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Shrinking of spatial hand representation but not of objects across the lifespan

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Abstract

Perception and action are based on cerebral spatial representations of the body and the external world. However, spatial representations differ from the physical characteristics of body and external space (e.g. objects). It remains unclear whether these discrepancies are related to functional requirements of action and are shared between different spatial representations, indicating common brain processes. We hypothesized that distortions of spatial hand representation would be affected by age, sensorimotor practice and external space representation. We assessed hand representations using tactile and verbal localization tasks and quantified object representation in three age groups (20-79 yrs., total n=60). Our results show significant shrinking of spatial hand representations (hand width) with age, unrelated to sensorimotor functions. No such shrinking occurred in spatial object representations despite some common characteristics with hand representations. Therefore, spatial properties of body representation partially share characteristics of object representation but also evolve independently across the lifespan.

Keywords

- Spatial representation, body representation, hand, sensorimotor functions

Highlights

- Spatial hand representation evolves systematically across the lifespan

- Hand representations shrink with increased age independently from tactile sensitivity
- **Distortion of objects in external space** share characteristics with hand representation
- But contrary to the hand, objects representation does not shrink across the lifespan

Introduction

A continuous and persistent spatial representation of the body is necessary to physically interact with the world and to interpret somatosensory information. For example, in order to plan a movement, such as reaching an object, knowledge of the initial location of the hand and fingers in external space is necessary to plan their trajectories (Kamper et al., 2003; Peviani & Bottini, 2018). Thus, movement planning depends on spatial body representation, and conversely body spatial configuration depends on movement. In general, extracting positional information from somatosensory stimuli requires spatial body representation (Bolognini & Maravita, 2007; Heed et al., 2012; Longo, Mancini, et al., 2015), as shown in haptics: when touching an object, the localization in space of the tactile stimulation (contact points) is based on the relative spatial position of the fingers, which then allows the identification of object shape in absence of vision.

However, studies have found that spatial representations (of body and movement or in perception) are not necessarily physically veridical. They show systematic deviations from the physical spatial properties. In particular, several studies have shown structural distortions of body representation, specifically of the hand (Ingram et al., 2019; Longo, 2017; Tamè et al., 2017), typically with a wider hand and shorter finger representations compared to the physical hand, a distortion observed from childhood (Van der Looven et al., 2021). Discrepancies between representation and physical spatial properties have also been observed in the haptic domain which depends on the relation between movement, body configuration and somatosensory information. Furthermore, when subjects are instructed to position, with their hands but without support of vision, two bars in parallel in external space, a systematic deviation of Euclidian parallelism is observed (Kappers, 1999; Kappers & Liefers, 2012; Kappers & Viergever, 2006). In addition, some of these spatial distortions have been found to be related to the use of different reference frames (e.g. body-, head- or hand-centered deviations) in the coding of movement (Cohen & Andersen, 2002; Dupin et al., 2018; Ghafouri & Lestienne, 2005) or somatosensory information (Ho & Spence, 2007; Pritchett et al., 2012). Altogether, this suggests a

strong dependence between body position and perception and action, as well as the presence of distortions in spatial body representations.

This disparity between the physical hand and its spatial representation raises (at least) two key questions: first, what factors affect spatial body representation? And, second, are the discrepancies observed with respect to the body (the hand) similar to those seen for external space **and consequently for object representation?** Moreover, the origin and cause of these discrepancies between spatial body representation and physical body configuration have generated growing interest, particularly regarding the potential link with sensorimotor functions, e.g. movement planning, proprioception or spatial perception (Caggiano & Cocchini, 2020; Medina & Coslett, 2016; Peviani & Bottini, 2018, 2020). Indeed, Aristotle's illusion accounts for a functional role of the discrepancies between body configuration and its representation (Benedetti, 1988): **the** hand representation for tactile spatial perception does not take into account the (highly unusual) crossing of two fingers. **In Aristotle's illusion, an object positioned into the cleft of the crossed index and middle finger is perceived, without vision, as two objects rather than one, when in contact with the uncrossed fingers.** Overall, even if different spatial representations are associated to specific functions (like body representation, motor or perceptual function), it is likely that these specific representations also share some of their spatial characteristics since their functions are not fully independent from each other (Peviani & Bottini, 2018).

In order to understand the origin of the discrepancies between spatial body representation and the physical spatial characteristics of the body, a first step is to identify what factors can affect these representations. Here, we focus on the spatial representation of the hand since most of our interactions with the external world are accomplished through (skilled) hand movements. Information concerning the localization of the fingers in space and their relative location is indeed necessary to produce dexterous movements, such as grasping an object (Butler et al., 2019; van Duinen & Gandevia, 2011), but also to identify object shape through touch (Yau et al., 2016). **This study aims to identify quantitative aspects of different factors that could affect spatial hand representation potentially related to sensory and motor functions. We first investigated here the effects of ageing. Age is known to affect motor and sensory functions (Carp et al., 2011; Heft & Robinson, 2017; Isokoski & Springare, 2012; Kuehn et al.,**

2018; Rossini et al., 1992; Ruitenberg et al., 2019) as well as spatial object representation not related to the body (Lepelley et al., 2010). We thus hypothesized that age would affect the spatial representation of the hand. We further investigated the effect of daily activities and of light touch sensitivity on the metrics of hand representations.

In the present study, we investigated the spatial characteristics of hand representation in 60 healthy participants from 20 to 79 years of age, divided into 3 groups of age (20-39, 40-59 and 60-79 yrs). We tested two types of hand representations: the first representation assessed in this study was of implicit nature and indirect using the localization of tactile stimulation. Indeed, since the skin follows any configuration of the body (Mancini et al., 2011), tactile stimuli are a good candidate for identifying common characteristics of body representations. Furthermore, tactile localization is closely linked to motor function (Cataldo et al., 2021; Dupin & Haggard, 2019; Dupin et al., 2015). The second spatial representation we tested here was based on explicit information based on verbal instructions. This mode of target instruction resides on declarative information (Squire & Dede, 2015) and relies on conceptual knowledge (memory) of the physical structure of the hand (Longo, 2015). This condition also served as a control, since it was used in previous studies (Ingram et al., 2019; Longo, 2015; Longo & Haggard, 2010).

To assess body representations, participants with eyes closed had to point with one hand to different locations (nail or metacarpophalangeal joint of each finger) of the other resting hand. Pointing was accomplished by using a stylus pen on a graphic tablet (see Figure 1A, B). The experimenter indicated the target location either verbally (VERBAL condition) or by a tactile cue on the target location (TACTILE condition). We excluded vision from all our assessments since even non-informative vision can modify tactile localization (Eads et al., 2015). Furthermore, vision also acts on position sense by providing a visual reference frame and/or conceptual knowledge of hand characteristics (Longo, 2015). Thus, contrary to previous studies, our tasks were performed in absence of vision. The order of the targets to be localized was randomized to ensure that no reference induced by the experimental procedure (visual or other) would bias perception.

