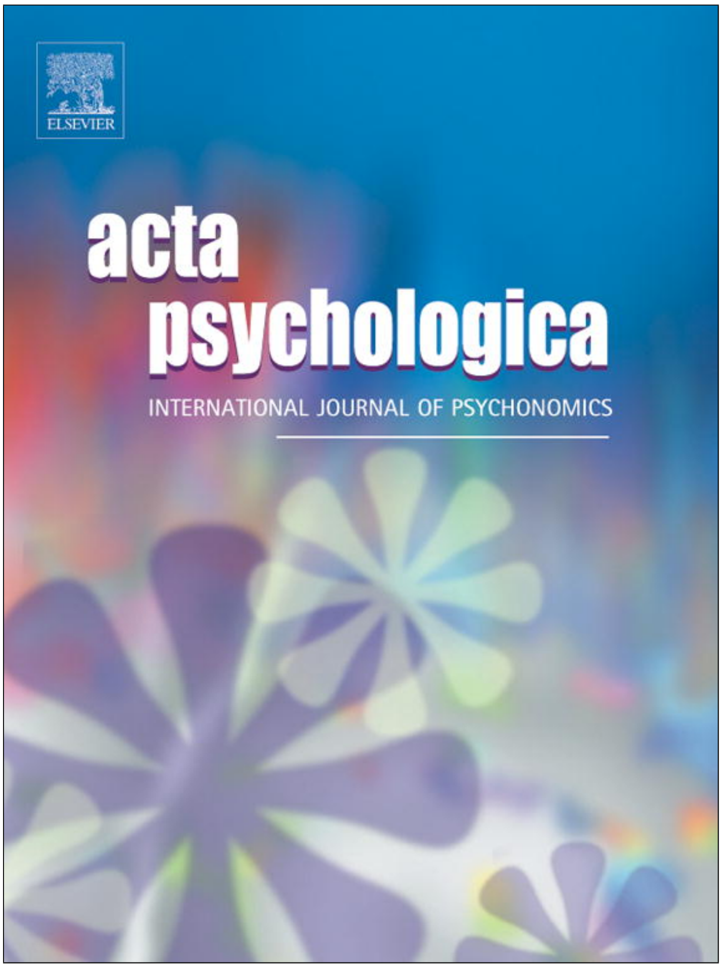
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The effects of healthy aging on mental imagery as revealed by egocentric and allocentric mental spatial transformations

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ABSTRACT

Previous studies suggest that mental rotation can be accomplished by using different mental spatial transformations. When adopting the allocentric transformation, individuals imagine the stimulus rotation referring to its intrinsic coordinate frame, while when adopting the egocentric transformation they rely on multisensory and sensory-motor mechanisms. However, how these mental transformations evolve during healthy aging has received little attention. Here we investigated how visual, multisensory, and sensory-motor components of mental imagery change with normal aging. Fifteen elderly and 15 young participants were asked to perform two different laterality tasks within either an allocentric or an egocentric frame of reference. Participants had to judge either the handedness of a visual hand (egocentric task) or the location of a marker placed on the left or right side of the same visual hand (allocentric task). Both left and right hands were presented at various angular departures to the left, the right, or to the center of the screen. When performing the egocentric task, elderly participants were less accurate and slower for biomechanically awkward hand postures (i.e., lateral hand orientations). Their performance also decreased when stimuli were presented laterally. The findings revealed that healthy aging is associated with a specific degradation of sensory-motor mechanisms necessary to accomplish complex effector-centered mental transformations. Moreover, failure to find a difference in judging left or right hand laterality suggests that aging does not necessarily impair non-dominant hand sensory-motor programs.

1. Introduction

Mental imagery (MI) is the distinctive human ability to create and transform mental representations of self and external objects. The debate on the underlying cognitive mechanisms of MI has emphasized the relevance of different classes of mental transformations (see Zacks & Michelon, 2005). A mental image can be mentally transformed, for instance, in order to process its visual features without the need for the observer to physically move the object or himself. In this case, an allocentric transformation, based on the updating of the object's intrinsic coordinate frame, is applied. It is also possible to use MI in order to transform our whole body image rotating or translating in the space. This latter process constitutes a form of egocentric transformation that involves the updating of the observer's reference frame (i.e., eye and head centered) like, for instance, during perspective taking tasks. When MI is applied to a specific body part, an effector-based transformation based on the effector reference frame (e.g., hand centered) is applied. This different form of egocentric transformation updates the coordinate frame of a specific body part relative to an object, to another body part or to the environment frame of reference making use of sensory-motor brain mechanisms that occur also during action planning and rehearsal (e.g., Michelon, Vettel, & Zacks, 2006; Parsons et al., 1995).

One very fruitful way of studying MI has been trough mental rotation (MR) paradigms. MR has been first systematically explored by Shepard and Metzler (1971) in a series of experiments in which they visually presented participants with identical or mirror-image pairs of solid objects and recorded reaction times (RTs) for same-different judgments. They found that participants' RTs monotonically increased with the increase of angular disparity between the two objects and argued that, in order to decide whether they are the same or different, participants mentally rotated one of the objects until it matched the position of the other. Similar results have been documented using laterality judgment about mirror-symmetric visual stimuli. For example in the "hand laterality task" observers were shown with a rotated picture of a hand and were asked to decide if the stimulus represents a left hand or a right hand. To perform this task it typically takes longer for larger hand rotations (Sekiyama, 1982; Parsons, 1987). However, it has also been shown that, differently from MR of solid abstract objects, MR of hands is strongly influenced by body part's somatic and kinesthetic aspects (Sekiyama, 1982; Parsons, 1987, 1994). Indeed, the hand laterality

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judgment takes longer when hands are rotated away from the body's midsagittal plane (i.e., lateral orientations) than when hands are rotated toward it (i.e., medial orientations). RTs associated with hand laterality judgments of left hand stimuli and right hand stimuli are asymmetric relative to 180° of stimulus angular departure. This non-monotonic distribution of RTs seems to reflect the physical constraints of the forearm and wrist movements toward the lateral side of the body midline, as the forearm movements crossing toward the body midline are easier to be executed. It has been argued that MR of hands is performed by mentally simulating one's own hand rotating it until it reaches the same position as the displayed hand stimulus (Cooper & Shepard, 1975; Gentilucci, Daprati, & Gangitano, 1998; Parsons, 1987). Parsons (1994) also showed that the time needed to make the left–right judgment is comparable to the time needed to actually move the hand into the same displayed hand posture. However, the medial–lateral RT difference also indicates the existence of a preferred tuning between the angular departure of the hand stimulus and its handedness. Indeed for some combinations of stimulus view, stimulus angular departure, and stimulus handedness, the laterality judgment is much faster than for others. This phenomenon is consistent with the idea that, for some given orientations (i.e., medial), participants rely less on sensory-motor processes (i.e., the mental transformation) and more on a direct proprioceptive-visual matching between the observer's felt hand and the visually presented hand. Coherently, RTs for medial hand orientations do not necessarily follow a linear relation with the stimulus angular departures (Parsons, 1994; ter Horst, Jongsma, Janssen, van Lier, & Steenbergen, 2012). In this sense, the difference between medial and lateral orientation response latencies for correct trials reflects the general degree of sensory-motor processing necessary to accomplish the mental spatial transformation. Indeed, when the stimulus angular departure and the stimulus view are not coherent with the observer's felt hand, the decision relies on sensory-motor mechanisms that are reflected in the typical RT-orientation dependent distribution observed during MR of hands.

