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A Breakdown of Imagined Visuomotor Transformations and Its Neural Correlates in Young Elderly Subjects

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Abstract

Several studies have shown age-related changes in motor imagery (MI) in older adults and the associated compensatory brain activation patterns; most of these studies have used explicit MI tasks or implicit MI tasks focused on mental rotation of body parts. Here, we address the effect of ageing on MI for the more complex visuomotor transformations entailed by mentally simulated hand-tool interactions triggered by a grip selection task (GST) for tools used in daily life. We studied 22 young and 22 elderly subjects performing the GST, in which they were asked to report whether they would grip a portrayed tool with an overhand or an underhand grip. We found a behavioral decline in the elderly group, accompanied by reduced activations of the left posterior parietal lobule, in a subregion associated specifically with reaching behavior by previous investigations. No differences were observed in the temporal cortices associated with object semantics. These results suggested a specific age-related vulnerability of the neural substrates, particularly for the imaginary reaching component of the task, rather than for the semantically driven grasping component. The combination of behavioral deficits and reduced activation of specific brain regions speaks in favor of a specific age-associated deficit for the complex imaginary movements required by the GST.

Key words: ageing, compensation, fMRI, grip selection task, motor imagery

Introduction

More and more people are living beyond their sixth, seventh, or even eighth decade. The quality of life of these populations is strongly associated with motor independence and efficient interaction with the environment. Reaching and grasping movements are an essential part of motor life and such interactions. The question arises as to whether these behaviors significantly change with ageing, how early this occurs and to what extent our neurocognitive system can address such changes. To test this issue and its possible neural underpinning in a setting compatible with fMRI investigations, we compared the performance of younger subjects and relatively young elderly subjects during a motor imagery (MI) task, that is, a grip selection

task (GST) that we discuss below. In this section, after a general introduction on MI, we present the GST, review the known impact of ageing on MI and discuss the rationale, the aims and the predictions of our experiment. As the reader shall see, this article represents the completion of a research program on MI of upper limb movements in early ageing based on 3 different paradigms that revealed different levels of compensation.

Motor Imagery as a Window on the Ageing Motor System

MI is a mental state during which movements are mentally evoked and rehearsed without overt actions (Jeannerod and Decety 1995).

There is compelling evidence to suggest that, during MI, subjects are capable of recruiting motoric representations (see, e.g., Héту et al. 2013), and this justifies the use of MI in basic research and clinical domains for the study of motor neurocognition as well as in rehabilitation programmes (review in Mulder 2007).

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

For example, in explicit MI tasks, subjects are directly asked to imagine themselves while executing the required action (Ehrsson et al. 2003), focusing on kinesthetic and bodily sensory information from a first-person egocentric perspective. These explicit MI skills are investigated with self-report questionnaires or mental chronometry paradigms; in particular, the isochronism of executed and imagined movements is taken as evidence that explicit MI has motoric components (Collet et al. 2011).

On the other hand, in implicit MI tasks, the imagery process is evoked without explicit reference to the concept of MI: for example, in the hand laterality task (HLT), subjects are asked to decide whether a hand portrayed in a picture (rotated at different angles) is 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 1987a, 1987b).

The contribution of a motoric component during these tasks is supported by PET and fMRI studies showing the involvement of the premotor cortices (the lateral premotor cortex and the supplementary motor area [SMA]), posterior parietal cortices (the superior parietal lobule and intraparietal sulcus) and cerebellum (Bonda et al. 1995; de Lange et al. 2005, 2006, 2008; Parsons et al. 1995; Vingerhoets et al. 2002; Seurinck et al. 2004; Zapparoli et al. 2014). Studies on implicit MI described in the literature mainly focused on mental rotation of body parts (Parsons 1987a, 1987b).

The Grip Selection Task

The GST represents an interesting variation of implicit MI tasks; here, subjects are shown pictures of different tools, and they are then asked to indicate whether these objects would have been grasped with an underhand grip or an overhand grip.

