlight only significant main effect between groups (black brackets) and interactions between the groups and sides (black dashed brackets). Data are represented through boxes indicating the first (lower hinges) and third quartiles (upper hinges), with internal lines for the median, whiskers for the largest (upper) and the smallest (lower) value ≥ 1.5 * the inter-quartile range, and black points for data beyond the end of the whiskers.

participants with respect to the young participants, for the left arm. Moreover, older participants perceived both hands as shorter than young participants with a higher distortion of the global shape of the hand that was higher on the right side in older than in young participants.

3.3. *Peripersonal space task*

The PPS task involves audio-tactile stimulation and thus, before assessing any multisensory interaction, we firstly analyzed participants' ability to process auditory (auditory localization task) and tactile (unimodal tactile perception) stimuli constituting the multisensory PPS task.

3.3.1. *Auditory localization tasks*

For the task of sound localization, we calculated, for each subject, the mean of the distances at which the sound was perceived when the tactile stimulus was given at each of the three temporal delays (see Fig. 6 A). The residuals of the model were normally distributed (Shapiro–Wilk normality test: W = .987, $p = .203$). The model ($R^2 = .77$) on the perceived distances revealed a significant interaction between temporal delays and group (F (2, 91.999) = 14.448; $p < .001$). Post hoc comparisons revealed that both groups were able to distinguish the source of the sound at the three different distances according to the different temporal delays (all $p < .001$, see Fig. 6 A). Moreover, it showed that young and older

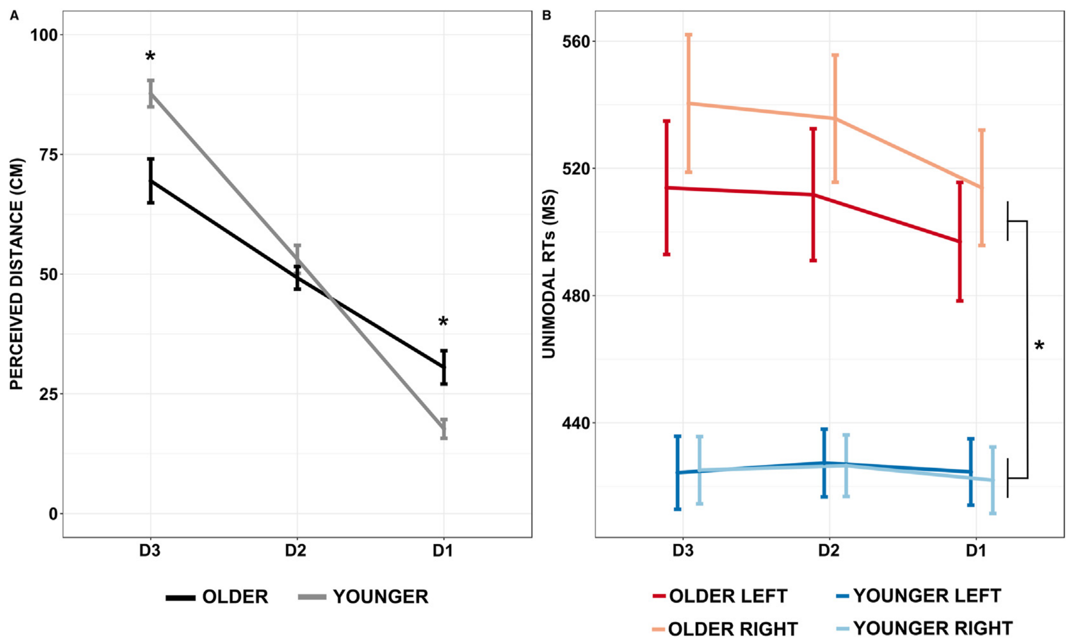

Fig. 6 – Age-related differences in auditory (left) and tactile (right) processing. The figure on the panel A shows the results of the localization task. Data represent the mean (±standard errors) of the estimated distances (cm) at which the sound was perceived when the tactile stimulus was given at each of the three temporal delays (D3, D2, and D1) corresponding to three sound distance (D3 = far; D2 = medium; D1 = near). The asterisks indicate significant differences between the two groups. The figure on the panel B shows means (±standard errors) RTs (msec) at unimodal tactile stimulus as a function of the three temporal delays (D3, D2, and D1). The black bracket with asterisk indicates a significant main effect between the two groups.

participants perceived at the same distance the sound at the medium temporal delays ($p = .372$), but they perceived the first and the last ones differently. In particular, older adults perceived sounds at the first temporal delay (D3) at a closer distance ($p < .001$, difference between older adults and young: 18.22 cm), and at the last (D1) at a farther distance ($p < .003$, difference between older adults and young: 12.85 cm) with respect to the young. To better characterize these effects, the perceived distances were fitted with a linear function (young: $R^2 = .99$; older adults: $R^2 = .99$) and individual slopes were compared between the two groups. Data revealed flatter slopes for older participants than for young participants (Shapiro–Wilk normality test, older adults: $W = .901$, $p = .027$; young: $W = .942$, $p = .328$; Wilcoxon rank sum test: $W = 119.5$, $p = .001$). To summarize, data from the auditory localization task confirmed that older participants were able to perceive the three different distances of the sounds in space corresponding to the three temporal delays, although with a decreased precision in sound distance estimation, as indicated by flatter slopes.