We then assessed whether the distortions observed were specific to parts of the body or whether distortions also affected the representation of external space. We hypothesized that if hand distortions are due to external space distortion, they would equally affect the spatial representation of objects and of the hand. We assessed the spatial representation of a commonly used object by asking participants to point successively to the 4 corners of a standard card (i.e., credit card, CARD condition), imagined to be positioned on the tablet. The task of the participant was to reproduce the size of the card by indicating the imagined position of the 4 corners using the stylus pen. The resulting card size was assessed with eyes closed and eyes open in order to quantify their dissimilarities. The eyes open condition aimed to assess (and control) what the participant thought to be a credit card size, with visual feedback of the movement while pointing the corners of the imagined card. We compared the resulting distortions of this object (card) representation with those of the body (hand).

Materials and Methods

We report how we determined our sample size, all data exclusions (if any), all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study.

1. Participants

Sixty participants took part in the experiment. All participants provided their written informed consent before testing. The experimental protocol was approved by the ethics committee (Comité de Protection des Personnes, 2017-A01875-48) and adhered to the ethical standards of the Declaration of Helsinki. Healthy participants were divided into 3 age groups (n=20 each): 20-39, 40-59 and 60-79 years, respectively. In each group half of the participants was females and the other males. Inclusion criteria: no hand motor deficit due to local trauma or central neurological disease, no disease potentially affecting sensory functions (such as diabetes), no psychiatric disorder. Participants were compensated with 20€ for their participation and the experiment lasted approximately 1h30. No part of the study procedures or analyses was pre-registered prior to the research being conducted.

2. Description of the groups

The sample size for the 3 age groups (n=20 each) was computed based on pilot data (difference between 20-40 and 60-80 year old subjects, power=0.8, alpha=0.05). Subject characteristics are detailed in Table 1.

	20-39 yrs. (N=20)	40-59 yrs. (N=20)	60-79 yrs. (N=20)
Mean age (yrs. \pm SD)	30 \pm 6.3	50.15 \pm 5.69	69.9 \pm 6.23
Laterality	17 RH, 2LH, 1A	18 RH, 2LH	17RH, 2LH, 1A
Computer use (hours/week)	30.5 \pm 21.20	23.75 \pm 11.47	23.53 \pm 17.92
Music instrument (hours/week)	1.05 \pm 3.43	0.15 \pm 0.49	0.35 \pm 1.09
Light touch detection threshold (in g)	0.11 \pm 0.14	0.20 \pm 0.16	0.33 \pm 0.28

Table 1: Subject characteristics for the three age groups. Age, laterality (short form of Edinburg handedness inventory; (Oldfield, 1971), daily manual activities, and light touch detection threshold (Weinstein, 1993). RH, LH, A: right-, left-handed or ambidextrous.

3. Apparatus

The device consisted of a graphic tablet (HUON WH1409) connected to a PC through USB. The graphic tablet was mounted on a support by means of two slides so that the tablet could slide away from the target hand in order to locate the physical position of the target (resting) hand and fingers. The software used to record data was developed in C++.

4. Procedure/Tasks

4.1. Main task

Participants sat on a chair with armrest. The armrest of the target hand was aligned with the centre of the device so that the target hand was positioned in the axis of the shoulder (Figure 1). The target hand was placed in the device (under the graphic tablet), palm down with the fingers abducted. The experimenter ensured that the position was sufficiently comfortable for the participant to maintain this

resting position without effort. Participants were instructed to keep the target hand relaxed during all testing conditions. After the target hand was positioned, measures of the first PHYSICAL condition were obtained.

4.2. Conditions

Five conditions were tested for each hand: 3 conditions (PHYSICAL, TACTILE, VERBAL) concerned the measure of the hand **and its** representation. Two further conditions involved (CARD-no vision, CARD-vision) the representation of an object in external space as control. The design of the experiment is illustrated in supplementary Figure S1. Hand and finger position was recorded based on 10 *target positions* on each hand: the position of the nail and of the metacarpophalangeal (MCP) joint of each finger.

4.2.1. PHYSICAL condition: real spatial hand configuration

Aim: to record the physical position of the 10 targets defining the hand and fingers. To record a given target, the graphic tablet was slid away from the hand so that the hand was visible. A laser pointer was positioned vertically pointing directly to the target to be measured. Then the tablet was moved to the closed position and the luminous point of the laser was recorded using the stylus pen of the graphic tablet. Each target was recorded once. In order to take into account possible involuntary movements of the target hand the PHYSICAL target points were measured at the beginning and at the end of the testing of each hand.

4.2.2. TACTILE condition: implicit representation of the hand based on touch

Aim: to assess the spatial representation of the hand based on tactile stimuli. The participant kept the eyes closed during the entire condition. In a given trial, the experimenter touched the participant at one of the 10 possible targets using a **pencil**. The participant had to position the stylus pen directly above the perceived tactile stimulation. **The tactile stimulation consisted in a continuous steady pressure applied to one target by the experimenter by the means of pencil padded with rubber at its end. The tactile stimulation lasted until the participant validated his/her response.** The order of the targets was randomized and each of the 10 targets was repeated 3 times (30 trials for each hand).

4.2.3. Representation of the hand based on VERBAL instruction

Aim: to measure the representation of the hand based on verbal instruction. This measure has been previously used for assessing spatial hand representations (Longo & Haggard, 2010). Here, the experimenter indicated the target verbally for each trial: nail or MCP joint for a given finger (for example: “joint of the index finger”, in French in the experiment).

For each participant, the VERBAL and TACTILE conditions were presented in a random order but this order was the same for the two hands of a given participant. No feedback of task performance (pointing error) was provided.

4.2.4. CARD-no vision and CARD-vision conditions

The two control conditions CARD-no vision and CARD-vision were presented in this order after TACTILE and VERBAL. The two tasks were similar except that CARD-no vision was done with eyes closed and CARD-vision with eyes open. In none of the conditions was the card physically present.

In these two conditions participants had to point with the stylus pen successively to the 4 corners of the imagined card, virtually located on the graphic tablet directly above the dorsum of the target hand. The card was of standard format (i.e. payment card, ISO/IEC 7810 ID-1, 85.6 x 53.98 mm) and participants were instructed to reproduce the size and the shape of this imagined card. Before the CARD no vision condition, the experimenter verbally checked that the participant knew this type of card (all participants acquiesced) and a standard card was shown to the participants for approximately 5 sec. During the task, the participant successively pointed to each corner of the imagined card. This was repeated 3 times.

4.3. Questionnaire regarding daily ‘dexterous’ activities

Before the main task, participants were asked to fill an online questionnaire about their weekly use of a computer and weekly practice of a music instrument involving dexterity (e.g. piano, guitar). Mean weekly number of hours (\pm SD) of computer use or music instrument practice are detailed in Table 1.