Behavioural, neurophysiological and neurofunctional findings support the idea that this task implicitly triggers the mental simulation of reaching and grasping movements. Johnson (2000b), for example, investigated the behavioral mechanisms of the GST by using tasks that involved either the actual reaching and grasping or the imagined reaching and grasping of a dowel presented in different orientations (Johnson 2000b); the time needed to make a grip selection decision was predicted by the angular distance between the effector's position and the end state of the simulated grip, following a biomechanically plausible pattern (Johnson 2000b).

The involvement of motor simulation in GST has been confirmed by a TMS study conducted by Pelgrims et al. (2005), who found an increase in corticospinal excitability while judging object-hand interactions in comparison to the control task.

Some interesting findings also came from studies on neurological patients with hemiplegia, whose performance was compromised by lesions specifically involving posterior parietal or

frontal motor regions. These findings are in line with the idea that imagined grasping involves a frontoparietal network, similar to actual grasping (Johnson 2000a).

This hypothesis was later specifically tested by Johnson et al. (2002), who showed in normal subjects that imagined grip selection specifically activates a frontoparietal circuit, which includes the premotor cortex bilaterally, the intraparietal sulcus and the right superior parietal lobule, regardless of the hand involved in the task (Johnson et al. 2002).

Daprati et al. (2010) further investigated this aspect and studied stroke patients with varying degrees of motor impairment and lesions either in the left or in the right hemisphere; subjects were tested with both the HLT and the GST task. While reaction times (RTs) were positively correlated with the severity of motor impairment, accuracy in the different tasks showed an interaction effect with hemisphere: left brain-damaged patients were more impaired in the GST, while the performance of right brain-damaged patients was more compromised in the HLT. Interestingly, when the judgment involved interaction with an object (GST), patients with severe motor impairments had worse performance (This surprising pattern of results was explained by postulating that the HLT and GST might depend on different cognitive strategies (and partially different neural substrates), with the GST being more dependent on motor simulation, and the HLT being feasible using also visual strategies. Accordingly, for the HLT, patients with severe motor impairment could still rely on alternative visual strategies and visual cues (e.g., the location of the thumb and pinkie). Such alternative strategies would not be applicable to solve the GST (Daprati et al. 2010).

Motor Imagery and Ageing

There is a growing literature documenting age-related patterns of brain activity associated with the changes in cognitive function that are typical of normal ageing (Park and Reuter-Lorenz 2009). The HAROLD model (hemispheric asymmetry reduction in older adults) hypothesizes that older adults have a more bilateral pattern of activations, particularly in the prefrontal cortex, to compensate for age-related cognitive decline (Cabeza 2002). Based on a similar logic, the PASA model (posterior-anterior shift in ageing) suggests that ageing is associated with a significant reduction of neural activity in posterior areas (mainly occipitotemporal areas) together with a significant increase of activations at the level of the frontal lobe (Davis et al. 2008). The CRUNCH hypothesis (compensation-related utilization of neural circuit hypothesis) proposes that, in tasks with lower cognitive load, older adults recruit greater neural resources to compensate and reach the same level of performance as young people; however, when the cognitive load is higher, they show equivalent or lower activation and worse behavioral performance compared with young adults (Reuter-Lorenz and Cappell 2008).

Most of the studies behind the HAROLD, PASA, and CRUNCH hypotheses addressed the domains of episodic memory, working memory or reasoning; on the contrary, motor cognition has been largely neglected until recently, with investigations primarily on the effect of ageing on MI.

For explicit MI tasks, behavioral chronometric studies have consistently shown a loss of temporal congruence between motor execution and explicit MI in elderly subjects, especially for unusual and constrained movements (Skoura et al. 2008). These changes were accompanied by neurofunctional changes documented with fMRI, for example, the over-recruitment of

occipitotemporal areas, which suggested the adoption of a complementary strategy based on visual imagery to compensate for MI decline (Zapparoli et al. 2013).

