When I am (almost) 64:

the effect of normal ageing on implicit motor imagery in *young elderlies*.

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Abstract

Motor imagery (M.I.) is a cognitive process in which movements are mentally evoked without overt actions. Behavioral and fMRI studies show a decline of explicit M.I. ability (e.g. the mental rehearsal of finger oppositions) with normal ageing: this decline is accompanied by the recruitment of additional cortical networks.

However, none of these studies investigated behavioral and the related fMRI ageing modifications in implicit M.I. tasks, like the hand laterality task (HLT).

To address this issue, we performed a behavioral and fMRI study: 27 younger subjects (mean age: 31 years) and 29 older subjects (mean age: 61 years) underwent two event-related design fMRI experiments. In the HLT, participants were asked to decide whether a hand rotated at different angles was a left or right hand. To test the specificity of any age related difference in the HLT, we used a Letter Rotation Task as a control experiment: here subjects had to decide whether rotated letters were presented in a standard or a mirror orientation.

We did not find any group difference in either behavioral task; however, we found significant additional neural activation in the elderly group in occipito-temporal regions: these differences were stronger for the HLT rather than for the LRT with group by task interactions effects in right occipital cortices.

We interpret these results as evidence of compensatory processes associated with ageing that permit a behavioral performance comparable to that of younger subjects. This process appears to be more marked when the task specifically involves motor representations, even when these are implicitly evoked.

1. Introduction

Motor imagery as a window on motor representations.

Motor imagery (M.I.) is a mental state during which movements are mentally evoked and rehearsed without overt actions (Jeannerod and Decety, 1995).

A functional equivalence between M.I. and real movement execution is suggested by several lines of evidence: for example, the isochronism of the physical and mental performances of the same action, (see for example Decety et al., 1989), and the impact of biomechanical constraints on M.I. performance (Sekiyama, 1982; Parsons, 1994). Moreover, TMS and EMG evidence show a pre-activation of motor pathways during motor imagery tasks (Li et al., 2004; Roosink and Zijdewind, 2010), while a partial overlapping of the neural networks activated during motor execution and imagination was revealed by PET and fMRI (see for example Hanakawa et al., 2003).

Motor imagery is also being used as a Trojan horse to explore the organization of the motor system where the presence of an explicit motor outflow might be not desirable (e.g. in clinical conditions characterized by involuntary movements like, Gilles de la Tourette Syndrome – see Zapparoli et al., 2015a; Zapparoli et al., 2015b) or, in combination with fMRI, as a tool to detect residual awareness in patients unable to do so, such as, for example, patients with a diagnosis of vegetative state (Owen et al., 2006).

An exciting new exploitation of motor imagery activity is being implemented in the area of neuroprosthetics: it has been shown that neural signals from posterior parietal cortex, decoded during a motor imagery behavior, can govern a robotic limb in a tetraplegic patient and encode complex aspects of motor planning, including motor goals (Aflalo et al., 2015) while signals decoded from motor cortex would encode continuous control signals as those needed for reaching tasks (Hochberg et al., 2006; Hochberg et al., 2012).

All this evidence is a clear vindication of the fact that during motor imagery subjects are capable of recruiting motoric representations and these findings provide the rationale for using M.I. in a variety of basic research and clinical domains for the study of motor neurocognition as well as in rehabilitation programs (for a review see Mulder, 2007) .

For example, M.I. trainings have been used in motor rehabilitation after stroke with variable fortunes (Wu et al.; Page et al., 2001; Jackson et al., 2003; Jackson et al., 2004; Dunsky et al., 2006), after brain injury (Liu et al., 2004; Sacco et al., 2011), in movement disorders (Braun et al., 2011; Heremans et al., 2011), but also as a complementary treatment of non-neurological patients to boost motor recovery after orthopedic surgery (Christakou and Yannis, 2007; Lebon et al., 2012).

M.I. has been also used to reinforce motor skills learning in healthy subjects (Lafleur et al., 2002; Gentili et al., 2006), including athletes (Moran et al., 2012).

Explicit and Implicit Motor Imagery

The action simulation involved in M.I. can be triggered explicitly or an implicitly, depending on the instructions and task characteristics.

In Explicit M.I., subjects are directly asked to imagine themselves executing the required actions (e.g., “Imagine flexing and extending your fingers” Ehrsson et al., 2003) and to focus on kinesthetic bodily sensation by taking a first-person egocentric perspective.

Explicit M.I. skills are indirectly investigated with self-report questionnaires or mental chronometry paradigms; the isochronism of executed and imagined movements is taken as evidence that explicit M.I. has motoric components (Collet et al., 2011).

On the other hand, in implicit tasks the M.I. process may be triggered without explicit reference to the concept of M.I. during “prospective action judgments” (Jeannerod and Frak, 1999), as in the Grip Selection Task, where subjects are asked to judge whether a tool is oriented conveniently for being grasped with the right or with the left hand (Seurinck et al., 2004; Jenkinson et al., 2009; Daprati et al., 2010); another example of an implicit M.I. task is the Hand Laterality Task (HLT), where subjects are asked to decide whether hands portrayed in a picture (rotated at different angles) are the left or right one. It is believed that during this task subjects unconsciously simulate a mental rotation of their own hand to match the position of the depicted hand stimulus, hence producing "motorically driven perceptual decisions" (Parsons, 1987b). The contribution of a motoric component during the HLT is supported by several PET and fMRI studies showing the involvement of the premotor cortices (the lateral premotor cortex and the SMA), of posterior parietal cortices (the superior parietal lobule and intraparietal sulcus) and the cerebellum (Bonda et al., 1995; Parsons et al., 1995; Kosslyn et al., 1998; Vingerhoets et al., 2002; Wraga et al., 2003; Seurinck et al., 2004; de Lange et al., 2005; Ferri et al., 2012; Zapparoli et al., 2014).

The motoric nature of implicit M.I. is also demonstrated by studies on patients with severe motor impairment: Conson et al. (2008, 2010) investigated the role of descending motor pathways on mental simulation of actions using the HLT in locked-in patients; in the first study (2008) they showed a specific impairment only in HLT, associated with the absence of visuo-motor compatibility or biomechanical effects, while normal performance was recorded in the mental rotation of external objects (Conson et al., 2008; Conson et al., 2010). More recently, Fiori et al. (2013) replicated these findings in patients with amyotrophic lateral sclerosis (Fiori et al., 2013a).

The involvement of motor representations seems to be view-dependent, with greater engagement of kinesthetic strategies and larger enrolment of motor cortical networks when hands are displayed in a palm-view perspective (ter Horst et al., 2010; ter Horst et al., 2012; Bläsing et al., 2013; ter Horst et al., 2013; Zapparoli et al., 2014).

Because of the implicit nature of the mechanisms whereby motor representations are evoked by tasks like the HLT, a specific potential use in rehabilitation could be envisaged for clinical conditions like hemiplegia accompanied by anosognosia in which patient cooperation with explicit strategies may be lacking in spite of some sparing of cortical motor regions and their function (Gandola et al., 2014).

Motor Imagery in the life cycle: behavioral and fMRI findings

There is also a well-documented decline or reshaping of M.I. as a result of normal ageing (Personnier et al.; Skoura et al., 2005; Personnier et al., 2008; Skoura et al., 2008; Saimpont et al., 2009; Malouin et al., 2010; Personnier et al., 2010; Zapparoli et al., 2013). Malouin (2010) reported age-related quality changes in explicit M.I. vividness, associated with an age-related decline in visuo-spatial and kinesthetic working memory (Malouin et al., 2010). Chronometric studies revealed a loss of temporal congruence between motor execution and explicit M.I., especially for unusual and constrained movements (Personnier et al.; Skoura et al., 2005; Personnier et al., 2008; Skoura et al., 2008; Personnier et al., 2010; Zapparoli et al., 2013). These changes were accompanied by neurofunctional changes, such as the over-recruitment of occipito-temporal areas, suggesting the adoption of a complementary strategy based on visual imagery to compensate for M.I. decline (Zapparoli et al., 2013).