4.4. Tactile sensitivity

Light touch sensitivity of the fingertips was assessed using Semmes-Weinstein monofilaments (Weinstein, 1993). For each participant the mean of the threshold of the 10 fingers (from both hands) in

grams was computed. The data are detailed in Table 1 and correspond to the mean over all participants of each age group (in grams).

5. Data Analysis

We used average hand width and finger length representations as main measures, since both were **doi** affected differently in previous studies (Longo & Haggard, 2010; Van der Looven et al., 2021). Data analyses were computed using Wolfram Mathematica 11.3 and IBM SPSS 23. **Study data and code** are available at <https://doi.org/10.17632/n8xyxwswf2.1>

5.1. Finger length

To determine mean finger length, the individual length of each finger (from MCP to its nail) was computed and averaged over the 5 fingers.

5.2. Hand width

Hand width was determined as the sum of the four successive distances between the MCP joints from finger I to V.

5.3. Hand width, finger length and card extents in all conditions

Table 2 presents the spatial representation (hand width and finger length) in all three **conditions as well as card width and length in the two conditions (vision/no vision)** of each age group.

	Age group	PHYSICAL	TACTILE	VERBAL	CARD Vision	CARD No vision
Mean width (cm \pm SD)	20-39 yrs.	11.60 \pm 0.91	11.95 \pm 2.36	12.49 \pm 2.85	7.76 \pm 0.84	6.24 \pm 1.22
	40-59 yrs.	11.53 \pm 0.98	10.74 \pm 2.35	11.82 \pm 3.31	7.55 \pm 1.38	6.54 \pm 1.81
	60-79 yrs.	11.46 \pm 0.89	9.32 \pm 1.40	9.88 \pm 1.79	7.86 \pm 1.23	6.20 \pm 1.61
	Mean	11.53 \pm 0.91	10.66 \pm 2.32	11.40 \pm 2.90	7.72 \pm 1.15	6.32 \pm 1.55
Mean length	20-39 yrs.	7.85 \pm 0.48	5.87 \pm 1.22	5.44 \pm 1.51	4.75 \pm 2.85	4.38 \pm 0.88
	40-59 yrs.	7.93 \pm 0.63	5.69 \pm 1.51	5.22 \pm 1.69	4.69 \pm 0.80	4.49 \pm 1.02

60-79 yrs.	7.89 ± 0.46	5.29 ± 1.27	5.02 ± 1.47	4.5 ± 0.64	4.06 ± 1.13
Mean	7.89 ± 0.52	5.61 ± 1.34	5.23 ± 1.54	4.65 ± 0.78	4.31 ± 1.01

Table 2: Averaged hand width and finger length for each age group in the three conditions (PHYSICAL, TACTILE, VERBAL) and card width and card length (in the two conditions CARD-vision and CARD-No vision). All values in cm. Hand measures averaged between the left and right hand of each subject.

5.4. Measures of response variability

The variability of responses was assessed across the 3 repeated measures for a given target. The area of the triangle consisting of the 3 repetitions for one given target was computed. The variability (or precision) measure was then calculated as the average area over all 10 targets for one subject.

5.5. Data normalization

Finger length and hand width in tactile and verbal conditions were normalized over (divided by) physical hand length and width, respectively. Then the lengths of the left and right hand were averaged.

For hand width, for one individual, and each hand, the distance between each MCP joint in TACTILE and VERBAL condition was divided by the respective distance in PHYSICAL condition. Then the widths of the left and right hand were averaged.

For the CARD condition: card representations obtained by each hand were averaged across the left and right hand. Data were normalized and expressed as ratios of width or length of CARD-No Vision relative to (divided by) CARD-Vision. Due to potential anisotropy in cardinal directions of space (and since hand width and finger length showed different properties) we compared card width and length separately.

5.5.1. Data normality

The normality of the data was tested using the Shapiro-Wilk test. Several datasets were not normally distributed (normalized hand width in tactile ($p=0.040$) and verbal conditions ($p=0.026$), normalized dominant hand width ($p=0.02$) and length ($p=0.36$) in tactile condition, normalized finger length ($p=0.023$) in verbal condition, length of the card ($p=0.004$), non-normalized finger length of left hand

in tactile condition ($p=0.025$)). For this reason, we used non-parametric statistical tests: Wilcoxon signed rank test for comparison and Kruskal-Wallis test for groups or factor effects analyses. Effect size r_e was computed for significant Wilcoxon signed rank test as $r_e = Z/\sqrt{N}$ and as η^2 for Kruskal-Wallis analyses (Rosenthal, 1994). Dunn's post-hoc p-values were adjusted by the Benjamini-Hochberg FDR method. 95% confidence interval computations were based on 1000 bootstraps.

5.5.2. Correlations and corrections

For the different correlations, we used Pearson correlations, except for cases without strong evidence for a linear relation, such as between sensitivity and spatial hand representation where we used Spearman Rho. All correlations were Bonferroni corrected for multiple comparisons. The threshold resulting from this correction is indicated after the p value of each test.

Results

We used individual hand width and finger length as main measures to quantify the spatial properties of tactile and verbal hand and finger representations and their changes with age. We also explored their potential relation to spatial object (rather than body) representations. 95% confidence intervals (CIs) are indicated in brackets after corresponding median values.

Normalized measures used in the Results section correspond to the dimension of the representation divided by the corresponding physical dimension. Thus, a normalized value of 1 indicates identical size of the representation and the physical size. Values <1 indicate a representation smaller than the physical size, and vice versa for values >1 . Normalization thus avoids any effect of individual differences in physical hand size on the dimensions of the spatial representation.

1. Properties of **implicitly-instructed** hand representation (TACTILE condition)

1.1. Tactile spatial representation versus physical hand dimension

Across all participants, the spatial hand representation obtained by tactile stimulation was significantly smaller (and more variable) than the physical dimension of the hand (Figure 2A). This was true for both finger length and hand width, and for both the right hand (median right length PHYSICAL: 7.85cm

[7.71–8.14] vs. length TACTILE: 5.65 cm [5.49–6.07], $Z=-6.434$, $p<0.0001$, $r_e=0.59$; right width PHYSICAL: 11.46cm [11.22–11.84] vs. width TACTILE: 10.71cm [CI 10.16–11.60], $Z=-2.893$, $p=0.004$, $r_e=0.21$, Wilcoxon signed-rank test) and the left hand (left length PHYSICAL: 7.80cm [7.71–8.12] vs. length TACTILE: 5.33cm [5.02–5.90], $Z=-6.427$, $p<0.0001$; left width PHYSICAL: 11.41cm [11.04–11.71] vs. width TACTILE: 10.32cm [9.43–11.29], $Z=-2.694$, $p=0.007$, $r_e=0.25$, Wilcoxon signed-rank test).