Hand laterality judgment is strongly influenced by the observer's hand posture during the task (Ionta & Blanke, 2009; Ionta, Fourkas, Fiorio, & Aglioti, 2007; Parsons, 1987; Shenton, Schwoebel, & Coslett, 2004), while individuals with congenital limb absence (Funk & Brugger, 2008), upper limb amputees (Nico, Daprati, Rigal, Parsons, & Sirigu, 2004), and chronic pain patients (Coslett, Medina, Kliot, & Burkey, 2010; Moseley, 2004; Schwoebel, Friedman, Duda, & Coslett, 2001) are impaired in performing this task. These findings suggest that proprioception and peripheral factors influence imagery and that sensory-motor mechanisms are essential in order to accomplish egocentric mental spatial transformations. The key role of the brain sensory-motor areas in supporting MR of hands has been recently demonstrated in a study in which patients with damage to the cortical somato-motor hand representation were selectively impaired in performing MR of hands but not MR of objects (Tomasino, Skrap, & Rumiati, 2011). In brain-damaged patients, dissociations between egocentric and allocentric transformations can be observed depending on the lesion site. For instance, Tomasino and Rumiati (2004) described patients whose abilities to perform MR based on "the visual strategy" or "the motor strategy" double dissociated as a consequence of a lesion either of the right- or left-hemisphere respectively. More specifically, right-hemisphere damaged patients were impaired when MR was based on the object reference frame but were able to perform egocentric-based MR, while left-hemisphere damaged patients showed the opposite pattern. This distinction has also received support from another neuropsychological study revealing a double dissociation between the two strategies (Sirigu & Duhamel, 2001).

Neuroimaging studies show that egocentric and allocentric transformations are supported by two complementary brain networks (see Zacks, 2008, for a recent review). In particular, the posterior parietal, the occipital and the superior temporal cortex are activated during allocentric transformations (e.g., Wraga, Shephard, Church, Inati, & Kosslyn, 2005; Zacks, Vettel, & Michelon, 2003). In addition, areas normally engaged in programming and executing movements (e.g., the supplementary motor area, the primary motor, premotor and parietal cortices, the cerebellum and the basal ganglia) are activated when the MR task is performed using an egocentric reference frame (e.g., Alivisatos & Petrides, 1997; Bonda, Petrides, Frey, & Evans, 1995; Kosslyn, DiGirolamo, Thompson, & Alpert, 1998; Kosslyn, Thompson, Wraga, & Alpert, 2001). Moreover, relative to objects, MR of hands was found to elicit stronger activity in the cortical motor areas (de Lange, Hagoort, & Toni, 2005; Kosslyn et al., 1998; Wraga, Thompson, Alpert, & Kosslyn, 2003; Wraga et al., 2005), and transcranial magnetic stimulation (TMS) applied over the motor cortex selectively impairs MR of hands (Ganis, Keenan, Kosslyn, & Pascual-Leone, 2000), but not MR of letters (Tomasino, Borroni, Isaja, & Rumiati, 2005). It has been demonstrated that within this wide brain network supporting MI, dissociation between egocentric and allocentric mental transformations can be found at the level of the posterior parietal cortex. Indeed, repetitive transcranial magnetic stimulation (rTMS) applied over the superior parietal lobule alters MR of letters while rTMS over the supramarginal gyrus impairs MR of hands (Pelgrims, Andres, & Olivier, 2009).

Like other cognitive abilities, MR seems to slowly degrade in elderly individuals. Age-related changes have been reported for MR of objects and alphanumeric characters (Berg, Hertzog, & Hunt, 1982; Cerella, Poon, & Fozard, 1981; Dror & Kosslyn, 1994; Gaylord & Marsh, 1975; Hertzog & Rypma, 1991; Kemps & Newson, 2005; Puglisi & Morrell, 1986; Sharps & Gollin, 1987), and MR of hands (Devlin & Wilson, 2010; Saimpont, Pozzo, & Papaxanthis, 2009). Elderly individuals have also been found to be slower than younger controls at explicitly imagining movements in a Fitts' like task (Personnier, Ballay, & Papaxanthis, 2010; Skoura, Papaxanthis, Vinter, & Pozzo, 2005), particularly when they imagined movements of the non-dominant hand (Skoura, Personnier, Vinter, Pozzo, & Papaxanthis, 2008). In this task, the time needed to imagine one's hand movement to a target increases with the distance and decreases with the size of the target, following the same physical law that regulates goal directed actions (Jeannerod, 1995). This is also consistent with their being less accurate and slower at executing movements with the non-dominant hand in highly demanding tasks (Francis & Spirduso, 2000; Mitrushina, Fogel, D'Elia, Uchiyama, & Satz, 1995; Teixeira, 2008).

However it remains unclear whether the age-related decline in MI hides a more specific deficit in applying either an egocentric mental transformation or an allocentric mental transformation. Indeed, the relationship between the type of stimulus and the mental transformation employed is not always necessarily so direct. Many studies suggest that MR of abstract objects can, to some extent, share the same cognitive and neural sources employed during egocentric transformations (e.g., de Lange et al., 2005; Wexler, Kosslyn, & Berthoz, 1998; Wraga et al., 2003). Thus, to date, the literature on the effect of normal aging on MR failed to clearly disentangle between potential differential effects of aging on the two mental transformation processes. Hence, the main purpose of the present study was to clarify the impact of normal aging on MR using either an egocentric (i.e., effector-centered) or an allocentric (i.e., object-centered) mental transformation. Differently from previous research, the paradigm employed in the present study allowed us to directly compare the two complementary mental spatial transformations by holding constant the stimuli to be mentally rotated and the type of response required. If the two classes of mental transformation differently decline with age, then we expected the group of elderly participants to perform worse in one of the two tasks. Instead, if healthy aging generally affects MR, then we expected impairments in both the egocentric and the allocentric task.

Since the functionality of the non-dominant hand changes with age (see e.g., Mitrushina et al., 1995; Francis & Spirduso, 2000; Teixeira, 2008), all our right-handed participants were asked to respond with their dominant hand (i.e., the right hand) irrespective of whether the response was left or right. This is at variance with Saimpont et al. (2009), in which elderly participants responded with the left hand or the right hand for left and right stimuli respectively. Thus, we also predicted that if normal aging specifically affects non-dominant hand sensory-motor programs, then our elderly participants' performance should be impaired for left-hand stimuli even when they respond with the dominant hand for both left and right handed stimuli.

Judging the laterality of a visually presented hand relies on limb-specific sensory-motor programs that are represented in the contralateral cerebral hemisphere (Parsons, Gabrieli, Phelps, & Gazzaniga, 1998; Parsons et al., 1995). Left-right judgments are faster when right hands are presented to the right visual field and when left hands are presented to the left visual field (Parsons et al., 1998). If elderly individuals were particularly challenged by engaging in sensory-motor programs to control their non-dominant hand during MI (Saimpont et al., 2009; Skoura et al., 2008), then they should be especially affected by the lateralized presentation of left hands. Furthermore, compared with young controls, elderly individuals may experience a greater interference when left hands are presented to the ipsilateral hemisphere (i.e., longer RTs for left hands presented to the right visual field), as well as a reduced advantage when left hands are presented to the contralateral hemisphere (i.e., longer RTs for left hands presented to the left visual field).