3.3.2. *Unimodal tactile perception*

We compared between young and older participants RTs to unisensory tactile stimuli for each temporal delay with respect to sound onset. The residuals of the model were not normally distributed (Shapiro–Wilk normality test: $W = .968$, $p < .001$), so the data were log-transformed for the analysis. The model ($R^2 = .95$) on unimodal RTs revealed a significant interaction between group and temporal delays ($F (2, 208) = 3.536$, $p = .031$) (Fig. 6 B). Post hoc comparison revealed faster RTs at near distance (D1) than at the medium (D2, $p = .004$) and the far distance (D3, $p < .001$), while similar RTs were found between medium and far distance (D2 *vs* D3: $p = .877$) in older but not in young participants (all p values > .574). Also, older participants were always slower in answering than young participants at all temporal delays (all p values < .001), as also shown by a significant main effect of group ($F (1, 52) = 24.63$, $p < .001$). These results indicate that older participants present a strong expectancy effect for unimodal tactile stimuli (i.e., faster reactions for later tactile targets – see (Kandula et al., 2017; Spaccasassi, Romano, & Maravita, 2019)), that was not present in young participants. Furthermore, not surprisingly, older participants were slower in responding to tactile cues than young participants, independently from temporal delays.

3.3.3. *Multisensory PPS task: audio-tactile interaction*

We first considered raw bimodal (audio-tactile) RTs to assess the effect of the sound distances on RTs to tactile stimuli in the two groups. The residuals of the model on raw bimodal RTs were not normally distributed (Shapiro–Wilk normality test: $W = .959$; $p < .001$) so the data were log-transformed for the analysis. The model ($R^2 = .97$) revealed a main effect of group ($F (1, 52) = 27.78$, $p < .001$) with generally slower RTs for the older group and an interaction hand X group ($F (1, 52) = 6.36$, $p = .015$), indicating slower RTs for the right side with respect to the left side in the older adults group ($p = .02$), but no difference in the young group ($p = .26$). Crucially, we found a main effect of distance ($F (2, 68.25) = 22.01$, $p < .001$) regardless of the group or the hand (distance X group: $F (2, 68.25) = 2.363$, $p = .102$; hand X temporal delays X group: $F (2,156) = .782$; $p = .459$). Post hoc comparisons revealed that in both groups, RTs at medium distance were significantly faster