For implicit MI tasks, such as the HLT, the picture is somewhat more complex: first behavioral deficits can be observed after the age of 70 (Saimpont et al. 2009a, Devlin and Wilson 2010; De Simone et al. 2013), while younger elderly subjects in their 60s, similar to the subjects studied here, may display MI abilities comparable to those of young subjects, if one controls for the general lengthening of RTs. Normal behavioral performance, however, is typically associated with significant additional brain activations for elderly subjects in occipitotemporal regions, much as for explicit MI tasks. These findings have been interpreted as evidence of compensatory processes associated with ageing to permit a behavioral performance comparable to that of younger subjects (Zapparoli et al. 2016).

Aim of the Study and Expected Results

One possible limitation of the experiments on MI described so far is that they do not have great ecological validity. In other words, it remains to be seen whether imaginary tasks that mimic daily life motor behavior are compensated for even better than the rather abstruse HLT or whether the visuomotor transformations required for imagined rehearsing reaching and grasping behaviors, a proxy for the study of the representation of semantically informed tool manipulation and use, are rather more vulnerable. On the basis of Daprati et al. (2010), one might anticipate different patterns of behavioral and fMRI results when compared with those seen in explicit MI or in the HLT, with less room for compensation. On the other hand, one may alternatively anticipate complete compensation for a GST, as such tool use is a daily life activity that may prove more resistant to the effect of normal ageing.

These were the alternative hypotheses addressed in our experiment together with the associated neurofunctional correlates. As the reader shall see, the outcome of the present experiment, together with our previous findings, permits a general discussion on the current models of compensatory processing in ageing in the domain of motor cognition and to frame our results in the context of one of the dominant models of normal ageing.

Materials and Methods

Participants and Neuropsychological Assessment

In total, 22 young subjects (mean age: 27.5 years, SD: 5.4 years) and 22 “young” elderly subjects (mean age: 61 years; SD: 6.6 years) underwent an event-related design fMRI experiment. The socio-economic status was the middle class from both groups; the educational level was not significantly different between the 2 groups (young subjects: 16 years, SD: 2.3; elderly subjects: 15 years, SD: 3.4).

None of the subjects had a history of neurological or psychiatric illness. They 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 Declaration of Helsinki (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 colored 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 visuospatial memory (Carlesimo et al. 2002), as well as the Frontal Assessment Battery (FAB, Dubois et al. 2000). None of the subjects had a single pathological score on the neuropsychological test battery; all raw, corrected and equivalent scores are provided in the supplementary materials section (Table S1).

Experimental Task

For the fMRI experiment, we used a GST, similar to the one proposed by Daprati et al. (2010).

Subjects were shown photos of different tools, all with a handle horizontally oriented and appearing on the right or left side of the image. The photos were preceded by a written indication (Fig. 1) of whether the grip selection judgment was meant for the right or the left hand (see below for a detailed description of the experimental task). If the tool's handle was oriented on the same side as the hand involved in the task, the handle was defined as “congruent,” otherwise it was labeled as “incongruent.” A total of