2. Material and methods

2.1. Participants

Fifteen elderly (mean age = 71.9 years, SD = 4.2, 8 female) and 15 young volunteers (mean age = 26.5 years, SD = 2.1, 8 female), with no history of previous neurological or psychiatric disease took part in the experiment. All participants were right-handed (elderly = 96 ± 4.8; young = 93.3 ± 6.1) according to the Edinburgh Standard Handedness Inventory (Oldfield, 1971). The elderly participants were well preserved both physically and cognitively (CRIq = 126.3 ± 7.2, Nucci, Mapelli, & Mondini, 2011; MOCA = 27.4 ± 1.1, Nasreddine et al., 2005). All participants who took part in the study gave written consent. The study was approved by the SISSA Ethics Committee.

2.2. Stimuli and task procedure

Presentation®14.9 software (Neurobehavioral systems, Albany, USA) was used to design and run the experiment. Participants sat in front of a PC screen (21″ and 70 EHz refresh rate) at a distance of 60 cm away. All participants responded with their dominant right hand by pressing a custom-made button box consisting of two pads located next to each other. Participants were told that the pad on the left was to be used for left responses and the pad on the right for right responses. Each image was a realistic picture of a hand and was the result of a rotation and/or reflection of two basic hand postures (back or palm). Each hand stimulus (left or right) was presented in six different angular departures (45°, 90°, 135°, 225°, 270°, 315°), and at three positions on the screen (left, LP; right, RP; and center, CP) (see Fig. 1a and b for an example of the stimuli and of the two tasks).

Each participant performed two laterality tasks, one requiring an allocentric transformation, and the other requiring an egocentric transformation. In the allocentric task, participants decided if a red dot was on the left or on the right side of the hand as it would be seen in the upright position (i.e., canonical orientation with fingers pointing upward), while in the egocentric task they were asked to decide whether the presented hand was a left or right hand. The red dot could be located either on the extremity of the little finger or ring finger, or of the index finger or thumb. The red dot was presented in both tasks however in the egocentric task it was not relevant.

Two blocks of the egocentric task and two blocks of the allocentric task were interleaved for each participant, while the order of presentation was counterbalanced across participants. Each block consisted of 144 trials for a total of 576 trials. Each trial began with a central fixation cross (1500 ms), followed by the presentation of a stimulus that was shown on a white background. After, a stimulus appeared randomly to the left, the right or on the center in the screen, each trial was timed-out upon the participant's response. Participants were required to make the laterality judgment as quickly and accurately as possible, and they did not obtain any feedback about their performance. The stimuli were presented in a random order except that the same stimulus could not appear twice within three successive trials. To make sure that participants understood the instructions, they were asked to perform ten practice trials prior to each block. During these training phases they were instructed and monitored by the experimenter to focus their gaze on the central fixation cross.

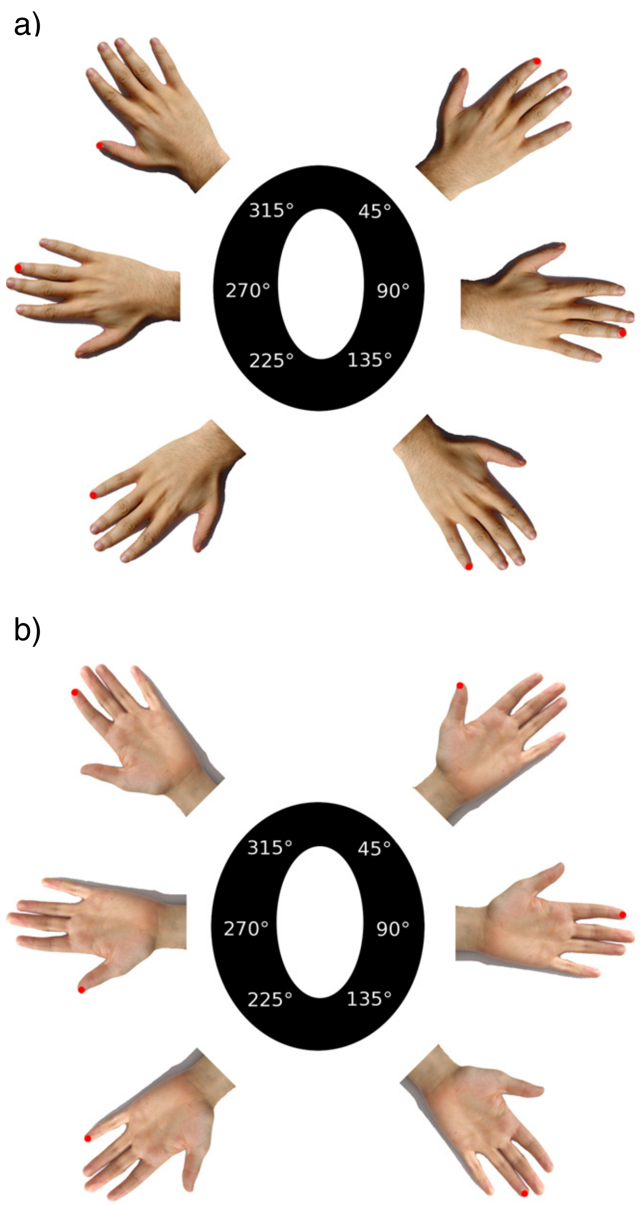

Fig. 1. a. Example of a right hand showed in back view at the different angles. b. Example of a left hand showed in palm view at the different angles.

2.3. Data analysis

A first analysis was carried out to check that MR processes were effectively engaged during both the egocentric task and the allocentric task. In order to do so, two mixed design ANOVAs were conducted on RTs separately for the egocentric and the allocentric task. Each ANOVA had Handedness (left/right), View (back/palm), Position (LP/CP/RP) and Angle (45°, 90°, 135°, 225°, 270°, 315°) as within-subjects factors, and Group (elderly/young) as between-subjects factor.

To test the effects of aging on sensory-motor components of MI, two mixed design ANOVAs on RTs and accuracy were conducted. Each ANOVA had Task (egocentric/allocentric), Handedness (left/right), View (back/palm), Position (LP/CP/RP), and Orientation (medial/lateral) as within-subjects factors, and Group (elderly/young) as a between-subjects factor. Lateral orientations correspond to hands rotated away from the participant's midsagittal plane (i.e., left hands when rotated counterclockwise and right hands when rotated clockwise), while medial orientations correspond to hands rotated toward the participant's midsagittal plane (i.e., left hands when rotated clockwise and right hands when rotated counterclockwise). Accordingly, medial orientations corresponded to the mean RTs of trials with 45, 90, and 135° of rotation for left hand stimuli, and with 225, 270, and 315° of rotation for right hand stimuli. Lateral orientations corresponded to the mean RTs of trials with 225, 270, and 315° of rotation for left hand stimuli and with 45, 90, and 135° of rotation for right hand stimuli. For each participant, and each combination of task, hand, view, position, and orientation, RTs were calculated as the average time of correct trials. RTs greater than two standard deviations above the mean and shorter than 500 ms were not included in any of the analyses (total loss, 6.8% of trials). Accuracy was calculated as percentage of correct trials before removing RTs outliers.