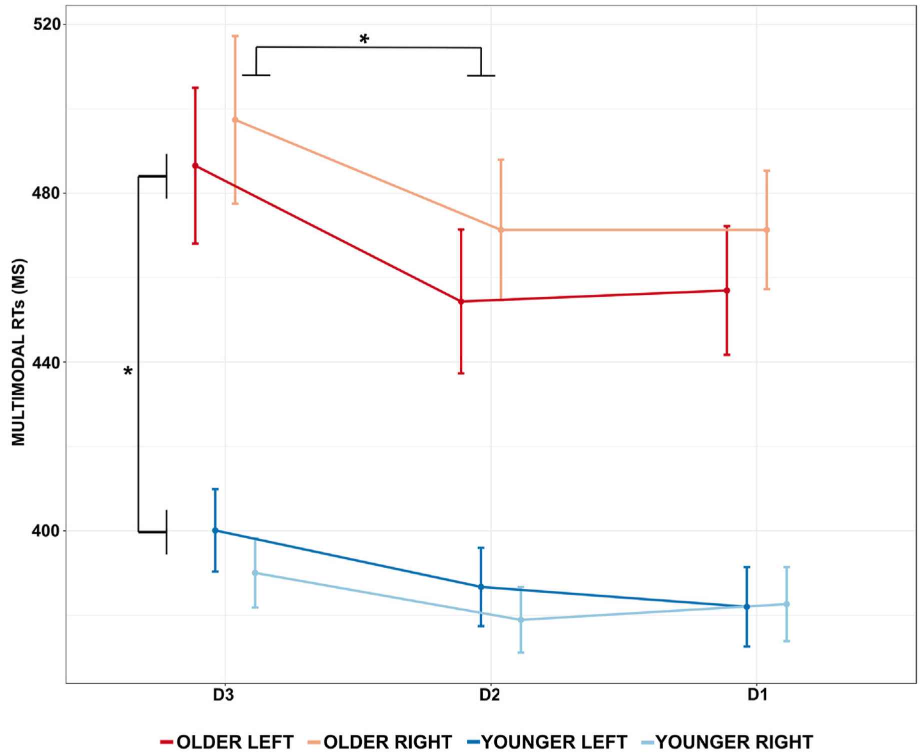

Fig. 7 – Bimodal responses capturing the distance-dependent multisensory facilitation characterizing PPS representation in young and older adults. The figure shows the raw bimodal responses in the audio-tactile interaction task. Data represent mean (±standard errors) RTs (msec) as a function of the temporal delays from the sound onset (D3, D2, and D1). Although older participants were generally slower than young participants (vertical bracket), higher facilitation in the RTs to tactile stimuli occurred when the sound was perceived at near (D1) or at a medium (D2) distance from the hand, with respect to far location (D3) (horizontal bracket) in both groups.

with respect to the far distance ($p < .001$), but not significantly different from RTs at the near distance ($p = .96$) (see Fig. 7). This indicates that although older participants were generally slower than the younger ones, the distance-dependent multisensory facilitation effect capturing PPS representation was not different in the two groups. This also suggests that bimodal responses in older participants do not only represent an expectancy effect, as observed for unimodal tactile responses where RTs associated to the medium distance were similar to those at far distance, but a multisensory facilitation effect related to PPS representation, with the sound at medium distance already facilitating RTs to tactile target.

Moreover, given the general slowness in unimodal and raw bimodal RTs in older rather than young participants, to directly compared the multisensory effect in the two groups, bimodal stimuli RTs were corrected by subtracting the baseline of the unimodal condition in each group (i.e., the fastest mean RT among the unimodal tactile conditions, see Method). The baseline correction allows us to calculate a facilitation effect on tactile RTs due to auditory stimulation with respect to the unimodal tactile RTs as an index of multisensory PPS (see e.g., Serino et al., 2015) to be compared between groups. The residuals of the model on baseline corrected multimodal RTs were not normally distributed (Shapiro–Wilk normality test: $W = .966$, $p < .001$) so the data were log-transformed for the analysis. The model ($R^2 = .88$) revealed a significant interaction between temporal delays and group ($F(2, 72.88) = 3.555$, $p = .034$) regardless of the stimulated hand (hand X temporal delays X group: $F(2,156) = .552$; $p = .594$). Post hoc comparisons revealed slower RTs for the older group in the far distance (D3), with respect to the young group ($p = .017$). In contrast, the distance at which sounds were able to affect the tactile RTs was similar in the two groups: indeed, in both groups, RTs at medium distance (D2, $p = .787$) and the near distance (D1, $p = .913$) were not different from each other, whereas, in both groups, RTs at medium distance were significantly faster with respect to the far distance (both p values $< .025$), but similar to the near one (both p values $> .99$) (see Fig. 8). Considering that the model showed no effect between the two sides, we merged the RTs between the two sides for each temporal delay and group. We then compared corrected bimodal RTs against zero (i.e., the fastest reaction time for unimodal tactile stimuli taken as a baseline) at each of the three temporal delays, by using one-sample Wilcoxon test, Bonferroni corrected (alpha set at $.05/3 = .017$). Comparisons showed that RTs in the young group are always different from the baseline (all p values $< .001$), i.e., young participants show multisensory facilitation at each of the three considered delays, while in older participants RTs differ from the baseline only at medium (D2) and at near (D1) distances (all p values $< .001$), i.e., older adults do not show multisensory facilitation ($W = 156$; $p = .601$) when they have to react to tactile stimuli on the hand while a sound is presented at far distance (D3).