To date, only a few behavioral studies investigated the influence of ageing on **implicit M.I.** processes, the focus of our investigation here. Saimpont and colleagues (2009), for example, reported a decline in the ability to implicitly simulate hands movements in elderly subjects, with longer RTs and lower accuracy, especially for the non-dominant hand and for stimuli presented in awkward positions with reference to the biomechanical constraints imposed by the stimuli. Devlin & Wilson (2010) found similar results, showing a decline in the elderly's performance in the HLT but also in a whole-body mental rotation task: they speculate that age-related changes in M.I. could be due to disruption of body schema (Devlin and Wilson, 2010).

A combination of the classical HLT in an egocentric reference frame and the same task in an allocentric-reference frame has been used in a recent study by De Simone et al. (De Simone et al., 2013) to compare multisensory, sensory-motor, and visual aspects of implicit M.I. in elderly and younger people. During both tasks subjects were shown pictures of rotated hands with a red dot depicted on the extremity of the little finger or ring finger, or the index finger or thumb. In the egocentric laterality task they were asked to report whether the presented hand was a right or a left one, while in the allocentric task subjects were asked to report whether the dot was on the left or on the right side of the hand as it would be seen in the upright position (De Simone et al., 2013). They showed that elderly participants were less accurate and slower for biomechanically awkward hand postures only when performing the HLT in an egocentric-reference frame; they concluded that ageing is associated with a specific degradation of the sensory-motor mechanisms necessary to perform complex effector-centered mental transformations (De Simone et al., 2013).

It is worth noting that the aforementioned studies are based on elderly subjects on average in their mid-seventies. It remains unknown what happens in younger elderlies, one and a half decades earlier[1]. Do they have preserved implicit motor imagery skills, and if so, are these subserved by the same functional anatomical patterns as in younger adults?

In the domain of healthy ageing, no study has yet investigated these issues nor is it known whether the eventual preservation of imagery abilities of young elderlies is based on compensatory mechanisms of some kind.

Given the rich literature on neurofunctional compensation processes in ageing, one could expect to observe a different pattern of activation in young elderly subjects, which could be considered a successful compensatory process or a compensatory attempt, depending on whether the performance reaches a level similar to that of younger subjects (Berlingeri et al., 2010).

On the basis of our previous work (Zapparoli et al., 2013), we hypothesize a greater activation of visual cortices in elderly subjects.

Aim of the study

The aim of this study was to investigate the behavioral and fMRI effects of normal ageing on implicit motor processes, by using a classical HLT paradigm (Parsons, 1987b; Zapparoli et al., 2014). We did so by comparing behavioral and fMRI patterns of 27 young (mean age 30 years) and 29 young elderly (mean age: 61 years) healthy subjects.

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[1] For a long time the seventh decade, perhaps because it coincides with retirement for most people, was considered synonimus of old age. Socio-economical and medical progress, and the increased proportion of surviving late elderlies may have moved the popular definition of senescense to the 8th decade in economically developed countries (Orimo H, Hideki I, Suzuki T, Araki A, Hosoi T, Sawabe M. Reviewing the definition of “elderly”. Geriatrics & Gerontology International 2006; 6(3): 149-58.)

In the same study we explored the specificity of any age-related change in the HLT behavior and/or functional anatomical patterns: to do so, the same subjects were also challenged with a Letter Rotation Task (LRT) during which they had to decide whether rotated letters were presented in standard or mirror orientation. On the basis of our previous work on ageing in explicit motor imagery on young elderlies of the same age we predicted a shift towards the visual cortices in the HLT for the elderly because of an impoverished ability to do imagery in a motor modality; this prediction would be fulfilled if such shift were greater for the HLT than for the LRT.

2. Materials and methods

2.1 Participants and neuropsychological assessment

27 young subjects (12 M/15 F; mean age: 31 years, SD: 9 years) and 29 elderly subjects (15 M/14 F; mean age: 61 years; SD: 7 years) underwent two event-related fMRI experiments. The socio-economical status was middle class in both groups; and the educational level was matched (young subjects: 16 years, SD: 2.9; elderly subjects: 15 years, SD: 3.7).

None of the subjects had a history of neurological or psychiatric illness. All were right-handed as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). The study was approved by the Local Ethics Committee (Comitato Etico Azienda Sanitaria Locale Città di Milano), and informed written consent was obtained from all subjects, according to the Helsinki Declaration (1964). All subjects participated after the nature of the procedure had been fully explained. A brief neuropsychological assessment was performed on each participant. The neuropsychological battery included a summary index of cognitive functioning, the Mini-Mental State Examination (Folstein et al., 1975), and a series of more specific neuropsychological tests assessing cognitive functions: Raven's Coloured Progressive Matrices to test abstract reasoning (Raven, 1984), short story recall (Novelli et al., 1986), and delayed recall on the Rey-Osterrieth complex figure for long-term verbal and visuo-spatial memory (Carlesimo et al., 2002), as well as the Frontal Assessment Battery (FAB, Dubois et al., 2000). None of the subjects obtained a single pathological score in the neuropsychological test battery.

2.2 Experimental task

2.2.1 Experimental Stimuli

Hand Laterality Task (HLT)

For the first fMRI experiment we used a classic hand laterality judgment task, similar to the one proposed by Parsons (Parsons, 1987b).

Subjects were shown photos of right or left hands, in palm or in back view, differently rotated their in 8 possible angles (starting at 0° and proceeding by 45° increments: 0°, 45°, 90°, 135°, 180°, 225°, 270°, and 315°). A total of 64 experimental stimuli were presented (2 x 8 angles of rotation x 2 hands x 2 [the palm or back of the hand]) (see also Figure 1).

The baseline stimuli were 64 scrambled pictures derived from the hands' experimental images. Each scrambled image had a green or a pink square in the centre.

We administered for the HLT a total of 128 stimuli (64 experimental stimuli and 64 baseline stimuli).

Letter Rotation Task

In the second fMRI experiment we used a Letter Rotation Task (LRT).

Subjects were shown photos of two different letters (J or F), rotated by different rotation angles (starting at 0° and proceeding by 45° increments: 0°, 45°, 90°, 135°, 180°, 225°, 270°, and 315°).

We chose these letters to be in line with recent studies investigating the same issue in Amyotrophic Lateral Sclerosis and in Spinal Cord Injury patients (Fiori et al., 2013a; Fiori et al., 2013b). As indicated in these papers, F and J were chosen because “their asymmetry was comparable to that of hands”. Subjects had to decide whether the letters were presented in standard or mirror orientation.

A total of 64 experimental stimuli were presented (2 x 8 angles of rotation x 2 letters x 2 orientations).

The baseline stimuli were 64 scrambled pictures derived from the letters' pictures.

Each scrambled image had a green or a pink square in the centre.

We administered for the LRT a total of 128 stimuli (64 experimental stimuli and 64 baseline stimuli).

2.2.2 Experimental Procedure

The participants practiced each task before the scanning session: subjects were familiarized with the stimuli by performing half of the trials (32 trials). We saw that this length made the subjects' enough confident with the task, as demonstrated by a short debrief directly after the training. Moreover, the number of experimental trials used during the training (32) was in line with the one used in previous behavioural studies on the same issue (see Saimpont et al., 2009). During this training, warning feedback was given in case of an error.

Each task was performed in a separate run, for a total of 2 fMRI runs; in each run experimental and baseline stimuli were randomly alternated according to an event-related design.

Each stimulus remained visible for 4000 ms and was preceded by a fixation point in the centre of the screen: the inter-stimulus interval (ISI) was jittered and it was randomly varied from 750 ms to 1250 ms. Subjects were asked to report whether they were shown a right or a left hand or whether they were shown a standard or mirrored orientated letter by pressing a button with their right or left index fingers. We did not give them any suggestion about the mental strategy to apply to solve the task, given the implicit nature of the task and according to the definition of implicit M.I. (see for example De Lange et al., 2005b in which they found that using different instructions for the same HLT task provides different results).

For the scrambled images, subjects had to respond with the right index finger when they saw a green square or with the left index finger when the square was pink. Accordingly, the contribution of the laterality of the motor response was controlled for in the analyses of each task. The experimenter reminded the participants to be fast and accurate in responding.

RTs and accuracy were recorded. The stimuli were delivered using the fibre-optic goggles (Visuastim, Resonance Technology Inc.). Responses were given through two response boxes (one for each hand).