In addition, we computed linear regression lines (i.e., slopes and intercepts) on RTs. The slopes were computed from the average RTs among angular departures equidistant from 0° (i.e., 45° with 315°, 90° with 270° and 135° with 225°), separately for medial and lateral orientations (medial orientations: left handed stimuli with 45°, 90° and 135°, right handed stimuli with 225°, 270° and 315°; and lateral orientations: left handed stimuli with 225°, 270° and 315°, right handed stimuli with 45°, 90° and 135°). The slope represents the average RT change produced by the stimulus angular departure reflecting the MR transformational process, with steeper slopes indicating slower speed of rotation. The intercepts were computed from the average RTs between angular departures equidistant from 0° (i.e., 45° with 315°, 90° with 270° and 135° with 225°). The intercept is thought to be related to processes such as visual perception, decision making, and response preparation (Shepard & Cooper, 1982). Earlier or later intercepts suggest that participants took shorter or longer time respectively to accomplish those processes. We then ran two ANOVAs on slopes, one for each task, with View (back/palm), Position (LP, CP, RP) and Orientation (medial/lateral) as within-factors and Group (elderly/young) as a between-factor. Even though RTs for medial orientations do not typically show a linear relation as a function of the rotational angle (Parsons, 1994; ter Horst et al., 2012; but see also Figs. 2 and 3), the slope analysis was planned to check if the laterally oriented hand stimuli were harder to be mentally transformed for the elderly group than for the young group. We also ran an ANOVA on intercepts of each participant with Task (egocentric/allocentric), Handedness (left/right), View (back/palm) and Position (LP, CP, RP) as within-factors and Group (elderly/young) as a between-factor. We set the alpha-level at 0.05; post-hoc comparisons were carried out using the Tukey HSD test. Partial eta squared (η^2) are reported where necessary.

3. Results

3.1. Angular departures

The following results (Sections 3.1.1 and 3.1.2) focus on the effects of the stimulus angular departures and its interactions with the other factors. The results of the full experimental design are illustrated in Table 3 in the Appendix section.

3.1.1. Egocentric task

The main effect of angle was found significant, $F\ (5, 140) = 41.51$, $p < .001$; $\eta^2 = .597$. There was a significant interaction between handedness and angle, $F\ (5, 140) = 28.80$, $p < .001$; $\eta^2 = .507$, and a significant three-way interaction between handedness, angle, and group, $F\ (5, 140) = 3.74$, $p < .005$; $\eta^2 = .118$. Both groups showed the expected RT asymmetry between left and right hand stimuli, with a preferred direction of rotation modulated by stimulus handedness (see Fig. 2). For the group of elderly participants, RTs were faster when left hand stimuli were shown with 45° and 90° than when left hand stimuli

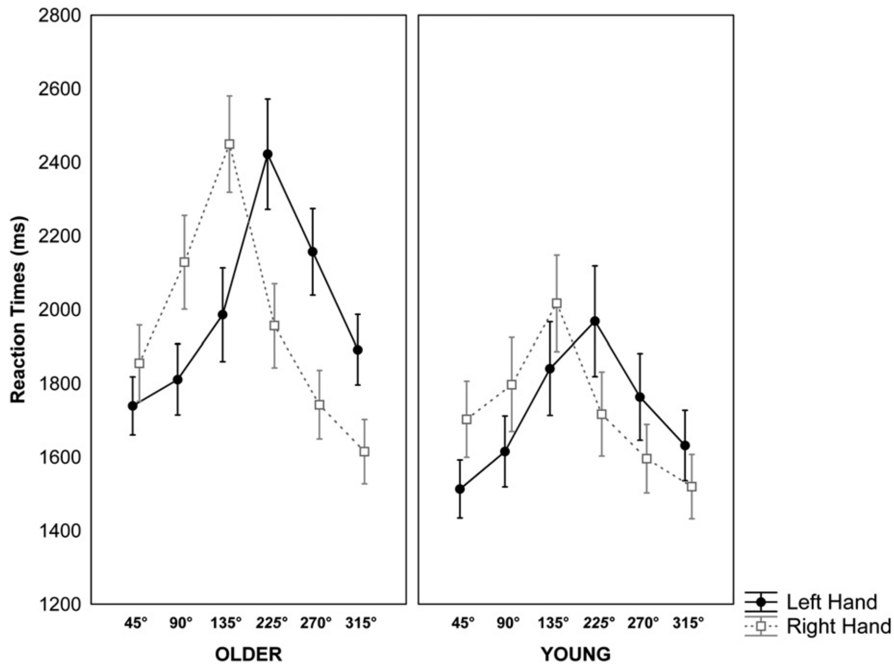

Fig. 2. Egocentric task. Mean RTs at the different stimulus angular departures (45°; 90°; 135°; 225°; 270°; and 315°) for the two stimulus handedness (left hand–right hand) and the two groups (elderly–young). Error bars depict the standard error of the mean.

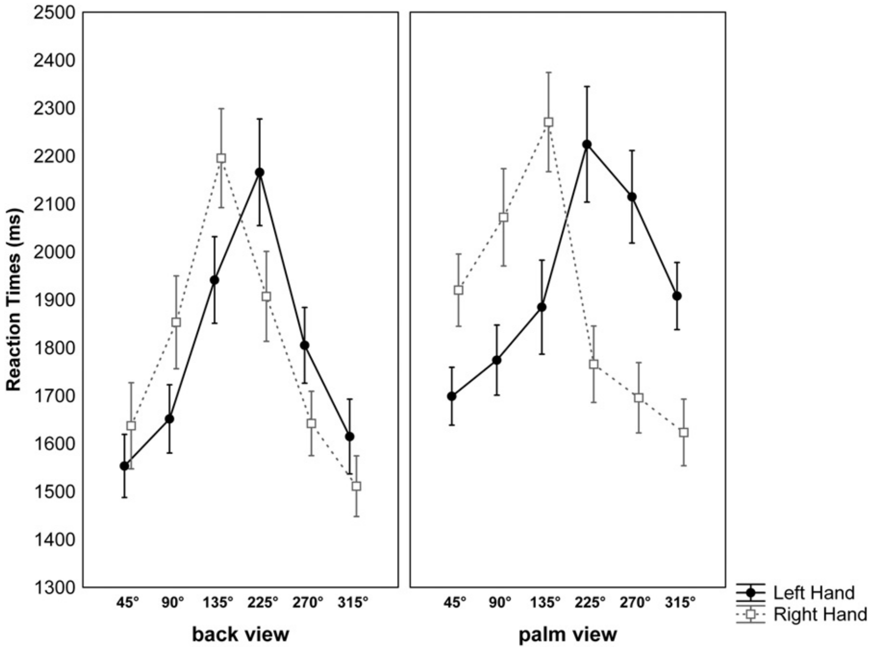

Fig. 3. Egocentric task. Mean RTs at the different stimulus angular departures (45°; 90°; 135°; 225°; 270°; and 315°) for the two stimulus handedness (left hand–right hand) and the two stimulus view (back–palm). Error bars depict the standard error of the mean.

corresponded to 225° and 270° of angular departures (*ps* < .005), and RTs were faster when right hand stimuli were shown with 270° and 315° than when right hand stimuli corresponded to 90° and 135° of angular departures (*ps* < .001). For the group of young participants, RTs were faster when left hand stimuli were shown with 45° and 90° than when left hand stimuli corresponded to 225° of angular departure (*ps* < .005), and RTs were faster when right hand stimuli were shown with 270° and 315° than when right hand stimuli corresponded to 135° of angular departure (*ps* < .05). Moreover, elderly participants' RTs for left hand stimuli with a rotation of 225° were slower than young participants' RTs for left hand stimuli with a rotation of 45° (*p* < .05), and for right hand stimuli with a rotation of 315° (*p* < .05). Elderly participants' RTs for right hand stimuli with a rotation of 135° were slower than young participants' RTs for left hand stimuli with a rotation of 45° and 90° (*ps* < .05), and for right hand stimuli with a rotation of 270° and 315° (*ps* < .05). For the group of elderly participants, the