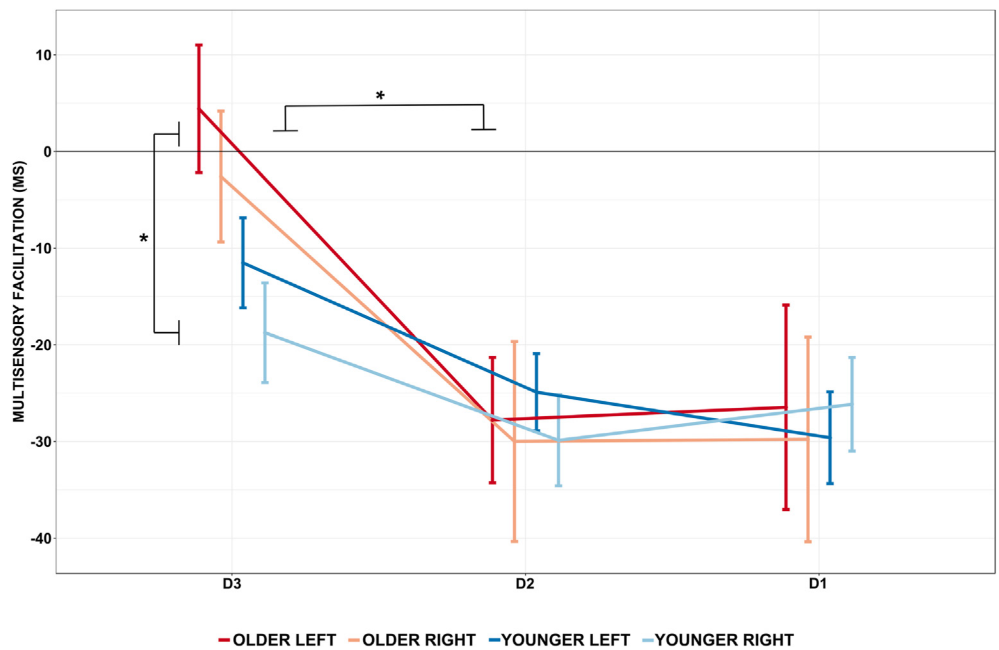

Fig. 8 – Peripersonal space representation is resistant to ageing. The figure shows the results of the audio-tactile interaction task with data (mean ± standard errors) corrected for the baseline (i.e., the fastest RTs to unimodal tactile stimulation, baseline, 0 solid line). Negative values indicate a multisensory facilitation effect. Slower RTs, not different from the baseline, emerged in the far distance (D3) in the older rather than young participants (vertical bracket). Crucially, in both groups, higher facilitation in the RTs to tactile stimuli occurred when the sound was perceived at near (D1) or at a medium (D2) distance from the hand, with respect to far location (D3) (horizontal bracket).

Taken together, and in line with previous works (Noel et al., 2015; Serino et al., 2015), these findings indicate that higher facilitation in the RTs to tactile stimuli occurred when the sound was perceived at near or at a medium distance from the hand, with respect to far location. Importantly, this effect was similar in both groups. Nevertheless, while young participants seem to show multisensory facilitation already at the farthest distance, even if this was less pronounced than at the medium or at the near distance, older participants did not show this facilitation with respect to the baseline in the far space. These results emerged beside a general slowing down effects in the processing of unisensory tactile stimuli in older with respect to young participants.

3.4. *Correlation analyses*

To test a possible effect of age within each group, we performed Spearman correlations (Shapiro–Wilk normality test revealed significance deviation from normality, p values always < .05) between age and some indexes of interests from the three tasks (i.e., parameters that revealed significant differences between the two groups): BL task: arm length, arm and hand shape index, all parameters averaged between the two sides; AAT: left arm length, hand length averaged between the two sides, left arm shape index, right hand shape index; PPS task: the difference between the RTs to bimodal trials associated to near and far sounds, RTs to bimodal trials associated to far sounds, both parameters averaged between the two sides. We found no significant correlations between age and the AAT (young adults: p values always > .07; older adults: p values always > .30; significant threshold set at .05/4 = .0125) or the PPS task (young adults: p values always > .11; older adults: p values always > .07; significant threshold set at .05/2 = .025) or the BL task, although a numerical positive relation (in the expected direction, higher distortion at increasing age), not surviving correction for multiple comparisons, emerged between age and only one parameter extrapolated from the BL task (hand shape index) in older adults (young adults: p values always > .21; older adults: p values always > .041; significant threshold set at .05/3 = .017).

Moreover, we investigated possible correlations between the BL task and the AAT. The parameters of interest listed above (arm length, hand length, arm shape index, hand shape index) were considered on both sides (left and right, significant threshold set at .05/8 comparisons = .006). No significant correlations between the two tasks emerged (all p values > .007).

4. Discussion

A decline in the processing of sensorimotor information that seems fundamental to maintaining updated body and space representations (Bassolino et al., 2014; Berlucchi & Aglioti, 2010; Canzoneri et al., 2013; de Vignemont, 2010) has been described previously in older adults (Costello & Bloesch, 2017; Kuehn et al., 2018). This would suggest the presence of less accurate body and space representations in older participants. In the present study, by focusing on the upper limbs, we explored this hypothesis by comparing the performance of healthy young and older participants in three tasks aiming to assess implicit and explicit perceived body dimensions and the PPS representations. Overall, our findings show more substantial distortions in BR observed both in the implicit and explicit tasks in the older adults rather than in young participants. Comparable multisensory facilitation for stimuli presented near the body was found in young and older adults, suggesting a similar PPS representation around the hand, while a reduced multisensory interaction for far stimuli, less accurate auditory localization and slower tactile processing were found in older participants.

4.1. Distortions in the implicit and explicit metric body representation in normal ageing

4.1.1. Implicit body metric

The findings from the BL task, aiming to capture implicit metric representations of the upper limbs, suggest that with respect to the young group, older participants underestimated the arm length (Fig. 4) and have a greater distortion in the global shape of the upper limbs (hands and arms), with a greater bias on the overall ratio between the estimated width and the estimated length (see Fig. 3).