2.3 Statistical analyses of the behavioral data

Mean accuracy and response time (RT) were calculated for each participant. Accuracy was defined as the proportion of correct responses, while RTs corresponded to the interval between the onset of the stimulus and subjects' button press. Individual performance was considered above chance level when the overall accuracy was greater than 60% (Saimpont et al., 2009). Two elderly subjects did not reach this criterion for the LRT task and so was excluded from the study.

The accuracy data were analyzed by means of a non-parametric test (Kolmogorov-Smirnov test for independent samples).

We excluded from the analyses inaccurate trials (9.7% for the HLT, 8% for the LRT) and outliers (+/- 2SD: 2.7% for the HLT, 4.1% for the LRT).

Then, for each subject, we subtracted from the RTs of each experimental trial the RTs of the associated baseline trial (simple RTs). This was done to ensure that the potential differences between groups were not related to a generalized age-related decrease of speed in giving motor responses (see for example Nebes, 1978).

The resulting RT data were analyzed as follows:

- HLT: RTs of the participants recorded inside the scanner were analyzed by means of a repeated-measures 2 x 2 x 8 ANOVA with "Hand" (Right/Left), "View" (Palm/Back) and "Angle" (the eight aforementioned angles of rotation) as within factors and "Group" (Elderly/Young) as a between factor. We had to exclude two elderly subjects to perform this analysis. The different hands' views were then classified as medially oriented or comfortable, that is, pointing towards the body midline or laterally oriented or awkward, that is, pointing laterally (see Figure 1). To analyze these effects we performed an ANOVA, with “Position” (Awkward/Comfortable), “Hand” (Left/Right) and “View” (Palm/Back) as within-group factors and “Group” (Elderly/Young) as a between-group factor.

- RTs of the participants recorded inside the scanner were analyzed by means of a repeated-measures 2 x 2 x 8 ANOVA with “Letter” (Right/Left), “Orientation” (Canonical/Mirror) and “Angle of Rotation” (the eight aforementioned angles of rotation) as within factors and “Group” (Elderly/Young) as a between factor.

2.4 fMRI data acquisition and analysis

MRI scans were performed using a 1.5 T Siemens Avanto scanner, equipped with gradient-echo echo-planar imaging (flip angle 90°, TE=60 msec, TR=3000 msec, FOV=280 x 210 mm and matrix= 96 x 64).

We collected 225 volumes for each task, in two separate runs. The first 10 volumes of each sequence (corresponding to task instructions) did not correspond to any stimulation and were discarded from the analyses.

Preprocessing

After image reconstruction, raw data visualization and conversion from DICOM to the NIFTI format were performed with MRIcron (www.mricro.com) software.

All subsequent data analyses were performed in MATLAB 2013b (Math Works, Natick, MA, USA), using the software Statistical Parametric Mapping (SPM8, Wellcome Department of Imaging Neuroscience, London, UK). First, fMRI scans were realigned to correct for any movement during the experiment; the realigned images were then stereotactically normalized into the MNI-EPI fMRI template to permit group analyses of the data (Friston et al., 1995; Ashburner and Friston, 1999). At this stage, the data matrix was interpolated to produce voxels with the dimensions 2 x 2 x 2 mm.

The stereotactically normalized scans were smoothed using a Gaussian filter of 10 x 10 x 10 mm to improve the signal-to-noise ratio.

Statistical analyses of the fMRI data

The BOLD signal associated with each experimental condition was analyzed by a convolution with a canonical hemodynamic response function (Worsley and Friston, 1995). Global differences in the fMRI signal were removed from all voxels with proportional scaling. High-pass filtering (128 s) was used to remove artifactual contributions to the fMRI signal, such as physiological noise from cardiac or respiratory cycles.

A fixed-effect analysis was done for each subject to characterize the BOLD response associated with each task, as opposed to its baseline condition[2], before entering the relevant contrast images into a random-effect analysis. Specific regressors were defined for each of the four classes of events (for the HLT: palm or back view, left or right hand; for the LRT: canonical or mirror view, F or J letter) and the time locked baseline conditions. Error trials (errors and missing responses), outliers and the time-matched baseline trials were excluded from the analysis.

Group levels analyses were done by using a second-level full factorial design conforming to a random-effect analysis in order to make a population-level generalization of the statistical inferences (Holmes and Friston, 1998; Penny and Holmes, 2004).

Four contrast images were brought to the second level analysis, one for each condition of interest; for the HLT: Hand (Right or Left); View (Palm or Back); for the LRT: Letter (F or J), Orientation (Standard or Mirror), after subtracting out the BOLD response for the time matched events of the baseline condition.

The full factorial ANOVA generated F-contrasts for the main effect of view and hand, and for the hand x view interaction effects and similar effects for the conditions of the LRT. Post-hoc analyses to examine the direction of the aforementioned effects were performed using linear contrasts to

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[2] Accordingly, the contribution of the laterality of the motor response was controlled for in the analyses of the M.I. task at the second level as well.

generate SPM[t] maps. To minimize the impact of the RTs on the results, these were treated as a confounding covariate.

Well-known general effects like the main pattern of activation for the HLT or for the LRT are described in Supplementary Table 1 and in Supplementary Figure 1.

In the following section we rather describe all the effects whose relevance was anticipated by the behavioral results. The specificity of the between group differences were then assessed by comparison with the LRT data.

1. HLT

1a. Effects shared by young and elderly subjects: regardless of the experimental group, we first evaluated the neurofunctional counterparts of the main behavioral effects such as for example the effect of view, of hand or the interactions between these factors.

1b. Between-groups differences: activation pattern differences between the two groups for the HLT.

1c. Correlations between fMRI and behavioral HLT measures: the behavioral measures were used as a predicting covariate of the fMRI patterns;

2. LRT: between group comparison of the LRT.

3. Group by task interaction effects: the magnitude of the between group activation difference for the HLT was compared with that of the same between group difference for the LRT.

Moreover, we ran a further full factorial ANOVA with the same approach on the HLT data, looking characterize the neural underpinnings of the biomechanical effects; “Position” (Awkward/Comfortable) and “View” (Palm/Back) were the within factors and “Group” (Elderly/Young) the between factor.

Each effect was visualized at the voxelwise threshold of $p<0.001$ (uncorrected). We further considered only cluster significant at $p<0.05$ for its spatial extent. In the paper we describe also the level of correction for multiple comparisons met by each peak of these clusters.

3. Results

3.1 Behavioral results

3.1.1 Hand Laterality Task

We first determined whether there were behavioral differences between the two groups in terms of accuracy: there were none. The Kolmogorov-Smirnov test for independent samples did not highlight any significant difference in any of the experimental conditions (Right back: p=0.4, Right palm: p=0.6, Left back: p=0.9, Left palm: p=0.6). The mean accuracy was 89% for the elderly group and 92% for the young group.

Then, we looked at the RTs, by means of a 2 x 2 x 8 repeated-measures ANOVA on RTs with "Group" (Elderly/Young) as a between factor and "Hand" (Right/Left), "View" (Palm/Back) and Angle (from 0° to 315° in steps of 45°) as within factors.

These results are also summarized in Figure 2.

<u>Main effects</u>

Hand: F(1, 52)=12.7; **p=0.001**; η^2=0.19, with faster RTs for the right hand.

View: F(1, 52)= 55.72; **p<0.001**; η^2=0.52, with the longest RTs for the palm view.

Angle: F(4.6, 242.9)=42.7; **p<0.001**; η^2=0.45, with the RTs increasing with respect to increasing angles of rotation.

Group: F(1, 52)=0.9; p=0.36; η^2=0.002.

<u>Across Group Interactions</u>

View*Angle: $F(4.3, 223.2)=23.16$; **$p<0.001$**; $\eta^2=0.31$.

For the back-of-the-hand views, there was a similar inverted U-shaped response, with the longest RTs at 180° degrees; for the palm views, the longest response time was for the 90°L rotation. As described in Figure 1, these views correspond to the most unnatural or less-frequently observed views of the palms because these can be produced only by a very artificial intra-rotation of a supinated hand with the elbow facing the sternum. See Figure 2a.

Hand*View: $F(1, 52)=4.3$; **$p=0.04$**; $\eta^2=0.08$, with a significantly larger view-dependent difference for the right hand (see Figure 2b).

Hand*Angle: $F(5.77, 300.42)=2.83$; **$p=0.012$**; $\eta^2=0.52$, with RTs generally faster for the right hand with the exception of the angle 270° in which the left hand was slightly faster than the right one; Hand*View*Angle: $F(5.03, 261.55)=2.01$; $p=0.08$; $\eta^2=0.037$.