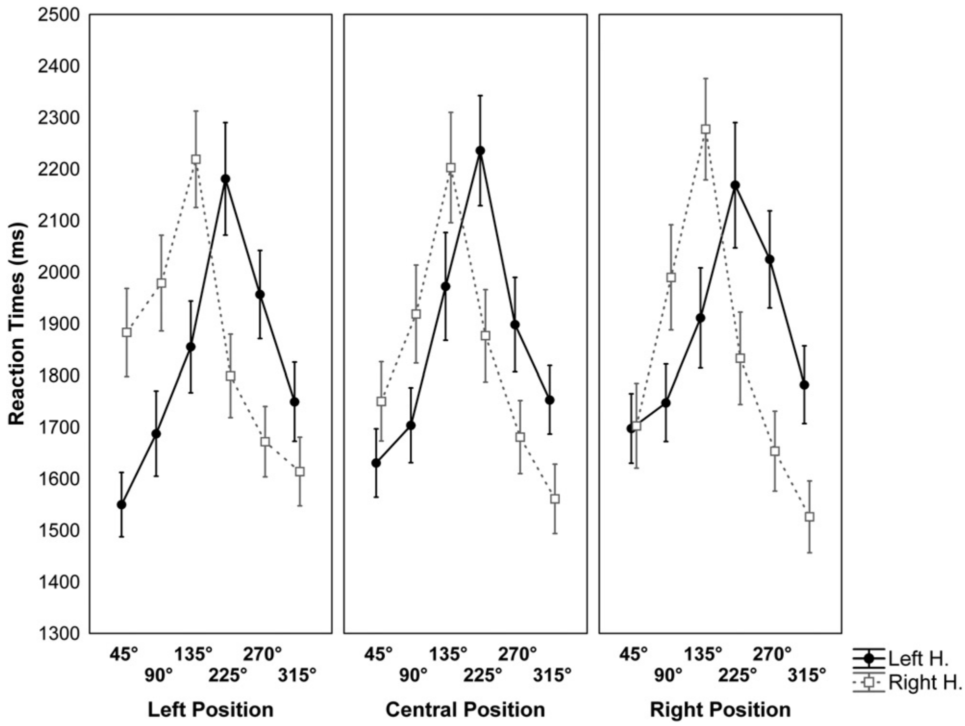

Fig. 4. Egocentric task. Mean RTs at the different stimulus angular departures (45°; 90°; 135°; 225°; 270°; and 315°) for the two stimulus handedness (left hand–right hand) and the three positions of stimulus presentation (LP–CP–RP). Error bars depict the standard error of the mean.

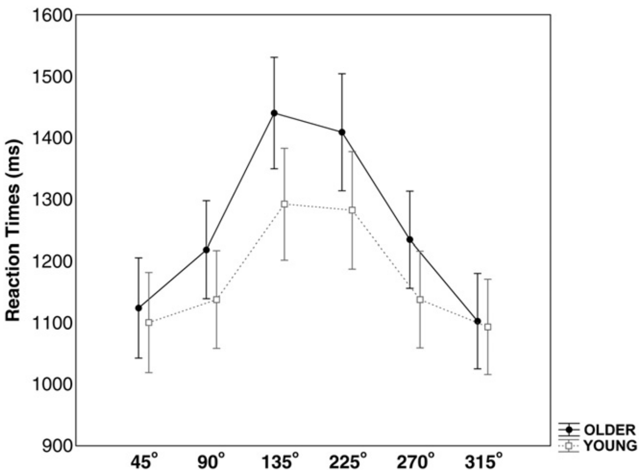

Fig. 5. Allocentric task. Mean RTs at the different stimulus angular departures (45°;90°;135°;225°;270°; and 315°) for the two groups (elderly–young). Error bars depict the standard error of the mean.

differences between left and right hand stimuli, for each angle of rotation, were always significant ($ps < .05$), except that for 45° of stimulus angular departure ($p > .05$). Instead, the group of young participants did not show such difference between left and right hand stimuli for each stimulus angular departure ($ps > .05$).

The main effect of stimulus view was significant, F (1, 28) = 12.05, $p < .005$; $\eta^2 = .300$. The view × angle, F (5, 140) = 6.03, $p < .001$; $\eta^2 = .177$, and the handedness × view × angle, F (5, 140) = 5.04, $p < .001$; $\eta^2 = .152$, interactions were also significant (see Fig. 3). For stimuli showed in back view, RTs differed between left and right hands with faster RTs for left hands at 135°, and with faster RTs for right hands at 225° ($ps < .05$). For stimuli showed in palm view, RTs differed between left and right hands with faster RTs for left hands at 45°, 90° and 135° ($ps < .05$), and with faster RTs for right hands at 225°, 270° and 315° ($ps < .05$). The handedness × position × angle interaction was also significant, F (10, 280) = 2.15, $p < .05$; $\eta^2 = .071$. When stimuli were presented centrally (CP), the 45° and the 315° of angular departures did not differ between left and right hand stimuli ($ps > .05$). When presented on the left (LP), trials with 45° of angular departure did significantly differ between left and right hand stimuli, with faster RTs for left hand stimuli ($p > .001$). When presented on the right (RP), trials with 315° of angular departure did significantly differ between left and right hand stimuli, with faster RTs for right hand stimuli ($p > .005$) (see Fig. 4).

3.1.2. Allocentric task

The factor angle led to a significant main effect, F (5, 140) = 65.93, $p < .001$; $\eta^2 = .701$, with a significant angle × group interaction, F (5, 140) = 3.78, $p < .005$; $\eta^2 = .119$. The group of young participants did not show a linear increment in RTs as a function of stimulus angle of presentation. Differently from elderly participants, their RTs slowed-down only for 135° and 225° of angular departures. Elderly participant RTs showed a linear increment as angular departures were further from the upright (0°): trials with an angle of 45° were faster than all other angles ($ps < .05$), except for 315° ($p = .999$); trials with an angle of 90° were faster than 135° and 225° ($ps < .005$) but they were not different from 270° ($p = .999$); trials with an angle of 135° were slower than all other angles ($ps < .001$), except for 225° ($p = .994$). The group of young participants was faster for trials with 45°, 90°, 270°, and 315° compared to RTs for trials with 135° and 225° of angular departures ($ps < .001$), while RTs for trials with 45° and 90° did not differ from those with 270° and 315° of angular departures ($ps > .05$). RTs are plotted as a function of stimulus angular departures for each group in Fig. 5.

The handedness × angle interaction, F (5, 140) = 5.16, $p < .001$; $\eta^2 = .155$, revealed that RTs were modulated by the angular departures and by the laterality of the visual marker. When the visual marker was located on the left side of the stimulus, RTs significantly increased between 90° and 135° of angular departures ($p < .001$), while RTs between 135° and 225° of angular departures did not differ from each other ($p = .446$). RTs then decreased from 225° to 270°, and to 315° of stimulus angular departures ($ps < .001$). When the visual marker was located on the right side of the stimulus RTs significantly increased between 90° and 135° of angular departures ($p < .001$). RTs then decreased from 135° to 270° ($ps < .005$), while RTs between 270° and 315° of angular departures were not significantly different ($p = .127$). A direct comparison between left and right sided markers revealed a significant difference at 225° of angular departure, with right located marker stimuli faster than left located marker stimuli ($p < .001$).