The present results show a distorted global shape of the hand (with overestimation of the width and underestimation of the length) and are in agreement with several earlier studies evaluating hand representations in young participants (Longo & Haggard, 2010, 2011, 2012a; Longo, Morcom, Pia, Preston, & Romano, 2016; Peviani & Bottini, 2018). Our findings expand this work by showing that the hand bias seems even higher in older adults rather than in young participants. Also, while global shape distortions have been reported mainly for the hand with similar effects for the forearm in tasks based on tactile stimuli perception (Canzoneri et al., 2013; Longo, 2017; Miller, Longo, & Saygin, 2014), the present results extend the bias to the arm only in older participants, thus suggesting that those distortions involve the whole upper limb (i.e., hand and arm) in normal ageing.

Although the overall distorted characteristics of the hand shape have been replicated under different versions of the body-landmarks localization task (e.g., motor *vs* purely perceptual responses; Longo, Long, & Haggard, 2012; Longo, 2018; Peviani & Bottini, 2018) by different laboratories (e.g., Cocchini, Galligan, Mora, & Kuhn, 2018; Longo & Haggard, 2010; Longo, Mattioni, & Ganea, 2015; Medina & Duckett, 2017; Peviani & Bottini, 2018; Saulton, Dodds, Bülthoff, & de la Rosa, 2015) and, even using other tasks (e.g., Canzoneri et al., 2013; Ferrè, Vagnoni, & Haggard, 2013; Longo & Haggard, 2011; Longo et al., 2015; Lopez, Schreyer, Preuss, & Mast, 2012), the mechanisms underlying such a bias remain uncertain (Ambroziak, Tamè, & Longo, 2018; Longo, 2018). Multiple, non-exclusive, factors have been proposed to be responsible for these distortions (Longo, 2017; Longo et al., 2015; Saulton, Longo, Wong, Bülthoff, & de la Rosa, 2016). One hypothesis suggests that this distorted global shape of the hand found in the general population relies on a stored implicit body model which is mostly influenced by somatosensory maps in the primary somatosensory cortex (Longo et al., 2015), such as the greater tactile acuity on the medio-lateral rather than proximo–distal axis of the hand dorsum and the anisotropy of the receptive fields of somatosensory neurons (Cody, Garside, Lloyd, & Poliakoff, 2008; Longo & Haggard, 2011). This effect might be even magnified in older adults. Evidence, indeed, suggests that primary somatosensory maps decline with age, resulting in a decrease of tactile acuity (e.g., Kalisch, Ragert, Schwenkreis, Dinse, & Tegenthoff, 2009) and associated with a degradation of peripheral mechanoreceptors on the skin (e.g., Kuehn et al., 2018). This is also supported by studies about ageing in animal models which reported an increase in the dimension of the receptive fields of somatosensory neurons (David-Jürgens, Churs, Berkefeld, Zepka, & Dinse, 2008; Spengler, Godde, & Dinse, 1995). These probable changes in primary somatosensory maps during ageing may explain the observed amplified distortions in the BL task in the older adults.

Moreover, in the general population, it has been proposed that such a stored body model is maintained and updated through multiple sensory and motor inputs, i.e., proprioceptive, tactile, visual and efference copies (Longo & Haggard, 2010; Schwoebel & Coslett, 2005). An age-related decline is also observed in peripheral mechanoreceptors at the levels of muscles and joints associated with alterations in proprioception (Adamo & Brown, 2007; Carmeli et al., 2003; Costello & Bloesch, 2017; Kuehn et al., 2018; Shaffer & Harrison, 2007), which in turn could affect the accurate updating of the implicit body model. In this sense, the body model in older participants could result more distorted because not efficiently supported by the contribution of on-line afferent proprioceptive and somatosensory information. The hypothesis that the distortions observed in the implicit body metric representation in older participants could be linked to a not efficient updating through the information coming from the body is in line with studies on motor imagery in normal ageing. Authors have demonstrated that the accuracy in mental imagery (i.e., the temporal correspondence between executed and imagined movements, e.g., Collet, Guillot, Lebon, MacIntyre, & Moran, 2011; Marchesotti, Bassolino, Serino, Bleuler, & Blanke, 2016) declines with ages (Personnier, Kubicki, Laroche, & Papaxanthis, 2010; Skoura, Papaxanthis, Vinter, & Pozzo, 2005; Skoura, Personnier, Vinter, Pozzo, & Papaxanthis, 2008), in particular in cases in which a newly changed state of the body has to be taken into account during action simulation, as when a load is worn on the arm (Personnier, Paizis, Ballay, & Papaxanthis, 2008). This behavior has been interpreted as difficulty in accurately updating the changed configuration of the musculoskeletal system through peripheral signals. Such a decline in updating the body model could also be linked to a decrease in the flow of sensorimotor information from/to the body due to a relative underuse of limbs in the older adults because of different motor capabilities and reduced daily life necessities. This hypothesis was also proposed in a previous study using an arm bisection task and showing an underestimation of the perceived arm length in older participants, in line with our results (Garbarini et al., 2015). A comparable underestimation of the perceived arm length has also been described in a few studies in pathological conditions of reduced or absent sensorimotor information such as amputees or stroke patients with motor deficits (e.g., Rognini et al., 2018; Tosi, Romano, & Maravita, 2018). However, while in patients the bias was restricted to the affected side, in our study older participants showed a similar underestimation of the perceived arm length for both the left and the right sides, in line with the non-lateralized hand distortions typically reported in young healthy participants (see Longo & Haggard, 2010, Experiment 3). This common result on both limbs suggests that the distortions reported in older participants at the BL task are not related to manual dominance or any cognitive lateralized mechanism.