Group by task Interactions

View*Group: $F(1, 52)=2.42$; $p=0.13$; $\eta^2=0.04$; Angle*Group: $F(4.6, 242.8)=1.2$; $p=0.2$; $\eta^2=0.02$; Hand*Group: $F(1, 52)=0.21$; $p=0.65$; $\eta^2=0.004$; Hand*View*Group: $F(1, 52)=0.22$; $p=0.64$; $\eta^2=0.004$; Hand*Angle*Group: $F(5.7, 300.42)=0.36$; $p=0.89$; $\eta^2=0.007$; Hand*View*Angle*Group: $F(5.03, 261.6)=0.82$; $p=0.53$; $\eta^2=0.02$.

The second ANOVA, with "Position" (Awkward/Comfortable), "Hand" (Left/Right) and "View" (Palm/Back) as a within-group factor and "Group" (Elderly/Young) as a between-group factor yielded the following results (see Figure 2c). Significant effects presented in bold.

Main effects

Position: $F(1, 52)=82.9$; **$p<0.001$**; $\eta^2=0.61$, with slower RTs for awkward or lateral positions.

View: $F(1, 52)=75.1$; **$p<0.001$**; $\eta^2=0.59$, with the well-established slower RTs for the palm view.

Hand: $F(1, 52)=9.3$; **$p=0.004$**; $\eta^2=0.15$, with faster RTs for the right hand.

Group: $F(1, 52)=0.06$; $p=0.85$; $\eta^2=0.001$.

Across Group Interactions

View*Position: $F(1, 52)=24.9$; **$p<0.001$**; $\eta^2=0.32$, with a **longer RTs particularly for awkward positions for the stimuli presented in the palm view** (cfr. our previous data: Zapparoli et al., 2014 and Figure 2c); Hand*View: $F(1, 52)=1.2$; $p=0.26$; $\eta^2=0.02$; Hand*Position: $F(1, 52)=0.14$, $p=0.7$; $\eta^2=0.003$; Hand*View*Position: $F(1, 52)=1.6$; $p=0.21$; $\eta^2=0.03$.

Between Group Interactions

Hand*Group: $F(1, 52)=0.16$; $p=0.69$; $\eta^2=0.003$; View*Group: $F(1, 52)=4.56$; $p=0.04$; $\eta^2=0.08$, with stronger differences between the two groups for the palm view; Position*Group: $F(1, 52)=2.3$; $p=0.14$; $\eta^2=0.04$; Hand*View*Group: $F(1, 52)=0.23$; $p=0.63$; $\eta^2=0.004$; Hand*Position*Group: $F(1, 52)=1.77$; $p=0.19$; $\eta^2=0.032$;View*Position*Group: $F(1, 52)=1.81$; $p=0.19$; $\eta^2=0.03$; View*Position*Hand*Group: $F(1, 52)=0.31$; $p=0.58$; $\eta^2=0.006$.

3.1.2 Letter Rotation Task

The Kolmogorov-Smirnov test for independent samples did not highlight any significant difference between the two groups in terms of accuracy in any of the experimental conditions (F Canonical: p= 0.4, F mirror: p=0.2, J Canonical: p=0.9, J mirror: p=0.4). The mean accuracy was 90% for the elderly group and 94% for the young group.

The repeated-measures 2 x 2 x 8 ANOVA with “Letter” (Right/Left), “Orientation” (Canonical/Mirror) and “Angle of Rotation” (the eight aforementioned angles of rotation) as within factors and “Group” (Elderly/Young) as a between factor yielded the following results (see Figure 3). Significant effects presented in bold.

Main effects

Letter: $F(1, 52)=34.32$; **$p<0.001$**; $\eta^2=0.4$, with faster RTs for the letter “F”; **Orientation**: $F(1, 52)=79.53$; **$p<0.001$**; $\eta^2=0.6$, with faster RTs for the canonical orientation; **Angle**: $F(5.2, 266.8)=49.48$; **$p<0.001$**; $\eta^2= 0.49$, with the RTs increasing with respect to increasing angles of rotation (See Figure 3); Group: $(1, 52)=0.74$; $p=0.39$; $\eta^2=0.14$.

Across Group Interactions

Letter*Angle: $F(5.8, 300.1)=6.65$; **$p<0.001$**; $\eta^2=0.11$, with faster RTs for the letter "F" with the exception of the angle 45°; **Letter*Orientation**: $F(1, 52)=4.47$; **$p=0.39$**; $\eta^2=0.81$; Letter*Angle*Orientation: $F(5.7, 290.99)=2.99$; $p=0.009$; $\eta^2=0.05$.

Between Group Interactions

Letter*Group: $F(1, 52)=0.001$; $p=0.99$; $\eta^2=0.001$; Orientation*Group: $F(1, 52)= 2.43$; $p=0.12$; $\eta^2=0.04$; Angle*Group: $F(5.2, 266.8)=0.80$; $p=0.56$; $\eta^2=0.01$. Letter*Angle*Group: $F(5.9, 300.3)=0.82$; $p=0.55$; $\eta^2=0.02$. Letter*Angle*Orientation*Group: $F(5.7, 290.9)=0.8$; $p=0.56$; $\eta^2=0.02$.

3.2 fMRI results

3.2.1 Hand Laterality Task

Across groups effects.

The effects shared by both young and elderly subjects were in line with our previous findings and supported the behavioral effects (Zapparoli et al., 2014).

The **factor "VIEW"** was highly significant: post hoc analyses (by means of linear t-contrasts) revealed that these were all due to greater activation for **the palm view** stimuli with stronger activity at the level of the left superior and middle frontal gyri, the left SMA, and the left inferior and superior parietal lobule; on the other hand, **the back-view** stimuli were associated with specific recruitment of the lingual gyrus bilaterally and the right precuneus (see Figures 4a and 4b and Tables 1a and 1b).

The **factor "HAND"** was also highly significant**,** with larger BOLD signal for stimuli depicting **left hands** in bilateral anterior regions (middle frontal gyrus, precentral gyrus), in right mid cingulum, and postcentral gyrus. As subjects responded with the left hand during the baseline as many times as during the experimental task, this effect cannot be explained by the mere implementation of the motor response. Further left hand larger activations were also found in posterior regions including fusiform gyrus, lingual gyrus and cerebellum in the left hemisphere (see Figure 4c and Table 1c). These results confirm our previous observations on the greater neural labor needed to process hand stimuli in palm view and depicting left hands.

The "View by Hand" interaction was also significant with specific effects in bilateral SMA, due to a comparatively smaller BOLD response for both elderly and young subjects for the back view of the right hand (see Figure 5 and Table 1d). A plot of the hemodynamic responses is illustrated in Figure 5.

Importantly, there were also **between-group differences**: the elderly subjects showed larger activations in the bilateral inferior frontal gyrus (opercular region), the superior parietal lobule and in the angular gyrus. Further hyperactivations were found in the precentral gyrus and in the inferior parietal lobule of the left hemisphere. Additional recruitments were also observed in the occipital lobe (superior and middle occipital gyri, lingual gyrus), in the calcarine fissure and in the fusiform gyrus bilaterally (see Figure 6a and Table 2a). On the other hand, the comparison Young > Elderly did not yield a significantly increased BOLD signal in any brain region.

To further explore the relationship between the hyperactivations recorded in the elderly subjects and their behavioral performance, their fMRI data were correlated with the RTs during the HLT in a linear regression analysis.

The analysis was restricted to the regions of significant hyperactivation in the elderly. A $p<0.005$ significant negative correlation was found in the left lingual gyrus whereby the higher the neural activity the better the behavioral performance (see Figure 7).

3.2.2 Hand Laterality Task: biomechanical constraints effect

The results showed a significant main effect of the factor "Position", with greater recruitment of motor regions associated with comfortable positions; moreover, we also recorded a significant

"Position by View" interaction: the greater recruitment of motor regions for comfortable positions was more marked for hands presented in palm view, in line with the behavioral results (see Figure 8 and Table 1e).