In order to identify any differences between the left and right tactile hand representations, we correlated the two. The spatial dimensions of the left and right hand were strongly correlated, for finger length (Pearson $r=0.59$, $p<0.00001$) and for hand width ($r=0.71$, $p<0.00001$, Figure 2B). Left and right representations were not significantly different (finger length: $Z=-0.567$, $p=0.57$; hand width: $Z=-0.648$, $p=0.52$, Wilcoxon signed-rank test), indicating that any individual bias (namely, underestimation of the size) in tactile hand representation is shared between the two hands.

Similarly, when comparing the width and length of the dominant to the non-dominant hand, we found no difference in hand width (dominant: 10.83cm [16–11.71] vs. non-dominant: 10.22cm [9.47–11.09], $Z=-0.995$, $p=0.320$ Wilcoxon signed rank test) or finger length (dominant: 5.60cm [5.45–6.08] vs. non-dominant: 5.51cm [5.07–5.85], $Z=-0.159$, $p=0.874$ Wilcoxon signed rank test), respectively (two ambidextrous subjects excluded).

Since finger length was highly correlated, and did not differ between the left and right hands, in subsequent analyses we averaged this measure across the two hands of a given subject. This was also done for hand width. Thus, normalized values provide a direct measure of the discrepancies between tactile or verbal hand representation and the physical dimension of the hand.

1.2. Comparison between hand width and finger length discrepancies (TACTILE)

Normalized tactile hand width (median width TACTILE: 0.98 [0.90–1.05]) and finger length (median length TACTILE 0.70 [0.67–0.75]) of spatial representations were strongly correlated (Pearson $r=0.63$, $p<0.00001$, see Supplementary Figure S2) but significantly different ($Z=-6.5$, $p<0.0001$, $r_e=0.59$, Wilcoxon signed-rank test), indicating that the underestimation in length and width share a common

factor, while the difference (smaller length) indicates the existence of an additional factor affecting hand width and finger length differently.

2. Properties of hand representation based on VERBAL instructions

2.1. Verbal spatial representation versus physical hand dimensions

In the verbal condition, the normalized mean finger length across participants was significantly lower than 1 (median=0.64 [0.59–0.72], $Z=-6.212$, $p<0.001$, $r_e=0.57$, Wilcoxon signed-rank test), indicating a smaller (shranked) representation of finger length compared to the physical hand. However, the normalized hand width representation in the verbal condition was not significantly different from 1 (median=1.09 [1.01–1.15], $Z=-1.804$, $p=0.071$, Wilcoxon sign rank test). **Data comparison between the two hands and physical hand size are illustrated in Figure S3.**

2.2. Comparison between hand representations based on tactile vs. verbal instructions

The reduction of normalized finger length in the verbal condition was significantly greater ($Z=-2.326$, $p<0.02$, $r_e=0.21$, Wilcoxon sign rank test) than that in the tactile condition. The finger length representation in the verbal condition strongly correlated to finger length in the tactile condition (Pearson $r=0.70$, $p<0.0001$).

The normalized hand width was significantly greater in the verbal compared to the tactile condition ($Z=-4.314$, $p<0.001$, $r_e=0.39$, Wilcoxon signed-rank test), but strongly correlated with that in the tactile condition (Pearson $r=0.69$, $p<0.0001$) suggesting a partly common processing **of explicitly instructed (verbal) and implicitly instructed (tactile) representations.**

3. Factors potentially affecting tactile and verbal hand representations

3.1 Effect of age

The tactile representations of hand width and finger length varied with age (Figure 3A, B). There was a significant effect of age on hand width (width TACTILE $H(2)=10.909$, $p=0.004$, $\eta^2=0.16$, Kruskal-Wallis), but not on finger length (length TACTILE $H(2)=1.853$, $p=0.396$). Dunn's post-hoc analyses on hand width showed a significant difference between the younger (median=1.06 [0.98–1.15]) and the

older group (0.89 [CI 0.79–0.92], $p=0.003$) indicating that hand width representation becomes smaller with increasing age (Figure 4A). Based on confidence intervals, while tactile width was not significantly different from physical hand width for the two age groups 20-39 years and 40-59 years, it was significantly smaller for the oldest group. In contrast, finger length was smaller than physical finger length in all age groups.

Given that hand width and finger length were normalized to physical hand size, we controlled for any age-related changes in real hand size (Figure 3B). However, the physical size of the hand did not change with age, for either hand width ($H(2)=0.001$, $p=1.0$) or finger length ($H(2)=0.488$, $p=0.783$, Kruskal-Wallis), confirming that the effect of age on tactile spatial hand representation is not related to changes in physical hand size.

The hand representation based on verbal instruction varied with age for hand width (width VERBAL $H(2)=10.201$, $p=0.006$, $\eta^2=0.14$) but not for finger length (length VERBAL $H(2)=0.857$, $p=0.652$). Dunn's post-hoc comparisons showed a difference of hand width related to age between the younger (median=1.18 [1.02–1.37]) and older group (0.95 [0.86–1.04], $p=0.008$, Figure 4B), similarly to what has been found under the tactile condition. Using confidence intervals, hand width based on verbal instructions was significantly larger than that of the physical hand for the two age groups of 20-39 and 40-59 years, but not for the 60-79 years group. In contrast, finger length was smaller than physical finger length in all age groups.

Finally, the effects of age on the size of the hand representation may reflect a genuine alteration of cerebral spatial representations; one clue in support of this idea would be an increase in response variability with age. However, precision (i.e., variability) in the tactile (mean in cm² (SD) 20-39 years: 2.1(0.8), 40-59 years: 1.62(0.73), 60-79 years: 1.72(0.78)) and verbal (20-39 years: 1.4(0.6), 40-59 years: 1.79(0.78), 60-79 years: 1.85(1.13)) conditions were not significantly affected by age (respectively $H(2)=3.933$, $p=0.14$ and $H(2)=0.507$, $p=0.77$, Kruskal-Wallis). Moreover, variability measures significantly, albeit weakly, correlated between tactile and verbal conditions (Pearson $r=0.29$, $p=0.023$).

3.2 Effects of tactile sensitivity

We analyzed whether normalized hand width and finger length obtained in the tactile and verbal conditions correlated with the degree of light touch sensitivity. Although non-significant, we found a similar negative trend for the effect of touch sensitivity on hand width in both TACTILE (Spearman $\rho=-0.28$, $p=0.032$ Bonferroni corrected p threshold $=0.017$ for three comparisons) and VERBAL conditions (Spearman $\rho=-0.27$, $p=0.034$ Bonferroni corrected p threshold $=0.017$ for three comparisons), indicating that the higher the sensitivity threshold, the smaller the hand width. There was no significant correlation with finger length (all $p>0.39$), but higher touch sensitivity threshold correlated with increasing age ($\rho=0.55$, $p<0.0001$, Bonferroni corrected p threshold $=0.017$).