Another factor recently proposed to explain perceived distortions in body metrics is related to general conceptual distortions linked to mistaken beliefs or visual memory of the location of different landmarks (Longo et al., 2015; Saulton et al., 2016). Although it is not possible to discard this hypothesis at the moment, this proposal is unlikely in explaining the age-related effects for at least two reasons. First, typically conceptual distortions have been reported at the level of the hand knuckles (Longo et al., 2015), while the present distortions in the older adults also refer to the arm. Secondly, similar bias was found in a different task, the AAT, not based on landmark localization. Finally, previous studies have demonstrated that visual-spatial memory of simple task mainly requiring maintenance of spatial information is not altered with age (Iachini, Iavarone, Senese, Ruotolo, & Ruggiero, 2009), not supporting the hypothesis that a decline in this function could be at the basis of the observed higher distortions in older participants.

4.1.2. *Explicit body representation*

Results similar to that obtained in the BL task have also been found in a more explicit task aiming to evaluate the perceived dimension of the upper limb by manipulating the corresponding body parts on an avatar (AAT). In particular, in line with BL findings, older participants showed a greater bias (underestimation) for the arm length and the global shape of the upper limbs. Also, the underestimation of the hand length was higher in the older than in young participants. However, while in the BL task differences between the two groups of participants emerged independently of the side, in the AAT, the difference between the two groups was limited to one of the two limbs, i.e., the left arm concerning the arm length and the Normalized Shape Index, and the right hand for the Normalized Shape Index. Thus, overall, although the age-related effects observed in the two tasks go in the same direction, the degree of distortions seems different, with modifications in older participants limited to one side in the explicit task. We can speculate that such differences in the results obtained at the AAT and the BL task are related to the contribution of different sensory modalities sub-serving these tasks and the underlying body representations. It has been demonstrated that while evident distortions in the representation of the hand emerge using implicit tasks (Longo & Haggard, 2010, 2012b), similar effects but with reduced magnitude have been reported in an *explicit metric* task, the "line length task" (Longo et al., 2015; Longo & Haggard, 2012b) where participants have to provide explicit judgment of the hand dimension, by referring to their own body. In this sense, the present AAT may resemble the "line length task" by tapping into a combination of somatosensory representations of one's own body and *explicit metric* judgment in terms of width and length. Moreover, in both tasks, participants have to provide their metric judgments by modifying the visual characteristic of a model (the avatar in our task, lines in the "line length task"). It is thus possible that in AAT with respect to the BL task, the influence of somatosensory representation is reduced in favor of additional visual information that typically appears to be less biased (see "the template matching task", Longo & Haggard, 2010; Longo et al., 2015; Longo & Haggard, 2012), thus leading to a reduced pattern of distortions. This interpretation could also account for higher bias in the older than young participants because the additional contribution of the visual component in this task could be not sufficient to completely compensate for the already higher distorted somatosensory representations captured at the BL task in the older group. It is also possible that older participants could not properly decrease the weight of the declined somatosensory inputs in favor of the visual information, in line with evidence showing difficulties in adjusting the weights of sensory bodily signals with ageing (Kuehn et al., 2018). We also note that probably visual characteristics of the avatar matching the participants' age and gender could have had a role, accordingly to previous studies showing distortions in the estimation of the length of others persons' body parts with greater distortions if the others were of the same gender (Linkenauger et al., 2015; Linkenauger, Kirby, McCulloch, & Longo, 2017).

Concerning the lateralization of the distortions, and differently from the results at the BL task, in the AAT we found an overall reduced distortion of the dominant right side, evident in the estimated global shape of the limbs (Normalized Shape Index) in both groups, except for the hand in the older participants. This seems to mimic the dominant-hand advantage typically reported in the motor domain in young participants (Kalisch et al., 2006). Such hand dominance has been described to decline with ageing, so that performances of the two hands become balanced and comparable in the older adults (Kalisch et al., 2006), in line with the similar Normalized Shape Index of the left and right hand, found here only in older participants. Although, considering the visuo-somatosensory nature of the AAT, the fact that participants did not execute any upper limb movement to perform this task, and the absence of such lateralization at the BL task (according to Longo & Haggard, 2010, Experiment 3), this side–related effect is unlikely to be directly linked to motor information contributing to the task, but could reflect some visual dominance–related differences, as visual feedback during motor experience. Alternatively, one could hypothesize that the side differences found in the older adults can be due to attentional bias. However, a rightward attentional bias (i.e., lower attention on the left) in the visual domain recently proposed in ageing (Zeller & Hullin, 2018) would predict opposite results with always higher distortion for the left side in older participants (effect present here in both groups, but with the exception of the hand for the older adults).