3.2.3 Letter Rotation Task

We found an over-recruitment in the elderly group at the level of the left middle occipital gyrus, the left calcarine fissure and the left superior parietal lobule in elderlies compared with youngers, whereas the opposite contrast (Young > Elderly) did not reveal any significant hyperactivation in the young group (see Figure 6b and Table 2b).

The other comparisons (letter F vs letter J or canonical view vs mirror view) did not yield a significantly increased BOLD signal in any brain region.

3.2.3 Group by task second order interaction effect.

We found a significant second order interaction effect, with the elderly group having increased hyperactivation for the HLT task that was significantly greater than for the LRT. These effects were in the right lingual gyrus and in the right superior occipital gyrus (see Figure 6c and Table 2c).

5. Discussion

The aim of the present study was to investigate the influence of normal ageing in its early stages on implicit motor imagery processes. To do so, we used the classic Hand Laterality Task. The specificity of any ageing related finding in the HLT was tested by comparison with another visual mental imagery task, the letter rotation task, which was delivered both in a behavioral setting and during fMRI. The presence of this control task and the relatively large sample of subjects (58 overall) makes our inference on aging effects in implicit motor imagery specific and solidly-grounded.

HLT is considered an implicit motor imagery task: it is widely believed that during the task subjects rely on a mental rotation of their own hand to match the position of the one presented on the screen (Parsons, 1987a). This task has been largely used for studying motor representations in both normal subjects or brain-damaged patients (McAvinue and Robertson, 2008), as it provides measureable indexes of motor imagery processes in the form of RT and accuracy and, importantly, their dependencies from biomechanical constraints (Parsons, 1987a; Parsons, 1987b).

The results of our study demonstrate for the first time the existence of significant neurofunctional effects of early ageing on the neural substrates of these implicit motor mechanisms.

We start this section by discussing our behavioral findings, considering both across- and between-group effects: the behavioral component of the study was important for interpreting the fMRI patterns, because it allowed us to determine whether any hyper- or hypo-activation in ageing was a sign of successful compensation or an unsuccessful compensatory attempt (for discussion and illustration of multiple behaviour fMRI scenarios, see Berlingeri et al., 2010).

We then address the meaning of the neurofunctional differences associated with ageing, that were mainly located in occipital regions; brain areas whose hyperactivations have already been associated with successful compensation in other studies on ageing (Berlingeri et al., 2010; Zapparoli et al., 2013).

Finally, we will discuss the relevance of our findings for the more general understanding of the effect of ageing on motor control.

Behavioral findings

Our findings suggest that the HLT is performed via a combination of cognitive strategies including visual, somesthesic and motoric ones. Given a fixed set of instructions, each of these may have prevailed depending on the view and rotation angle of each stimulus and the ensuing biomechanical constraints on any motor simulation strategy. As we shall discuss, the relative weight of each component, and their age-related changing weight, can be inferred, at least in part, from the behavioral pattern and by some form of educated reverse inference on the fMRI data. We start here with the behavioral patterns.

For both young and elderly subjects, we observed that the view of the back of the hand was associated with faster reaction times; this was particularly true for the right hand. Moreover, a significant view-by-angle interaction effect was detected: for the back view, there were longer RTs for the 180° rotation pointing downwards, with RTs showing an inverted U-shape on the basis of the orientation angle; one possible explanation for these particular RTs distribution is that hand orientations around 0° conform to an egocentric perspective being "motorically familiar", whereas those around 180° are treated as external objects according to an allocentric perspective; these stimuli would be "motorically unfamiliar" as they would imply positions that are awkward or even impossible to take. Brady et al. (2011) maintained this hypothesis and used d' and RT measurements, to find a clear split in performance for egocentric and allocentric views of the back of the hands (Brady et al., 2011)[3].

On the contrary, for the palm view, the longest RTs were for hand rotations that, if imagined with one's own hand, would require an awkward intra-rotation of the elbow to face the sternum with the hand in a supinated position.

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[3] Brady et. al (2011) considered only back-viewed stimuli: several of these were explicitly cueing to someone else's hand (e.g. hands in hand-shacking position pointing to the observer), therefore cuing quite obviously to an "extra-personal" perspective. Our stimuli were canonical 2D stimuli with an equal number of back- and palm views of the hands.

Finally, for the different hand rotations classified into the categories described by Parsons et al. (1987b), we found a significant effect of the biomechanical constraints, with slower RTs for awkward positions, and interaction effect whereby the awkward positions required longer processing times especially for the palm view.

Taken together, these observations suggest that both groups were performing the task according to expectations based on data collected from different subjects in previous experiments who were behaving in more ecological settings (Parsons, 1987a)see also Zapparoli et al., 2014).

The crucial part of our behavioral findings was the exploration of the between-group effects which revealed that the elderly group was comparable to the group of younger subjects, both in terms of accuracy and normalized RTs; these findings may seem in contrast with previous studies that explored the same issue (Saimpont et al., 2009; Devlin and Wilson, 2010; De Simone et al., 2013).

Saimpont and colleagues (2009), for example, found that elderly subjects were overall nearly as accurate as younger subjects while performing the HLT (90 % overall accuracy in elderlies vs 96% in youngers); however, they had longer RTs and a closer look at the accuracy data reveals that the older subjects were less precise particularly for stimuli corresponding to biomechanically awkward positions, like the palm of the hand at 90° or the back of the hand at 180° (see for example ter Horst et al., 2010). The authors concluded that elderly subjects suffer from an impairment in visuo-perceptual processing in ways that are constrained by biomechanical motoric factors, with a specific decline when hands were depicted in awkward positions (Saimpont et al., 2009).

In line with Saimpont et al.'s (2009) findings, De Simone et al. (2013) also showed that elderlies were less accurate and slower while preforming HLT in an egocentric-reference frame (De Simone et al., 2013). On the other hand, Devlin & Wilson (2010) found that elderly people are slower but not less accurate (Devlin and Wilson, 2010).

However, the discrepancy between our findings and the aforementioned studies may be explained by two main factors: first, the different mean age of the elderly participants in the studies: 61 years in our study versus 78 in Saimpont's study (2009), 72 in De Simone et al. (2013) and 74 in Devlin et al. (2010); it is well documented that a decline in motor performance with healthy ageing can be detected only in fairly old subjects while in young elderly subjects, such as the ones in our sample, performance may remain similar to that of young subjects (see for example Mattay et al., 2002; Wu and Hallett, 2005). This does not deny the possibility that the equivalent behavior could be generated by a re-organized brain, as we will discuss below.

Second, in aforementioned studies, only absolute RT values were considered; to avoid the confound of a global lengthening of RTs for the elderly (see for example Nebes, 1978). Instead, we analyzed "ΔRTs" (RTs associated with experimental trials minus RTs for baseline trials). We adopted this approach because we observed longer absolute RTs in the elderly group that were mirrored by longer RTs also in the baseline conditions, suggesting a general lengthening of motor responses rather than a specific decline in mental motor representations[4].

Taken together, our results suggest that in normal early ageing behavioral performance in implicit motor tasks may stay close to a young-like level; the fMRI experiment allowed us to further explore this finding, investigating whether the two groups also show similar neural patterns (suggesting that early ageing does not affect the domain of implicit motor representation) or different fMRI patterns, a finding that could be explained in terms of successful compensation.

Neurofunctional counterparts of the behavioral data

Across groups effects

We identified view-specific fMRI patterns in motor mental imagery of hands. As revealed by the direct comparison Palm view > Back view, visuo-perceptual judgments for hands displayed in palm view were associated with increased BOLD response at level of left premotor cortices (superior frontal gyrus and SMA) and left somatosensory cortices (postcentral gyrus) as if responses for this class of stimuli were more "motorically driven" (Jeannerod & Frak, 1999) or in need of motoric

[4] In addition, as we will argue, ΔRTs were the appropriate covariate measures for the fMRI analysis as the fMRI dependent variables were differential responses for the HLT and its baseline.

strategies. Indeed, the involvement of these areas in both motor execution and M.I. tasks has been extensively demonstrated (for a meta-analysis, see Hétu et al., 2013).

On the other hand, the contrast Back view > Palm view yielded specific activations in occipital cortices, which have been observed in visual imagery tasks (Guillot et al., 2009), suggesting at least a partial dissociation between the cognitive strategies used to process hand stimuli from different views, as already highlighted by previous literature on young subjects (ter Horst et al., 2010; Bläsing et al., 2013).