3.3. Effect of dexterous daily activities

We found no significant correlation of hand width or finger length with daily computer use or other dexterous activities (all $|r| < 0.17$, $p>0.18$; see Methods for details). This held for both tactile and verbal hand representations.

3.4. Effect of sex

The physical size of the hand (length and width) was different between male and female (all $Z<-4.332$, $p<0.0001$ $r_e>0.40$, Wilcoxon signed-rank test). However, we found no effect of sex on distortions of hand representations in both TACTILE (all $Z>-0.68$, $p>0.496$, Wilcoxon signed-rank test) and VERBAL conditions (all $Z>-0.887$, $p>0.375$, Wilcoxon signed-rank test).

4. Comparison of spatial hand and object representations

4.1. Properties of object representations (external space) vs. body representations

In order to investigate whether the observed changes in spatial hand representation with age were specific to body representation, we also assessed the properties of object (i.e. non-body) representations. For this, participants had to point to the corners of an imagined object (credit card). Mean card shapes obtained for pointing with the left and right hand are illustrated in Figure 5A. Card distortions for CARD no-vision and CARD-vision are independently illustrated in Figure S4. Individualized distortion of card

length representation was computed as the ratio between card length without vision and card length with eyes open, and similarly for card width.

Across participants, distortions of card length and width were both significantly smaller than 1 (median length 0.90 [0.85–0.94], $Z=-2.966$, $p=0.003$, $r_e=0.27$; median width 0.83 [0.76–0.87], $Z=-5.706$, $p<0.001$, $r_e=0.52$; Wilcoxon signed-rank test), indicating that the distortions applies to both body and objects. Distortions of card length and width were significantly different ($Z=-4.91$, $p<0.0001$, $r_e=0.45$, Wilcoxon signed-rank test) but strongly correlated (Pearson $r=0.70$, $p<0.0001$, Bonferroni corrected p threshold =0.017).

In order to explore the similarity between hands and object representations, we correlated the size of the card dimensions with those of the hand, i.e. with hand width and finger length in the TACTILE condition (Figure 5B). Card width shrinking correlated significantly with both hand width shrinking (Pearson $r=0.42$, $p=0.001$, Bonferroni corrected p threshold =0.017; Figure 5B) and finger length shrinking of their representations (Pearson $r=0.41$, $p=0.001$, Bonferroni corrected p threshold =0.017). However, card length did not correlate with either hand width or finger length (all Pearson $r<0.13$, $p>0.30$).

Hand width and finger length of the hand representation in VERBAL condition significantly correlated with normalized card width (Pearson $r=0.59$, $p<0.0001$ and $r=0.37$, $p<0.0001$, respectively, Bonferroni corrected p threshold =0.017). Card length also correlated with finger length (Pearson $r=0.36$, $p=0.005$) but not with hand width ($r=0.15$, $p=0.25$).

These results suggest that hand width is partially related to spatial distortions that are not specific to the body.

4.2. Effects of age on dimensions of object representation

We also investigated potential age effects on spatial object (card) representation (Figure 4C). No significant effect of age group on card length ($H(2) = 1.537$, $p = 0.464$, Kruskal-Wallis) was found, suggesting that the observed age effect on the reduction of hand representation is specific to the body (but not to the object) representation. Age did not affect card width either ($H(2) = 2.178$, $p = 0.337$).

Finally, the extent of card width and length with or without vision (non-normalized) did not correlate with age (all $|r| < 0.15$, $p > 0.27$).

Discussion

In this study, we aimed to identify the factors that affect the spatial representation of the hand, focusing on age effects. Since tactile perception, movement and spatial perception are functionally related, we designed an experimental paradigm that linked these three domains, and used the localisation (pointing to the sites) of tactile stimulation or verbal cues (all with eyes closed) to assess spatial body (hand) representation. We found that hand representations showed clear deviations from physical hand size: finger length and hand width were smaller than those of the real hand. This underestimation or shrinking was invariant for the representations of the left or right hand (distortions strongly correlated), suggesting that common factors operate in the spatial representation of the two hands. This also suggests that hand dominance does not influence hand representation. Indeed fMRI studies showed that digit representation in primary somatosensory cortex does not differ between the left and right side (Schweissfurth et al., 2018). The size (width) of spatial hand representation decreased as age increased and this was not observed for object representation. Finally, spatial properties of object representation were also partially shared with spatial hand representation characteristics.

Distortion of body-related spatial representations (i.e., of the hand)

Representations of hand length and finger width showed partly similar distortions (shrinkage), as shown by the correlation between these two measures. However, an unknown additional factor appeared to affect hand width differently from finger length representations, since the latter was more affected than the former. This difference may be related to a potential anisotropic effect of hand position relative to the body: a radial metric such as finger length may be affected differently compared to hand width (a tangential metric). Indeed, the distortions affecting card perception also showed differences between width and length, although these differences departed from those of the hand (namely, card length distortions did not correlate with hand distortions, while card width correlated with hand width and finger length). Controlling for hand position would help to understand if the additional factor depends on the orientation of the hand in space or if it is genuine to the representation. Also, no such anisotropic

effect was found in a previous study (using a different paradigm) when the hand was positioned in rotated positions (Ingram et al., 2019; Longo & Haggard, 2010; Saulton et al., 2015). However, this is reminiscent of the reported veridical estimation of tactile distance on the dorsum of the hand, with an underestimation of distance in the radial axis (Longo, Mancini, et al., 2015). Such a general width/length difference is consistent with the observed differences found in other studies with respect to hand width, but not finger length (Longo & Haggard, 2010; Longo, Mancini, et al., 2015).

Comparing hand representation based on tactile stimuli vs. verbal instructions, we found a smaller hand width in the tactile than in the verbal condition, but conversely for finger length (**longer** in tactile vs. verbal condition). **Even though these deviations shared some properties (as shown by their correlations), it is clear that the two types of instructions involved different processes: (i) since tactile stimulation lasted during the trial, memory related to the stimulation was not involved in that condition, while in the verbal condition, long term language-based conceptual memory was involved; (ii) furthermore, the difference observed here between tactile and verbal hand representations may be related to indirect (tactile) vs. explicit memory (knowledge) of hand configuration. Only the latter is likely to use general conceptual information about hand structure (Saulton et al., 2017, 2016) and could explain the difference in body representations obtained through verbal or tactile instructions. Indeed, the fact that distortions of body representation varied in magnitude as a function of the instruction (but different from those of the current study) has been previously found (Ingram et al., 2019; Mattioni & Longo, 2014).**