4.2. *Age-related differences in tactile and auditory processing, but comparable peripersonal space representation in young and older participants*

Our results show significant differences between older and young participants in auditory and tactile processing. More precisely, in the auditory distance perception task assessing sound localization, older participants were able to perceive the source of the sounds at the three different distances, but they were less sensitive to discriminate the three locations, as they perceived the farthest distance as significantly closer and the closest distance as more distant (with no difference at the middle position), with respect to the young participants (see Fig. 6 A). This resulted in a flatter slope in the linear function between temporal delays and sound localization in older adults rather than in young participants. Changes in the sound localization ability from young adulthood to old age (Abel, Giguère, Consoli, & Papsin, 2000; Dobreva, O'Neill, & Paige, 2011) and a reduction of perceived spatial volume have been reported in older adults (Ghafouri & Lestienne, 2000). However, it is difficult to compare this result with related work on age-related effects in distance perception because, so far, different protocols have mainly employed static visual objects (e.g., Bian & Andersen, 2013), whereas the present study is one of the few studies using acoustic dynamic stimuli. Age-related unimodal perceptual differences were confirmed in the perception of unimodal tactile stimuli. First, tactile RTs were, in general, slower in the older adults, in line with previous studies showing age-related changes in tactile perception (Carmeli et al., 2003; Costello & Bloesch, 2017), as well as in reaction times and speed processing in different modalities (e.g., Cespón, Galdo-Álvarez, & Díaz, 2013; Kuehn et al., 2018; Murray et al., 2018). Also, in older participants, and not in young participants, RTs to unimodal tactile stimuli varied as a function of the delay of tactile stimuli administration. In particular, in older adults RTs became faster with longer delays, an effect indicating a form of cognitive expectancy (Kandula et al., 2017): as the trial's time increases, the probability of receiving touch also increases, and thus subjects are more ready to respond for late delays. The two effects on auditory and tactile processing might not be fully independent of each other. Given that participants had to judge sound distance by indicating at which location the sound was when they perceived a tactile cue, a slower general tactile processing, and an increased expectancy could have a role in explaining the results in the auditory localization task. Slower tactile processing might explain why the auditory space is contracted for the far stimuli, as touch is processed later. This effect, however, could be compensated when the tactile cues were administered at further delays during the trial (i.e., medium position), and it could even produce the opposite effect (the closer position is perceived further away) because of increasing expectancy in the latest delay (near, i.e., the tactile processing is anticipated, and thus the sound is perceived farther away).

Crucially for this study, despite these differences in the elaboration of auditory and tactile stimuli in the two groups, we found comparable multisensory facilitation in older adults and young participants for bimodal stimuli at near and at medium distance from the body. Importantly, in both groups, such facilitation was numerically higher in these two closer positions than at the far location. Previous multisensory studies (Noel et al., 2015; Serino, 2019; Serino et al., 2015) have interpreted such multisensory facilitation as a proxy of PPS boundaries. This result could thus suggest similar hand-PPS boundaries in the older adults and young participants. Although few previous studies have tried to describe older adults abilities in processing stimuli within the PPS (Costello & Bloesch, 2017; Kuehn et al., 2018), so far, this is the first work directly comparing PPS representations in young and older participants by exploring its multisensory proprieties.

The similar facilitation observed in the two groups could be based on comparable multisensory abilities. This is supported by results demonstrating that multisensory integration processes seem to be spared in older adults (Laurienti, Burdette, Maldjian, & Wallace, 2006; Mahoney, Li, Oh-Park, Verghese, & Holtzer, 2011) and similar to younger subjects in the audio-tactile task (Mahoney et al., 2011). Besides reduced unisensory abilities in processing external and bodily stimuli in older adults, an efficient PPS representation could play an important role to support actions in the near space and to protect the individual from incoming potential dangerous stimuli, in line with the proposed function of PPS (for recent reviews Bufacchi & Iannetti, 2018; Cléry & Ben Hamed, 2018; Serino, 2019).