It is important to highlight that the stronger premotor recruitment seen for the palm view could not be explained by longer RTs associated with this condition since the impact of RTs on the BOLD response was covaried-out in our fMRI analyses.

This finding was further explored by looking at the Interaction effect "Hand by View": both groups showed a significant interaction at the level of left SMA, with the lowest neural recruitment of this area for the right hand presented in back view, suggesting a minor engagement of kinaesthetic and motoric strategies in both young and elderly participants for a stimulus viewed from this perspective (see Figure 5).

Our findings therefore confirm the behavioral hypothesis of a "privileged status" for the back of the right hand, already seen in young people, and now also in elderly right-handed healthy subjects (Zapparoli et al., 2014).

Implicit motor imagery in healthy ageing: between group differences

Investigation of neurofunctional changes across the adult lifespan has been the aim of many fMRI studies (for a review, see Goh, 2011).

Modifications of fMRI patterns in the elderly have been interpreted as evidence of compensatory processes by a number of studies (Grady et al., 1994; Cabeza, 2002; Cabeza et al., 2002; Buckner, 2004; Davis et al., 2008). When the performance remains comparable with the younger counterparts, compensatory processes manifest themselves in the recruitment of additional brain regions (e.g. Zapparoli et al., 2013) or by a stronger activation of some of the constituent components (e.g., the present study). These patterns have been documented in several cognitive domains (e.g., working memory, episodic memory retrieval, perception, inhibitory control, etc.). This phenomenon was initially observed in the prefrontal cortex and inspired the so-called HAROLD model (Cabeza, 2002), but more recent evidence has shown that the compensatory hyperactivations of the elderly may involve brain regions also outside the frontal lobe, depending on the task (Berlingeri et al., 2010; Berlingeri et al., 2013).

fMRI compensatory processes have been previously described also in the domain of motor function, using a variety of motor tasks, ranging from simple to complex (Mattay et al., 2002; Ward and Frackowiak, 2003; Heuninckx et al., 2005; Zapparoli et al., 2013). These studies showed age-related differences, especially in non-motor brain regions associated with more cognitively demanding tasks, like pre-SMA, which may reflect increased cognitive monitoring of performance (see Nachev et al., 2008 for a review); these differences are usually greater when complex tasks are used (Heuninckx et al., 2005). These findings are interpreted as a sign of ‘‘an adaptable motor network able to respond to age-related degenerative changes in order to maintain performance levels’’ (Ward and Frackowiak, 2003).

Given the vast functional equivalence between motor execution and motor imagery at the cortical level, one would expect a similar scenario also for the motor imagery domain. Only few studies investigated this issue with evidence available only for **explicit** motor imagery processes: these previous studies showed stronger activation of M1 (posterior portion, Sharma and Baron, 2014), SMA and prefrontal regions (Allali et al., 2014), and occipital lobes (Zwergal et al., 2012; Zapparoli et al., 2013; Wang et al., 2014).

Our current findings on implicit processes are partially in line with this literature, reporting additional recruitment of occipital regions (superior occipital and lingual gyri) in elderly people. These regions have been associated with visual imagery of body part movements, which shares common occipital substrates with visual perception (Guillot et al., 2009). We thus confirm the elderly's need of an additional strategy or that they rely more heavily on visual areas to deal with the task, even in implicit motor imagery processes. The linear regression analysis on the elderly subjects' RT data confirmed this hypothesis: the greater the recruitment of these additional regions, the better the behavioral performance (i.e. faster RTs).

It is important to recall that the fMRI differences are specifically related to the domain of motor representation and could not be explained as a general difficulty to mentally manipulate visual stimuli, given the fact that they were significantly greater in the hand laterality task than in the letter rotation task (see Figure 6c).

The hypothesis of compensation processes that occur in the occipital regions is supported by studies investigating M.I. with implicit paradigms in Parkinson's disease (PD) patients: for example, Helmich et al. (2007) studied 19 strongly lateralized PD patients (i.e. one hand was clearly more affected by the disease than the other one) during the execution of the Hand Laterality Task. They reported decreased M.I. abilities in PD patients for the most affected hand, especially when depicted in awkward (i.e. biomechanically less plausible) positions. Moreover, the neurofunctional results showed increased activity in the occipito-temporal cortex (and especially in the extra-striate body area, EBA) during the imagination of movements with the affected hand. The authors concluded that in PD patients motor imagery of the affected hand exploits additional neural resources in the visual cortices to compensate for the decline in motor representations. Van Nuenen et al. (2012) further investigated this issue: they studied PD patients and healthy controls with TMS; they selectively inhibited the EBA or the dorsal premotor cortex during the execution of the HLT, testing in particular the posture congruency advantage (i.e., the improvement in subjects' performance when their current hand posture is congruent to the imagined movement). Inhibition of the EBA disrupted the posture congruency advantage (e.g. faster RTs in discriminating hands showed in positions congruent with the subject's body posture) in PD patients, while this did not happen during the inhibition of the dorsal premotor cortex. The reverse pattern was observed in healthy controls. Taken together, these findings suggest that the EBA plays a compensatory role in PD to compensate an impoverished contribution of premotor cortex to motor imagery.

As already discussed above, the elderly's hyperactivations in our task are not mirrored by substantial behavioral differences, in contrast with what was found in our previous study on explicit M.I. in a different but age-matched sample of subjects (mean age: 60 years).

It is possible that this discrepancy could be due to the different nature of the tasks. As already pointed out by De Lange et al. (2008), explicit and implicit motor imagery tasks present a differential load on self-monitoring of actions, which is increased when subjects are explicitly asked to imagine their hands moving. In their study, the authors showed how manipulating the degree of action monitoring in patients with conversion paralysis influences the imagery process and the ensuing cortical response: their basic finding was a reduced premotor activation for the hysterically paralyzed hand during implicit motor imagery. However, this effect was abolished when subjects were challenged with an explicit motor imagery task (de Lange et al., 2008).

Other evidence supporting this hypothesis comes from studies on explicit and implicit motor imagery in schizophrenic patients (Danckert et al., 2002): in explicit motor imagery tasks they show a poor relationship between imagined and real movement duration, as if they were unable to generate accurate internal images of their own actions; on the contrary de Vignemont et al. (2006), investigating the same issue using an implicit M.I. paradigm, found that implicit M.I. was preserved in schizophrenic patients (de Vignemont et al., 2006).

Our results suggest that in the early phase of ageing compensatory processes in the domain of motor representations could be successful primarily in M.I. tasks with a low degree of explicit action monitoring, like HLT, in which the "desired state" of the system is visually available; this results in a normal behavioral performance. That is not true for explicit motor imagery processes, where we found "unsuccessful" compensatory neural mechanisms with the loss of temporal congruency between real and imagined movements. In the advanced stage of ageing (after the age of 70 years) the compensatory process would not be sufficient, resulting in a behavioral decline for both explicit and implicit tasks as previously described (Saimpont et al., 2009; De Simone et al., 2013; Devlin and Wilson, 2010).

The group of elderly subjects studied here, the “when I am (almost) 64” subjects, belong to an age that could be called young elderly, as they belong to the age range when retirement normally begins. They reveal a pattern of graceful aging whereby cognitive performance remains within more than acceptable levels thanks to some compensatory brain processes. It remains to be seen what would be their behavioral and fMRI pattern in implicit motor imagery one decade later. Previous studies (Saimpont et al., 2009; De Simone et al., 2013; Devlin & Wilson, 2010) demonstrated significant changes in terms of behavioral proficiency one decade later. Also, as our group of young elderlies were taken from a relatively privileged social and educational background, it would be interesting to expand the study to more variable groups, in terms of education and occupation, whose aging process may follow a different trajectory.

Conclusions

In this paper we have shown that implicit M.I. in normal early ageing is not substantially modified at the behavioral level, even if it is characterized by a stronger recruitment of visual cortices and the neurofunctional level.

These findings may have implications in the domain of rehabilitation, to identify the best age-range that could take advantage from M.I., used as a complementary technique in motor re-learning with patients affected by neurological or orthopedic diseases. On the basis of our results it remains questionable and open to explicit testing whether young elderly subjects may still benefit from implicit motor imagery techniques, in spite of their qualitative shift in terms of brain activation patterns.