We found that hand **width** was underestimated, i.e. was smaller than the size of the physical hand in the tactile condition. However, in the verbal condition, **hand width was not significantly different from the physical hand width**. Both results are different from what was found in several previous studies on hand representation which reported a systematic overestimation of hand width (Longo & Haggard, 2010; Mancini et al., 2011; Peviani & Bottini, 2020; Tamè et al., 2017). **The difference between previous and our studies concerning the overestimation of hand width** is likely due to methodological dissimilarities (e.g. age of participants, conditions including vision). Our findings show that the size of the hand representation depends on age. Elder participants tended to have smaller representations, and younger to have larger representations, as compared to their physical hand (particularly for hand width). Thus,

in our study the younger group had a normalized hand width significantly greater than 1 in the verbal condition, indicating an overestimation. In some studies participants were about 18-76 years of age (Longo & Haggard, 2010; Mancini et al., 2011), but since the mean age was not available, a potential age effect cannot be ascertained. In other studies (Peviani et al., 2020; Tamè et al., 2017), however, the mean age was lower than 30 and this may therefore in part explain hand width overestimation. Furthermore, in these previous studies, the assessed hand was hidden from view but participants had eyes open. Finally, the use of visual information in previous studies compared to ours could also have affected the participants' responses. Given vision, the external landmarks covering the hand may have been used in addition to participants' beliefs of the hand configuration. However, this seems unlikely since the overestimation was still found even when instruction target participants' beliefs (Tamè et al., 2017).

Distortion of spatial object (non-body-related) representations

We investigated whether some properties of the spatial representation of the body would differ from those of an object. This internal – external difference in spatial representation may account for some of the results. We found that the spatial representation of an imagined rectangle (credit card size) with eyes closed was smaller than that with eyes open, although in both conditions the card was imagined (virtual). However, this reduction did not correlate with age (but it did with hand size), suggesting that the reduction in hand size as a function of age is specific to body representation, and does not apply to external objects. However, an indirect relation between internal and external space may exist, as suggested by the fact that the distortion in object representation (particularly with card width) correlated with that of the hand (both width and finger length). Since the spatial configuration of the hand and the card differed in their complexity and structure, the factor underlying this common distortion cannot rely on their respective shape as found in previous studies (Saulton et al., 2015, 2016), but is likely to reflect a more general spatial distortion.

Furthermore, there was a task-specific constraint between pointing to the hand and pointing to the card: the successive and systematic pointing from one corner to the next of the card allowed for estimation of distance (length) between the target points. In the hand task, in contrast, the random order of assignment

to different target points of the hand did not allow for estimation of distances, whether in terms of hand width or finger length. Therefore, the decrease in card size with eyes closed may be due to two distinct misestimations, firstly due to a general distortion of spatial metrics, and secondly to an interaction between representations of body space (internal, without distance cues) and object space (external, with distance cues). Since card size underestimation with eyes closed correlated with hand representation distortion, we can exclude that this common distortion is due to underestimation of distance based on estimated movement extent. The fact that the hand and object representations showed similar distortions suggests that the representation of the body is compatible and consistent with the representation of action (control of movement) in peripersonal space. Indeed, a previous study has found that objects that convey an action (as holding it), show distortions related to those of the hand (Peviani et al., 2021).

Finally, the hand representation task using verbal instruction is more comparable to the card corner pointing task, since these two tasks did not rely on continuous tactile stimulation but on structural/conceptual memory and/or spatial mental imagery of the hand or the card. In particular, card length correlated with finger length in the verbal condition and could reflect conceptual distortions (Longo, Mattioni, et al., 2015; Saulton et al., 2017, 2016), as previously found specifically for the conceptual knowledge of finger length (Longo, 2015). However, hand representation obtained through tactile stimulations showed similar correlations with card distortions as those obtained with verbal instructions. Since tasks were different (distance estimation vs. localization) and the physical shape of the card and hand were clearly dissimilar, this common bias in the distortions may reflect an idiosyncratic general distortion of space that might affect localization and distance regardless of the target (object or body part). In particular, this common bias may be related to the pointing task used in all conditions and may reflect a distortion of motor space. However, a motor bias cannot account for a general hand distortion effect (Longo, 2018).

Effect of age

We found that the representation of hand width decreased with age, and this was independent of the physical width of the hand. But, as expected (McIntyre et al., 2021; Stevens et al., 2003), touch sensitivity also decreased with age. However, the age-related reduction in hand representation only

showed a non-significant trend for correlation with touch sensitivity. Thus, age-related decrease of tactile sensitivity cannot account for age-related reduction of the hand representation. Furthermore, no correlation was observed between decrease of hand representation and amount of daily dexterous activities. Although the cause of this age-related reduction remains unclear, we may tentatively point to other factors, not addressed in our study, such as deterioration in tactile spatial resolution (two-points discrimination) or spatial accuracy of movement. The reported underestimation in movement extent during ellipse drawing under visual control in older adults is consistent with a compression of the representation of external space (Ghafouri & Lestienne, 2000). Task differences (with / without vision) may explain why we found an age-related compression in the representation of the body but not in external space (card size). However, in our study, the analysis of non-normalized card size, which might reflect the shrinking related to a motor command in both conditions with and without vision, showed no age-related effect.

Finally, the shrinking of the hand representation might reflect something different from functional alterations related to age. Furthermore, recent studies showed that distortions of body representation evolve from childhood on: first, hand size is underestimated (but not object size) using visual or haptic matching tasks. Then, hand size increases during childhood between 6-10 years (Cardinali et al., 2019). Moreover, based on verbal instructions, finger length underestimation was found to increase with age and from childhood (Van der Looven et al., 2021), consistent with our finding that finger length representation was already smaller in adulthood. However, this previous study (Van der Looven et al., 2021) found no shrinking of hand width: to the contrary, they reported an overestimation of hand width similar to our results for the two younger age groups in verbal condition. This difference may suggest that both width and length of hand representation decrease with age, each with a different time course. This would further suggest that the shrinking of the hand representation (width and length) may occur during the entire life span, and may indicate more general and use-dependant modifications of body representation (e.g. functional optimization) not specifically related to age-related functional decline.

Conclusions

In conclusion, we used an indirect method based on the localization of tactile stimuli without visual feedback in order to quantify the spatial representation of the hand. We found that the spatial representations differed from the physical dimensions of the hand. These spatial distortions of the representation were shared between the left and right hand. The width of the hand representation decreased with age, which was not linked to age-related decline in sensory functions (tactile sensitivity). In contrast, no age effect was found on spatial object representation, suggesting that compression of the body representation occurred independently from general (external) spatial distortions. Furthermore, some distortions of external (object) space shared characteristics with implicitly- (tactile) and explicitly-instructed (verbal) body representations, implying that despite some specific dissimilarities, different spatial body and object representations share, at least in part, a common cerebral substrate.

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Conflict of interests

The authors declare that they have no competing interests.