Table 1
Mean accuracy reported as percentage of correct responses for the two groups in the two tasks and hand conditions. Standard errors of the mean are printed in brackets.

	ELDERLY		YOUNG	
	Egocentric Task	Allocentric Task	Egocentric Task	Allocentric Task
Left hand	89% (.12)	98% (.07)	92% (.09)	98% (.02)
Right hand	87% (.15)	97% (.10)	93% (.10)	98% (.03)

3.2. Orientations

3.2.1. Accuracy

Significant main effects of task, F (1, 28) = 49.56, $p < .001$; $\eta^2 = .638$, with a better performance in the allocentric compared with the egocentric task, and of orientation, F (1, 28) = 4.81, $p < .05$; $\eta^2 = .146$, with MR being harder for lateral orientations than medial orientations were observed. Main effects were qualified by an interaction between these two factors, F (1, 28) = 5.23, $p < .05$; $\eta^2 = .157$. The orientation × group, F (1, 28) = 10.22, $p < .005$; $\eta^2 = .267$, and the task × orientation × group interactions, F (1, 28) = 9.27, $p < .005$; $\eta^2 = .248$, were significant. Post-hoc comparisons showed that the group of elderly participants was significantly less accurate during the egocentric task of lateral orientations (see Fig. 6) compared with all other conditions ($ps < .05$). For both groups, there was no difference between orientations during the allocentric task ($ps > .05$).

The task × position interaction, F (2, 56) = 7.83, $p < .001$; $\eta^2 = .218$, and the three-way task × position × group interaction, F (2, 56) = 4.52, $p < .05$; $\eta^2 = .139$, were both significant. Post-hoc tests revealed that, relative to young participants, elderly participants' accuracy significantly differed when they adopted the egocentric task than when they adopted the allocentric task, as a function of the position of the stimulus on the screen. Here, during the egocentric task, elderly participants made significantly more errors with LP than with CP stimuli ($p < .001$). Performance for RP stimuli was also worse than CP stimuli but this effect was only marginally significant ($p = .09$). Young participants were not affected by the lateralized presentation of hands when they applied the egocentric task ($ps > .05$). Moreover, for both groups, participants' accuracy during the allocentric task did not differ depending on positions ($ps > .05$).

The factor handedness, F (1, 28) = .66, $p = .42$, *ns*, and the interaction between handedness and group, F (1, 28) = 3.42, $p = .074$, *ns*, did not reach significance (see Table 1).

3.2.2. Reaction times

The ANOVA showed a significant main effect of task, F (1, 28) = 104.15, $p < .001$; $\eta^2 = .963$, with the allocentric task being faster than the egocentric task. There was a main effect of view, F (1, 28) = 16.01, $p < .001$; $\eta^2 = .363$. RTs during MR of palm view hands were slower than during MR of back view hands. A main effect of position, F (2, 56) = 3.60, $p < .05$; $\eta^2 = .114$, was found significant, with RTs

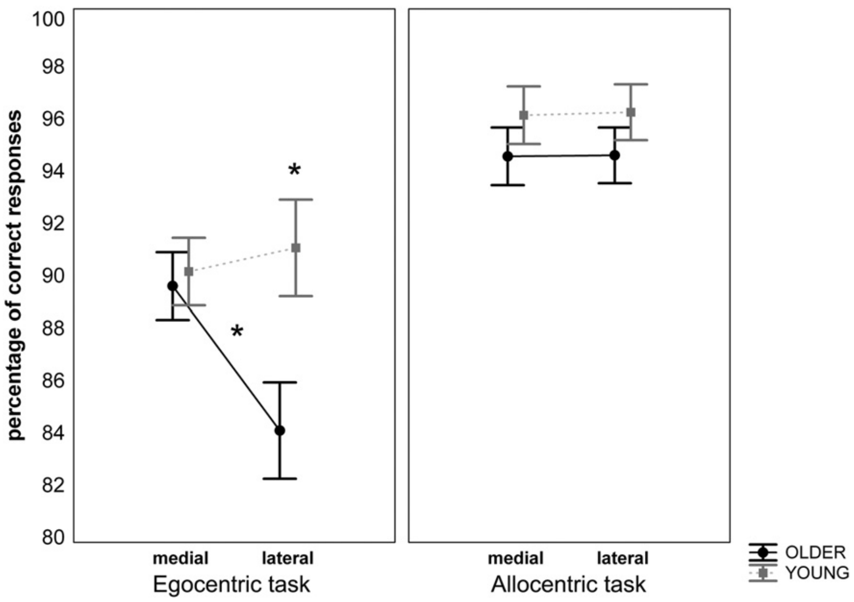

Fig. 6. Mean percentage of correct responses at the different orientations (lateral–medial) of the stimuli for the two groups (elderly–young) and the two tasks (egocentric–allocentric). Error bars depict the standard error of the mean.

being slower for LP and RP stimuli compared with CP stimuli, as well as a main effect of orientation, $F(1, 28) = 67.33$, $p < .001$; $\eta^2 = .706$, with RTs for lateral orientations being slower than medial orientations.

The task × view, $F(1, 28) = 4.43$, $p < .05$; $\eta^2 = .136$, view × orientation interactions, $F(1, 28) = 11.01$, $p < .01$; $\eta^2 = .282$, and the three-way task × view × orientation interaction, $F(1, 28) = 11.69$, $p < .01$; $\eta^2 = .294$, were found significant. Post-hoc analysis revealed that, during the egocentric task, RTs for lateral orientations were slower than RTs for medial orientations both for back view ($p < .001$) and palm view hands ($p < .001$). Moreover, for lateral orientations, palm view hands took longer compared to back view hands ($p < .001$), while there was no difference between RTs for back and palm view hands when showed with medial orientations ($p > .05$). View and orientation had no effect when participants performed the allocentric task (*ps* > .05).

The position × group interaction, $F(2, 56) = 4.66$, $p < .05$; $\eta^2 = .142$, was accounted for by the slower performance of elderly participants with LP and RP stimuli compared with CP stimuli (*ps* < .05). The significant handedness × position interaction, $F(2, 56) = 5.02$, $p < .05$; $\eta^2 = .151$, revealed that left hand stimuli presented to the right visual field took longer than right hand stimuli presented to the center and to the right visual field (*ps* < .05). The ANOVA also showed a significant three-way task × position × orientation interaction, $F(2, 56) = 3.50$, $p < .05$; $\eta^2 = .111$, which was driven by the factors' task and orientation: the different positions of the stimuli on the screen (i.e., LP, CP, RP) did not differ from each other depending on the type of task or orientation (*ps* > .05).

Table 2
Mean reaction times (RTs) (milliseconds) for the two groups in the two tasks and hand conditions. Standard errors of the mean are printed in brackets.