Our paper leaves a number of outstanding issues: it will be important, for example, to investigate whether, as already seen in the domain of the real motor execution, the effect of early ageing could be detected by using more complex implicit M.I. tasks (e.g. the grip selection task).

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Figure captions

Figure 1. Classification of the stimuli presented in the HLT

Figure 2. Behavioral Results for the HLT: (a) Interaction effect View by Angle; (b) Interaction effect View by Hand; (c) Interaction effect View by Position.

Figure 3. Behavioral Results for the LRT.

Figure 4. fMRI results (HLT): Across group effects. (a) Main effect View (brain areas more activated for the palm view); (b) Main effect View (brain areas more activated for the back view); (c) Main effect Hand (brain areas more activated for the left hand).

Figure 5. fMRI results (HLT): (a) Interaction View by Hand; (b) Plot of the hemodynamic response of the local maxima of the interaction.

Figure 6. fMRI results: between group effects (HLT and LRT). (a) Brain areas hyperactivated in the elderly's group during the HLT; (b) Brain areas hyperactivated in the elderly's group during the LRT; (c) Brain areas more hyperactivated in the elderly's group during the HLT than during the LRT (interaction group by task).

Figure 7. Correlation analysis between BOLD response and RTs for the elderly subjects in the region has showed a Group by Task interaction effect.

Figure 8. (a) Brain areas resulted more activated by comfortable positions and (b) plot of the hemodynamic response in the local maxima of the effect in (a), to show the interaction effect between position and view.

Figure 1

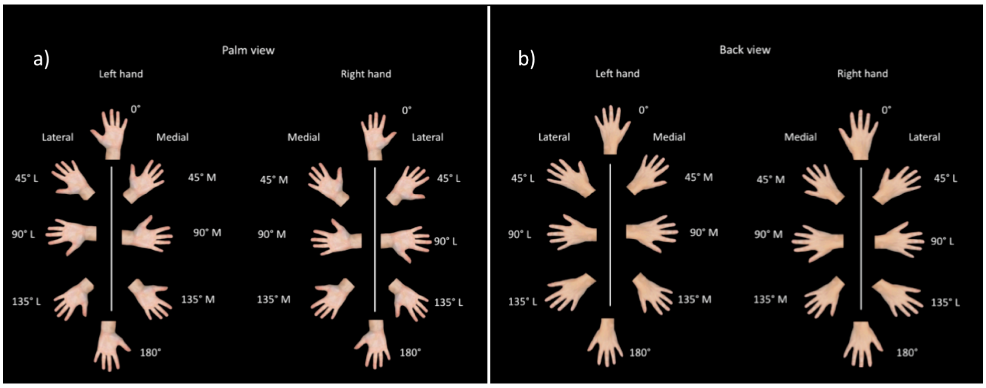
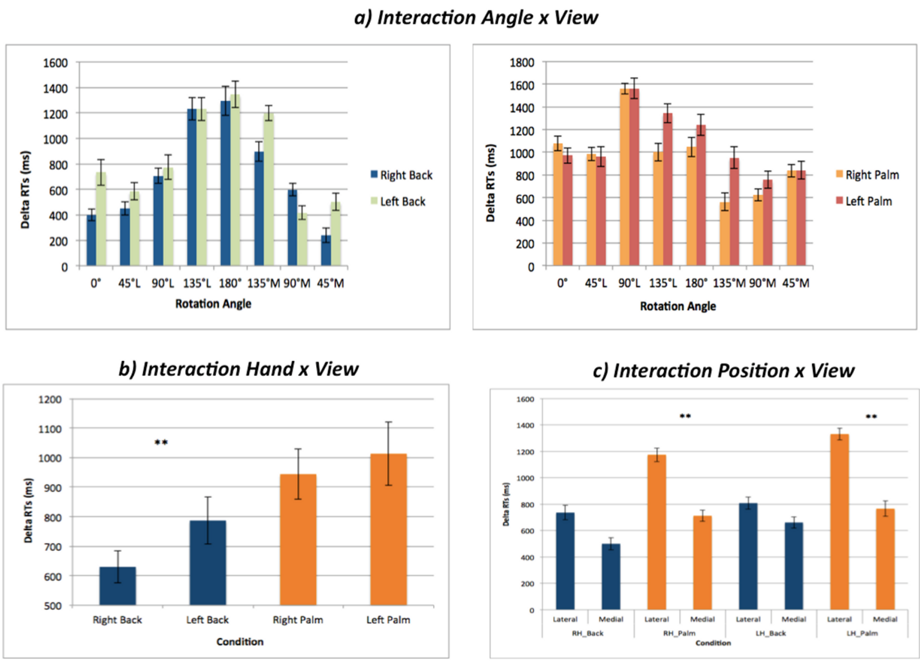


Figure 2



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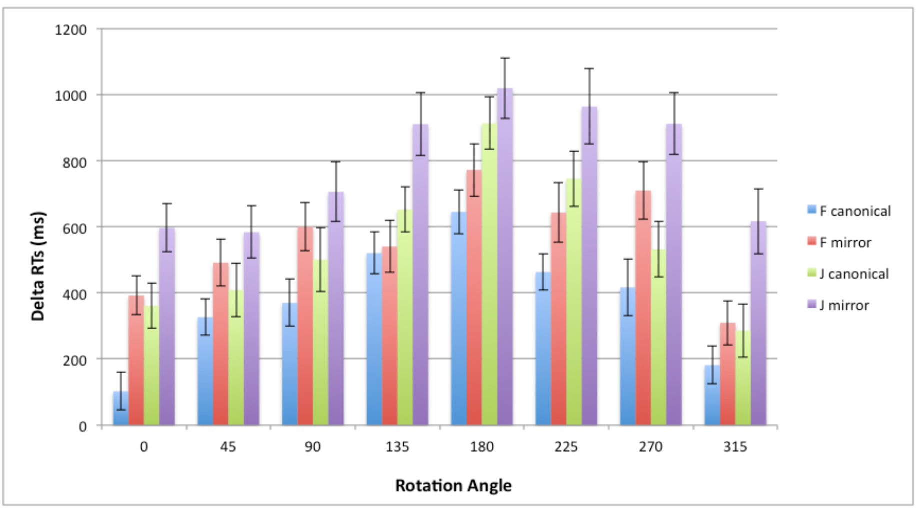

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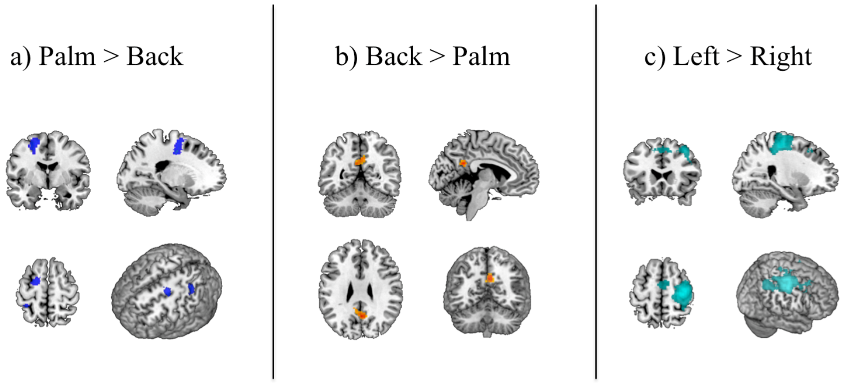