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Artwork and Tables

Figure 1

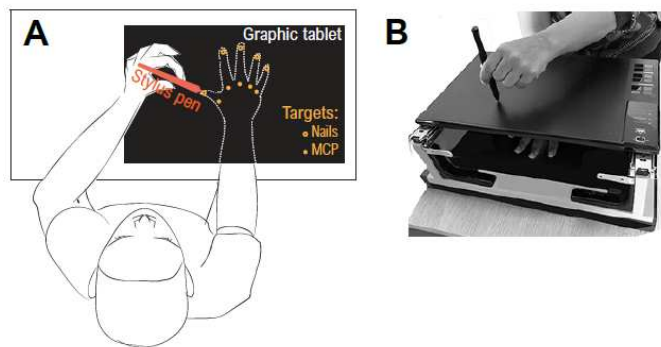


Figure 2

Figure 1: A. Schematic top-view of the set-up. The subject points with the left hand to the target position on the right hand, indicated either by tactile stimulation or by verbal instruction. B. Tablet device: the participant points with a stylus pen on the graphic tablet to the perceived position of a stimulated (or instructed) target on the hand below the tablet.

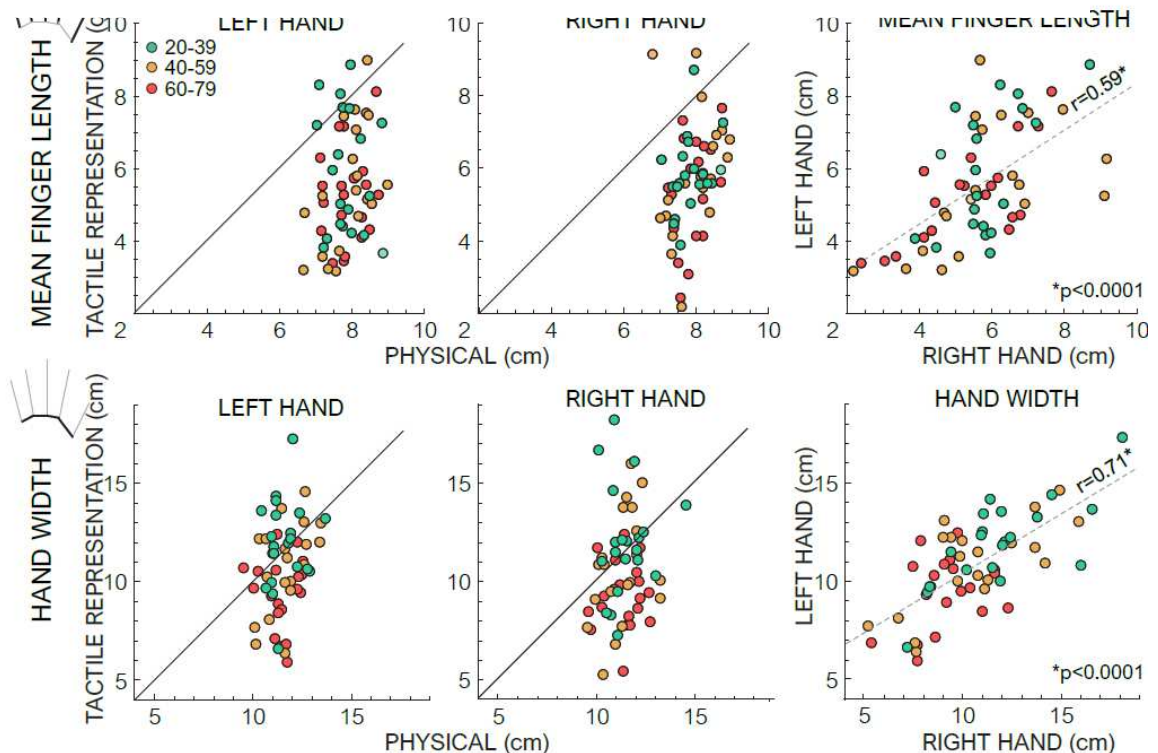


Figure 2: A. Finger length (top) and hand width (bottom) of left and right hands in TACTILE vs. PHYSICAL conditions. Each circle corresponds to a participant and colors represent age groups. Diagonal lines: identity line (dimension of representation equals dimension of the physical hand). Note: the variability between individuals is greater in the representation compared to the physical hand. B. Correlation between right and left finger length (top) and hand width (bottom) in TACTILE condition. Stippled line: regression line.

Figure 3

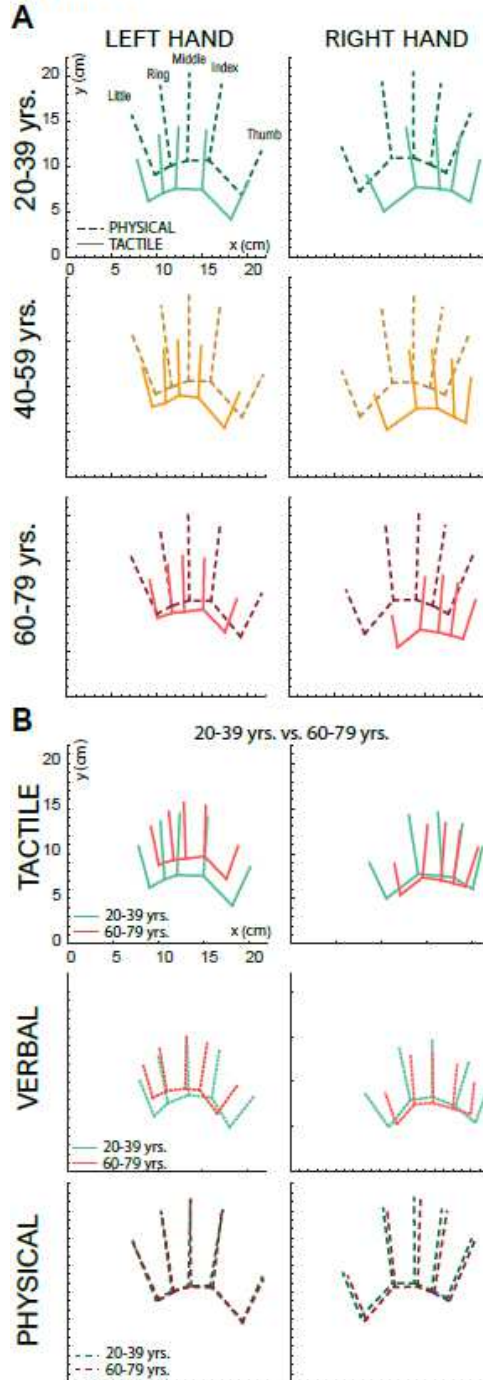


Figure 3: A: Comparison for each age group and each hand of the PHYSICAL hand (dashed lines) and TACTILE (solid line) in the reference frame of the graphic tablet. B Comparison of hand representations obtained in TACTILE (top) and PHYSICAL (bottom) condition between the 20-39 and 60-79 yrs group.