	ELDERLY		YOUNG	
	Egocentric Task	Allocentric Task	Egocentric Task	Allocentric Task
Left hand	2003 (463.1)	1263 (308.4)	1722 (469.1)	1185 (354.8)
Right hand	1959 (469.9)	1246 (298.7)	1725 (504)	1162 (352.6)

RTs were modulated by task and orientation, $F(1, 28) = 35.66$, $p < .001$; $\eta^2 = .560$. Lateral orientations were significantly slower than medial orientations when participants performed the egocentric task ($p < .001$) but not when they performed the allocentric task ($p > .05$). The orientation × group interaction, $F(1, 28) = 5.78$, $p < .05$; $\eta^2 = .171$, and the task × orientation × group interaction, $F(1, 28) = 4.22$, $p < .05$; $\eta^2 = .131$, were found significant. For both groups, during the egocentric task, lateral orientations took longer than medial orientations (*ps* < .005), while in the allocentric task, RTs for medial orientations were not significantly different from RTs for lateral orientations (*ps* > .05). Only for the egocentric task (see Fig. 7) was MR of laterally-oriented stimuli showed slower for elderly than young participants ($p < .05$), while MR of medially-oriented stimuli showed no difference between the two groups ($p > .05$).

Finally, the factor handedness, $F(1, 28) = 3.42$, $p = .074$, *ns*, and the handedness × group interaction, $F(1, 28) = .91$, $p = .34$, *ns*, failed to reach significance (see Table 2).

3.3. RTs linear regression

3.3.1. Slopes

For the egocentric task there were significant main effects of view, $F(1, 28) = 6.03$, $p < .05$; $\eta^2 = .177$, and orientation, $F(1, 28) = 8.85$, $p < .05$; $\eta^2 = .240$. The orientation × group interaction was found significant, $F(1, 28) = 4.07$, $p < .05$; $\eta^2 = .126$. During the egocentric task the group of elderly participants showed steeper slopes for lateral orientations compared to their performance on medial orientations ($p < .005$) and to both medial and lateral orientations performed by the young participants (*ps* < .05).

The ANOVA on the allocentric task revealed significant main effects of group, $F(1, 27) = 5.89$, $p < .05$; $\eta^2 = .179$, with the group of elderly participants showing steeper slopes than young participants, and of orientation, $F(1, 27) = 15.91$, $p < .001$; $\eta^2 = .371$, with steeper slopes for lateral orientations compared to medial orientations.

The significant interaction between position, orientation, and group, $F(2, 54) = 5.62$, $p < .05$; $\eta^2 = .172$, was significant. The older group had steeper slopes for stimuli showed to the right with lateral orientations compared to their performance with medially

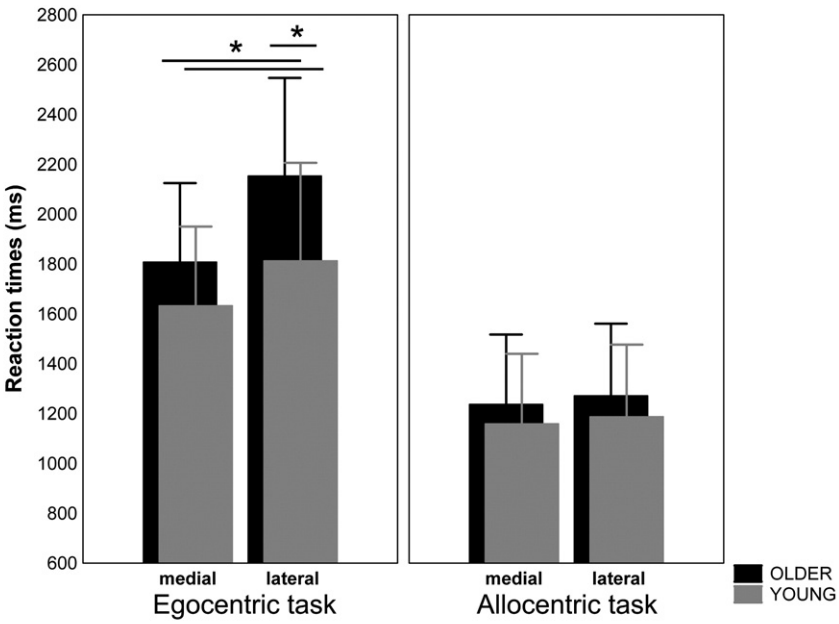

Fig. 7. Mean RTs at the different orientations (lateral–medial) of the stimuli for the two groups (elderly–young) and the two tasks (egocentric–allocentric). Error bars depict the standard error of the mean.

oriented stimuli showed to the right ($p < .05$), and to the young participants' performance with medially oriented stimuli presented to the left, to the center and to the right of the screen ($ps < .05$).

3.3.2. Intercepts

There were significant main effects of task, F (1, 28) = 87.11, $p < .001$; $\eta^2 = .756$, and view, F (1, 28) = 25.3, $p < .001$; $\eta^2 = .474$, and a significant task × view interaction, F (1, 28) = 21.23, $p < .001$; $\eta^2 = .431$. Later intercepts were found during the egocentric task for palm view hands with respect to back view hands in the allocentric and in the egocentric task ($ps < .001$). Intercepts during the allocentric task for back view and palm view did not differ ($p = 1.0$). Finally, a three-way task × handedness × position interaction, F (2, 56) = 3.95, $p < .05$; $\eta^2 = .123$, was found significant, thus highlighting the influence of the lateralized presentation on the hand laterality judgment. During the egocentric task, in the left visual field the intercepts for the left hand stimuli were smaller than for the right hand stimuli ($p < .05$) and, on the right visual field, the intercepts for the right hand stimuli were smaller than the left hand stimuli ($p < .05$). No differences were found between the left hand stimuli intercepts and the right hand stimuli intercepts when showed centrally ($ps > .05$). There was no such a relationship with the presentation side between left and right stimuli in the allocentric task ($ps > .05$).

4. Discussion

In the present study participants were requested to perform two laterality tasks. They had to judge either the handedness of a visual hand (egocentric task) or the location of a marker to be either on the left or right side of the same visual hand (allocentric task). We exploited the different involvement of MR processes in these two tasks in order to investigate multisensory, sensory-motor, and visual-related components of MI during healthy aging.

The egocentric task was characterized by the classic RT asymmetry between left and right hand stimuli with a non-monotonic relation with the angle of stimulus rotation. In this task, the group of elderly participants showed slower RTs for each angle of rotation (except for 45°) between left and right hand stimuli (see Fig. 2). The differences between left and right hand stimuli were coherent with a medial–lateral effect on RTs because left hand stimuli with 45°, 90°, and 135° of angular departures, and right hand stimuli with 225°, 270°, and 315° of angular departures were easier to be judged than right hand stimuli with 45°, 90°, and 135° of angular departures and left hand stimuli with 225°, 270°, and 315° of angular departures. This result was confirmed by the statistical analysis carried out taking into account the factor orientation. Indeed, while lateral orientations were slower than medial orientations for both groups, elderly participants were found to be significantly slower in judging the laterality of hands shown with lateral orientations (i.e., with awkward hand postures). Importantly, the specific impairment of our elderly participants for lateral orientations was present also when considering their accuracy. Here, relative to the young participants, they were significantly less accurate in judging hand laterality when the stimulus was shown with lateral orientations. Finally, we analyzed the speed of MR as expressed by the slope of the best-fitting RT lines. Coherently with what has been discussed above, during the egocentric task, the group of elderly participants showed steeper slopes for lateral orientations compared to medial and lateral orientations performed by the group of young participants.