Figure 5

Interaction View by Hand

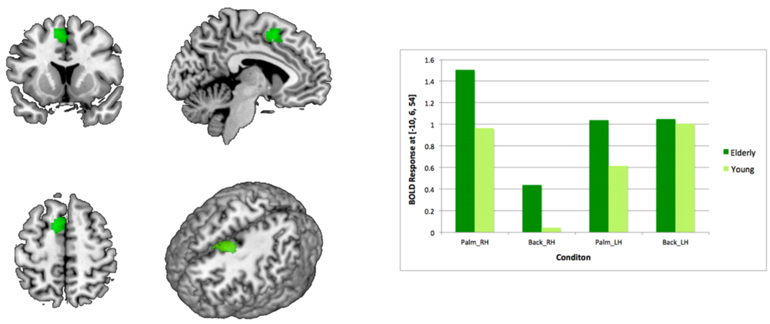

Figure 6

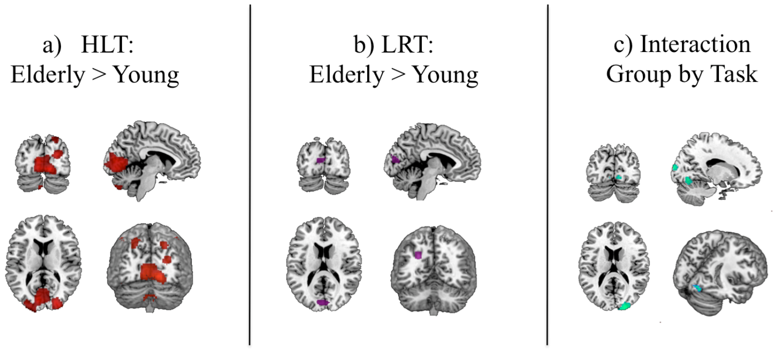

Figure 7

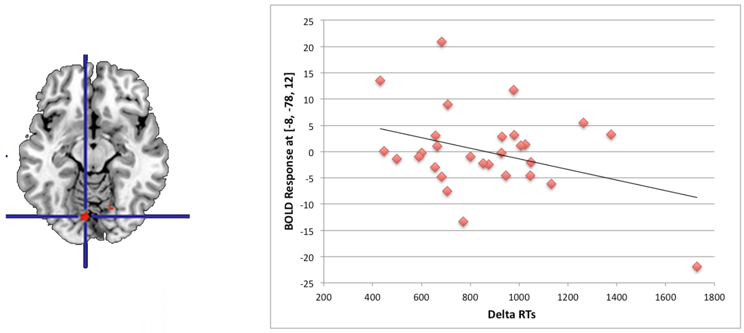

Figure 8

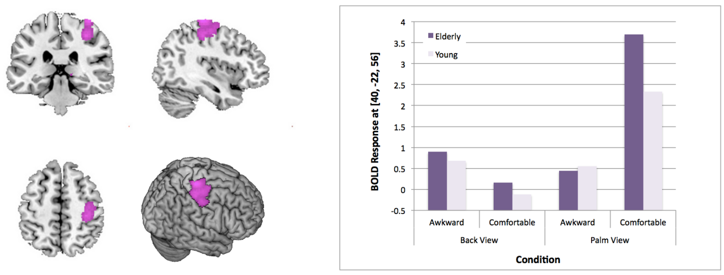

Table 1. fMRI across-group results (Hand Laterality Task)

Brain regions (BA)	MNI coordinates							
	Left hemisphere				Right hemisphere			
	x	y	z	Z-score	x	y	z	Z-score
a. Palm > Back								
Superior Frontal gyrus (6)	-22	-8	44	4.7#	--	--	--	--
Superior Frontal gyrus (6)	-20	-6	56	4.0	--	--	--	--
Middle Frontal gyrus (6)	-24	-4	52	4.0	--	--	--	--
SMA (6)	-12	4	62	3.2	--	--	--	--
Superior Parietal Lobule (2)	-32	-42	60	3.6	--	--	--	--
Inferior Parietal Lobule (40)	-36	-42	54	3.6	--	--	--	--
b. Back > Palm								
Lingual gyrus (18)	-6	-50	26	3.4	12	-58	26	2.7
Precuneus	--	--	--	--	6	-60	32	3.3
c. Left Hand > Right Hand								
Middle Frontal gyrus (9)	-30	10	48	3.5	38	20	50	4.9#
	-44	16	50	3.1	--	--	--	--
Middle Frontal gyrus (8)	-28	14	50	3.6	--	--	--	--
	-28	18	48	3.5	--	--	--	--
	-26	20	54	3.3	--	--	--	--
	-24	14	44	3.2	--	--	--	--
Precentral gyrus (6)	-38	8	34	4.7#	34	-14	58	6.1#
Precentral gyrus (6)	-44	4	38	4.5#	44	-14	52	5.6#
Precentral gyrus (6)	-48	6	38	4.2	42	-14	56	5.5#
SMA (6)	--	--	--	--	16	-8	68	4.6#
Mid. cingulum (24)	--	--	--	--	6	-16	46	4.7#
	--	--	--	--	6	-12	48	4.7#
	--	--	--	--	8	0	42	4.7#
	--	--	--	--	12	6	40	4.7#
	--	--	--	--	8	-4	46	4.6#
Precentral gyrus (4)	--	--	--	--	34	-20	52	6.1#
	--	--	--	--	34	-24	54	6.1#
	--	--	--	--	32	-20	56	6.1#
	--	--	--	--	48	-16	44	6.0#
Postcentral gyrus (3)	--	--	--	--	46	-20	48	5.9#
	--	--	--	--	38	-20	48	5.8#

Lingual gyrus (18)	-14	-88	-10	3.9	--	--	--	--
	-10	-84	-12	3.8	--	--	--	--
	-16	-86	-14	3.8	--	--	--	--
	-20	-80	-16	3.6	--	--	--	--
Fusiform gyrus (18)	-24	-72	-14	3.3	--	--	--	--
Fusiform gyrus (19)	-30	-68	-16	3.2	--	--	--	--
Cerebellum (18)	-20	-74	-16	3.4	--	--	--	--
d. Interaction View x Hand								
SMA (6)	-10	6	54	4.5	--	--	--	--
SMA(32)	0	14	48	3.9	--	--	--	--
	-8	-4	56	3.3	--	--	--	--
e. Comfortable >Awkward Positions								
Precentral gyrus (4)	--	--	--	--	38	-28	70	4.2
Postcentral gyrus (3)	--	--	--	--	34	-28	50	3.8
Precentral gyrus (6)	--	--	--	--	40	-14	60	3.3

FWE corrected

Table 2. fMRI between-group results.

Brain regions (BA)	MNI coordinates							
	Left hemisphere				Right hemisphere			
	x	y	z	Z-score	x	y	z	Z-score
a. Elderly > Young (HLT)								
Inferior Frontal op. gyrus (44)	-38	10	28	4.0	38	8	26	4.2#
Precentral gyrus (44)	-38	8	32	4.3#	--	--	--	--
Precentral gyrus (6)	-44	6	50	4.6#	--	--	--	--
Superior Parietal lobule (7)	-24	-72	48	4.0	24	-74	46	4.3#
Inferior Parietal lobule (39)	-44	-58	54	3.4	--	--	--	--
	-42	-56	48	3.3	--	--	--	--
Inferior Parietal lobule (40)	-42	-52	40	3.5	--	--	--	--
	-40	-48	48	3.5	--	--	--	--
	-40	-50	44	3.5	--	--	--	--
	-44	-50	54	3.5	--	--	--	--
	-48	-50	58	3.4	--	--	--	--
Angular gyrus (39)	-44	-52	36	3.4	46	-52	38	4.0
Fusiform gyrus (19)	--	--	--	--	24	-60	-14	4.8#
Fusiform gyrus (37)	-44	-56	-14	4.0	--	--	--	--
Superior Occipital gyrus (19)	-20	-98	16	4.2#	28	-66	28	4.2#
Middle Occipital gyrus (18)	-28	-90	10	4.0	26	-88	18	5.3#
	-28	-64	30	4.3#	--	--	--	--
Lingual gyrus (17)	-6	-72	6	4.5#	--	--	--	--
	-4	-72	2	4.4#	6	-70	6	4.1
Lingual gyrus (18)	-10	-80	-4	4.7#	14	-76	-6	5.6#
Calcarine fissure (17)	-8	-84	10	4.9#	--	--	--	--
	-8	-80	8	4.9#	--	--	--	--
Calcarine fissure (18)	-8	-84	-4	4.7#	--	--	--	--
b. Elderly > Young (LRT)								
Inferior Frontal op. gyrus (44)	-34	10	28	4.3	--	--	--	--
Superior parietal lobule (7)	-26	-72	52	3.5	--	--	--	--
Cuneus	-6	-92	22	3.1	--	--	--	--
Middle occipital gyrus (19)	-26	-62	34	4.8#	--	--	--	--
Calcarine fissure (17)	-6	-86	12	4.2	--	--	--	--
c. Elderly > Young (HLT > LRT)								
Lingual gyrus (18)	--	--	--	--	16	-72	-10	3.8
Superior Occipital gyrus (18)	--	--	--	--	22	-96	16	4.0

FWE corrected