Figure 4

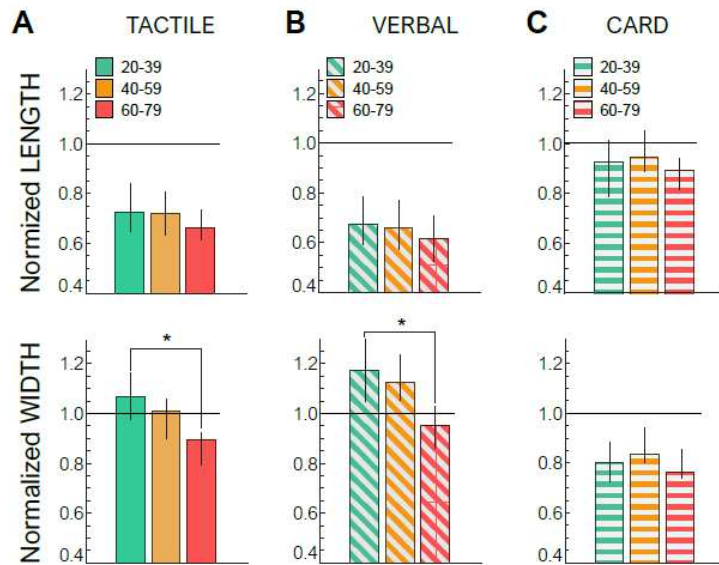


Figure 5: Effect of age on normalized finger length (top) and hand width (bottom) in TACTILE (A), VERBAL (B) and CARD (C) conditions (median values for each age group). Vertical bars represent the 95% confidence interval. Horizontal lines correspond to the case where the size of the respective representation is identical to the size of the physical hand (same for CARD).

Figure 5

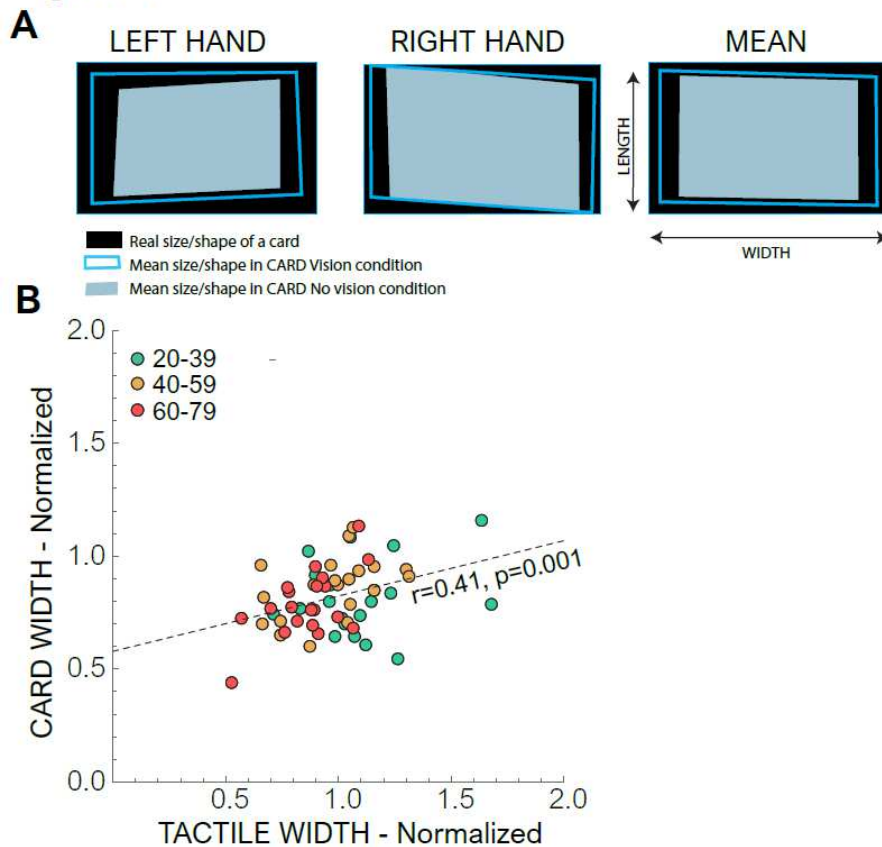


Figure 4: A: Mean size and shape of card representation with eyes open (blue line) and eyes closed (light blue filled shape) compared to real card size (black rectangle), separately for the left and right pointing hand. B: inter-individual correlation between distortion of hand width in the TACTILE condition and card width.

	20-39 yrs. (N=20)	40-59 yrs. (N=20)	60-79 yrs. (N=20)
Mean age (yrs. \pm SD)	30 \pm 6.3	50.15 \pm 5.69	69.9 \pm 6.23
Laterality	17 RH, 2LH, 1A	18 RH, 2LH	17RH, 2LH, 1A
Computer use (hours/week)	30.5 \pm 21.20	23.75 \pm 11.47	23.53 \pm 17.92
Music instrument (hours/week)	1.05 \pm 3.43	0.15 \pm 0.49	0.35 \pm 1.09
Light touch detection threshold (in g)	0.11 \pm 0.14	0.20 \pm 0.16	0.33 \pm 0.28

Table 1: Subject characteristics for the three age groups. Age, laterality (short form of Edinburg handedness inventory; (Oldfield, 1971), daily manual activities, and light touch detection threshold (Weinstein, 1993). RH, LH, A: right-, left-handed or ambidextrous.

	Age group	PHYSICAL	TACTILE	VERBAL	CARD Vision	CARD No vision
Mean width (cm \pm SD)	20-39 yrs.	11.60 \pm 0.91	11.95 \pm 2.36	12.49 \pm 2.85	7.76 \pm 0.84	6.24 \pm 1.22
	40-59 yrs.	11.53 \pm 0.98	10.74 \pm 2.35	11.82 \pm 3.31	7.55 \pm 1.38	6.54 \pm 1.81
	60-79 yrs.	11.46 \pm 0.89	9.32 \pm 1.40	9.88 \pm 1.79	7.86 \pm 1.23	6.20 \pm 1.61
	Mean	11.53 \pm 0.91	10.66 \pm 2.32	11.40 \pm 2.90	7.72 \pm 1.15	6.32 \pm 1.55
Mean length (cm \pm SD)	20-39 yrs.	7.85 \pm 0.48	5.87 \pm 1.22	5.44 \pm 1.51	4.75 \pm 2.85	4.38 \pm 0.88
	40-59 yrs.	7.93 \pm 0.63	5.69 \pm 1.51	5.22 \pm 1.69	4.69 \pm 0.80	4.49 \pm 1.02
	60-79 yrs.	7.89 \pm 0.46	5.29 \pm 1.27	5.02 \pm 1.47	4.5 \pm 0.64	4.06 \pm 1.13
	Mean	7.89 \pm 0.52	5.61 \pm 1.34	5.23 \pm 1.54	4.65 \pm 0.78	4.31 \pm 1.01

Table 2: Averaged hand width and finger length for each age group in the three conditions (PHYSICAL, TACTILE, VERBAL) and card width and card length (in the two conditions CARD-vision and CARD-No vision). All values in cm. Hand measures averaged between the left and right hand of each subject.