An intriguing hypothesis is that spared multisensory processing in the older adults is due to decrease in unisensory processes. This could be linked to one principle of multisensory integration: two stimuli in the two modalities more strongly interact when unimodal processing is weak – inverse effectiveness (Stein & Stanford, 2008). Even if the current results are compatible with it, our paradigm was not designed to test this hypothesis directly. Alternatively, it could be possible that efficient, or even greater, multisensory processing in older adults compensates for the age-related decline in unisensory abilities (de Dieuleveult, Siemonsma, van Erp, & Brouwer, 2017; Diaconescu, Hasher, & McIntosh, 2013; Diederich, Colonius, & Schomburg, 2008), in line with studies showing a more extended recruitment of brain areas during multisensory tasks in older versus young adults (Heuninckx, Wenderoth, & Swinnen, 2008; Townsend, Adamo, & Haist, 2006; Venkatraman et al., 2010).

Despite similar effects in older adults and young participants in PPS representation, differences between the two groups were found in the far space. Older participants showed less multisensory facilitation as compared to young participants when the tactile stimulus was coupled with far sound (see Fig. 7). This could be interpreted as a weaker effect of sound in the far space, not able to compensate for the slower RTs to the tactile stimuli in far rather than in near location in the older adults. However, a similar multisensory integration in the two groups has been observed at the medium distance, besides equivalent slow RTs to unimodal tactile stimuli in medium and far position in the older adults. Such difference in the far space between the two groups could also be seen as if young participants showed higher multisensory facilitation with respect to older adults in the far space, to more efficiently anticipate potential contact with external stimuli during their likely more frequent and more dynamic interactions with the environment, in contrast with decrease upper extremities range of motion and disuse in older adults (Daley & Spinks, 2000; Schultz, 1992).

4.3. *Different effect of ageing between BR and PPS representation in older adults*

The present results show important distortions in BR in older adults in perceiving the metrics of the upper limb using implicit and explicit BR tasks. On the other hand, no significant differences in the PPS representation between young and older participants emerged, despite age-dependent differences in unimodal tactile and auditory perception. The fact that BR and PPS were not tested in the same participants does not allow us to conclude for a strong dissociation between the two functions, as other factors might explain this difference (e.g., individual differences, the sensitivity of the tasks). Nevertheless, the present data are suggestive that ageing impacts more strongly on BR than PPS.

The present results with alterations in BL task, with mainly unaltered PPS representation in older adults, is opposite to that we found after immobilization. After immobilization, the perceived arm length remained unchanged (BL task), while multisensory facilitation within PPS decreased. In the case of immobilization, we interpreted those changes as due to unaltered afferent static information from the immobilized limb maintaining BR, associated with reduced possibility to act in space, driving modifications in the PPS (Bassolino et al., 2014). In normal ageing, the opposite effects could be related to a decline in afferent information from the body (Costello & Bloesch, 2017; Kuehn et al., 2018) not properly updating BR, and preserved actions in the close space, even if likely reduced in terms of frequency, supporting a comparable multisensory facilitation within PPS boundaries. The unaltered PPS representations could also be linked to compensation for the decline of unisensory and bodily information through preserved multisensory mechanisms, and to the protective function of predicting dangerous stimuli near the body, particularly necessary when perceptual processing is altered or slowing down as in the case of older adults.

4.4. *Study limitations*

The present study has potential limitations. First, as mentioned above, to avoid fatigue in older adults, we adopted two independent samples to test PPS (in one group) and body representations (BL task and AAT, in a second group). This prevents a direct comparison of the results at the three tasks in the same sample. Secondly, the age range for the older group is larger than the range in the young group. However, no significant correlations between age and the outcome of interests at the BL task, the PPS task, or the AAT were found for young or older participants.

5. Conclusion

To our knowledge, this is the first study describing BR and PPS representations in normal ageing by adopting tasks previously used to demonstrate the plasticity of these representations after tool-use and immobilization (Bassolino et al., 2014; Canzoneri et al., 2013). The present findings suggest the importance of introducing those tasks aiming to evaluate BR and PPS representations in the assessment of older people. Although the present sample of healthy, cognitively unimpaired and active older adults could not allow us to make inferences about pathological conditions during ageing and PPS or BR distortions, a topic that requires future research, the present study has the advantage to show that even in the absence of diseases, age-related effects are evident in BR and PPS representations. More generally, this work extends the concept of plasticity underlying BR and PPS by showing that these representations are not only modifiable after short or long experience of tool-use or disuse (Bassolino et al., 2010, 2014; Biggio et al., 2017; Maravita & Iriki, 2004; Martel et al., 2016; Serino et al., 2007), but even during the normal course of life.

Author contributions

MB and AS designed the study; GS, MF and CZ performed the experiments; GS, MF and MB analyzed the data; GS, MB, OB and AS wrote the manuscript.

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Cortex TOP guidelines

We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study. It has not been possible to pre-register any part of the study procedures or analyses prior to the research being conducted. Data and digital study materials are available at https://osf.io/p75yz/

Open practices

The study in this article earned Open Materials and Open Data badges for transparent practices.

Declaration of competing interest

The authors report no commercial or competing interest.

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