Performance in the egocentric task was characterized by longer RTs, steeper slopes and later intercepts particularly when the hand stimulus was shown in palm view (see also ter Horst, van Lier, & Steenbergen, 2010). The RT distribution for stimuli shown in palm view was markedly different from that of back view stimuli (see Fig. 3). While left and right hand stimuli shown in back view were different only at 135° and 225° of angular departures, for palm view stimuli the differences between left and right hands were significant for all angles of rotation. However, the analysis of the effect of medial and lateral orientations showed that the task took longer as the hand stimulus was pointing away from the observer's body midline (i.e., lateral orientations) for both back and palm view stimuli. The RT change as a function of the stimulus view is consistent with the notion that, when observers perform the hand laterality judgment, they integrate visual and proprioceptive information in order to establish the spatial coordinates (i.e., the rotational axes) on which to apply the mental transformation process. Indeed, when the hand stimulus is displayed with the same view (i.e., palm facing down) as that of the observer's felt hand (i.e., palm facing down), the required MR process operates on one axis that rotates around the horizontal plane. In contrast, when the hand stimulus is displayed with a view (i.e., palm facing up) different from that of the observer's felt hand (i.e., palm facing down), the required MR process operates on two axes that rotate one around the horizontal plane, and the other around the frontal plane.

We also found that the RTs distribution between left and right hands was sensitive to the lateralized presentation employed in the present study. Particularly, when stimuli were shown to the left or to the right visual field, the RT differences between left and right hand stimuli for some angles of rotation were inverted (see Fig. 4). Moreover, the significant interaction between task, hand and position confirmed classical findings (Parsons et al., 1995, 1998). Both the young group and the older group showed earlier intercepts during the egocentric task for hands presented to the contralateral hemisphere (i.e., left hands presented to the left visual field and right hands presented to the right visual field). This result bears resemblance to the central (i.e., contralateral) representation of overt motor behavior and motor imagery (Crammond, 1997; Jeannerod & Decety, 1995). However, this effect seems to be independent of the mental transformation process itself, as it was found for the intercepts of the RT linear function. For this reason we speculate that, even independently from the demands of the MR task, visual perception of body parts could automatically elicit the activation of cerebrally lateralized hand sensory-motor programs. Coherently with this result, a previous study showed that the left hemisphere advantage for right hand stimuli and the right hemisphere advantage for left hand stimuli are observed also in a simple detection task. Moreover, this contralateral bias is not due to a spatial compatibility effect between visual and proprioceptive information (Aziz-Zadeh, Iacoboni, & Zaidel, 2006). Interestingly, our elderly participants were neither affected by the ipsilateral nor by the contralateral presentation of hands. However, their ability to apply a mental transformation upon those sensory-motor representations was selectively affected for difficult and awkward effector-centered transformations. Besides, in contrast with Saimpont et al. (2009), in which a selective impairment for left hand stimuli was reported, in our study the ability of elderly participants to perform the hand laterality judgment task was equally affected for imagined left- and right-hand mental transformations. This finding cannot be due to their responding with the non-dominant hand because in our study they responded using only the dominant one.

In the egocentric task elderly participants performed significantly worse and slower when stimuli were presented to the left or right side of the screen rather than to the center. Importantly this effect was independent from stimulus handedness (i.e., left/right hand stimuli). This is consistent with the notion that elderly individuals experience difficulties when they have to apply difficult and longer effector-centered transformations (Personnier et al., 2010; Skoura et al., 2005, 2008). There are several reasons that allow us to rule out any influence of spatial attention in generating this effect. First, the spatial position effect was present only during the egocentric task and not during the allocentric task. Second, the kind of lateralized presentation we employed does not trigger any spatial attention bias toward left or right. Finally, it has been demonstrated that in spatial cuing tasks the shift of spatial attention is well preserved in older individuals (Greenwood, Parasuraman, & Haxby, 1993), especially when the task does not involve cue encoding (Folk & Hoyer, 1992).

During the allocentric task, we observed a different RT modulation with the angle of rotation for the two groups. While the group of elderly participants took longer to judge the laterality of the visual marker as the stimulus angular departure increased, young participants' RTs were affected only by two angles (i.e., 135° and 225°) of stimulus rotation (see Fig. 5). This finding suggests that the allocentric task was too easy for the young participants to cause a linear increment of RTs with the angle of stimulus rotation. Indeed, the allocentric task was performed always faster and with fewer errors than the egocentric task. It is also possible that the group of young participants may have applied a different strategy than MR in order to solve this task. Even though there were no significant differences between young and elderly participants' RTs in the allocentric task, the analysis of the slopes revealed that the speed of the mental transformation was slower for elderly participants. This result is in line with the classical finding that the speed of the mental transformation is disproportionally affected by aging (Dror & Kosslyn, 1994; Sliwinski & Hall, 1998). Differently from the egocentric task, RTs in the allocentric task were not modulated by stimulus orientation, thus demonstrating the fundamental difference between the egocentric and the allocentric mental transformation in our tasks: the egocentric task was subject to biomechanical constraints (i.e., the medial-lateral effect) while the allocentric task was affected only by the angle of stimulus rotation. However, we also found that the orientation of the visual stimulus influenced the speed of the transformational process (i.e., the slopes) also during the allocentric task. It is possible that, as already discussed for RT data, the young group was not applying MR strategies in this task, therefore modifying the linearity of the RT-distribution. Another possible explanation is that the allocentric transformation would have encompassed sensory-motor processes carrying-over the egocentric transformation from one experimental block to another.

Finally, we found that elderly individuals were selectively more impaired when they performed the egocentric task than when they performed the allocentric task. This effect was present even when the same stimuli and the same response were required in the two tasks. In particular, elderly participants were significantly less accurate and slower than young participants (see Figs. 6 and 7) in judging the laterality of hands shown with awkward hand postures (i.e., lateral orientations). This interaction suggests that the older participants in our study were selectively impaired at applying complex egocentric mental transformations. Our results cannot be explained with a general age-related decline in speed processing (Birren, 1974; McDowd & Craik, 1988; Salthouse, 1996). Rather, they suggest that aging selectively affects sensory-motor brain mechanisms.

It has been shown that older adults are more susceptible than young adults to an increase in memory load rather than an increase in the display load (Fisk & Rogers, 1991), and that they show deficits of visuospatial working memory (Jenkins, Myerson, Joerding, & Hale, 2000). However, the impairment showed by elderly participants cannot exhaustively be interpreted as a working memory deficit. The elderly participants in our study slowed down and performed less accurately with lateral, but not with medial hand orientations. There was no difference in the RTs and accuracy between the younger group and the older group in MR of medial hand orientations. Given that the amplitude of the angular departures for medial and lateral orientations is exactly the same, it is logical to assume that the working memory load is kept constant between the two factor levels. What differs between medial and lateral hand orientations is the relative involvement of multisensory and sensory-motor mechanisms respectively.

Dissociations such as the one we reported reveal that mental changes in aging are not always generalized. Indeed our study clearly shows that aged healthy individuals meet considerable difficulties in applying MI, especially when the egocentric frame to be updated requires biomechanically complex transformations. This notion is supported by a specific deficit in performing mental transformations to laterally-oriented hands, as measured by the slope of the RTs linear function. On the other hand, as revealed by the analysis of the intercepts, the hemispheric sensitivity for body parts in facilitating motor responses seems to be well preserved among healthy elderly individuals. Finally, the disproportionate medial–lateral effect on accuracy and RTs reported here directly suggests that aging is associated with a specific degradation of sensory-motor cerebral mechanisms that are critical for the ability to imagine and to program body movements.

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