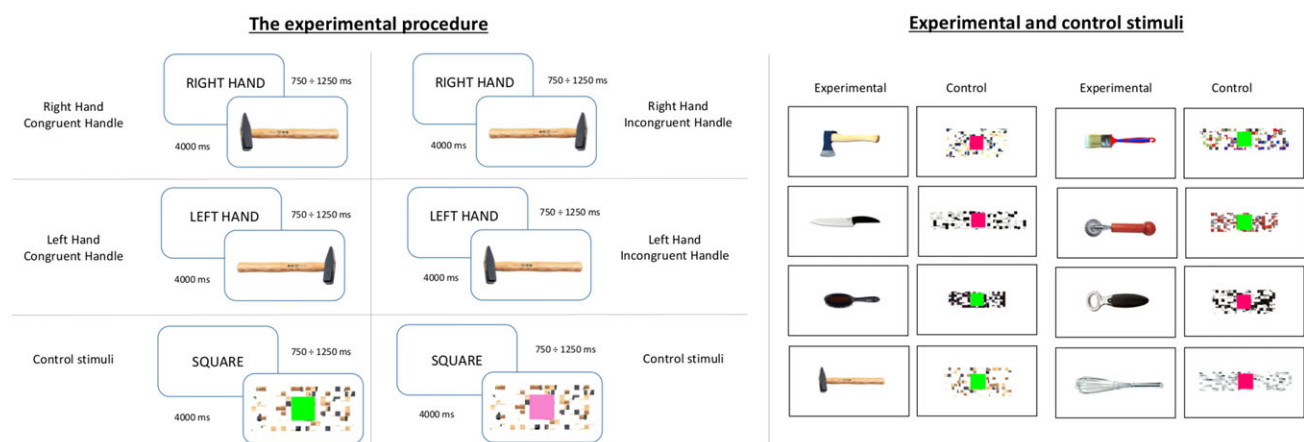


Figure 1. Graphical representation of the experimental procedure and experimental stimuli.

64 experimental stimuli were presented (8 objects \times 2 hands \times 2 handle orientations, each repeated 2 times).

The baseline control stimuli were 64 scrambled pictures derived from the tools' pictures. Each scrambled image had a green or a pink square in the center (The choice of a baseline task can be motivated in many ways. A strict hierarchical subtraction approach may have warranted having pictures of tools without any information on what to do with them (to not engage motor imagery processes). However, we decided to avoid the likely "visuo-priming" effects of seeing pictures of a graspable objects in the baseline as previous studies have shown that the mere observation of an object automatically activates motor representations and the object-specific affordances (see, e.g., Craighero et al. 1996). Accordingly, and by design, our baseline stimuli were meant to subtract out the most elementary aspects of the visual input (the stimuli were derived from a fragmentation of the original pictures) and a motor response for a simple nonobject-oriented discrimination task.

We reasoned that this would have best met our aim of providing a broad first test of the anatomy of the GST and any difference in the functional anatomy of elderly and young participants (Fig. 1).

Procedure

Participants practised the task before the scanning session: subjects were familiarized with the stimuli by performing half of the trials (32 experimental trials). During this training, a warning feedback was given in case of an error.

For the fMRI experiment, the stimuli were randomly alternated according to an event-related design. Each stimulus remained visible for 4000 ms, and the ISI was jittered and randomly varied from 750 to 1250 ms (interstimulus interval: ISI). This procedure guarantees a beneficial desynchronization between the stimuli onsets and the timing of volume acquisition specified by the repetition time of the fMRI protocol. Subjects were asked to report whether to use a given object properly, they would have gripped it with an overhand or an underhand grip; the reports were given by pressing a button with their right or left index fingers. 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. Visual stimuli were delivered using fiber-optic goggles (Visuastim, Resonance Technology Inc.). Responses were given through 2 response boxes (one for each hand).

Statistical Analyses of the Behavioral data

Mean accuracy and response time (RTs) 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 tool stimulus presentation and subjects' button press. Individual performance was considered above chance level when the overall accuracy was $>60\%$. Outliers (threshold = mean RTs \pm 2 SD) were excluded from the analyses.

For each subject, from the RT of each experimental trial, we subtracted the RT of the corresponding baseline control trial (simple RTs), that is, the trial containing the scrambled picture generated from a given experimental stimulus. This was done to assure that the potential differences between groups were not related to a generalized ageing-related decrease of speed in making motor responses (see, e.g., Nebes 1978). This was the same approach of our previous study on ageing and implicit MI (Zapparoli et al. 2016). Descriptive statistics are reported in Table 1a and 1b.

Accuracy and RTs data distributions were first formally checked by means of the Shapiro–Wilk test. Accuracy data were then analyzed by means of nonparametric independent samples *t*-test since the data were not normally distributed in any of the experimental conditions (Right hand, Congruent Handle: $W = 0.856$, $P < 0.001$; Right hand, Incongruent Handle: $W = 0.866$, $P < 0.001$, Left hand, Congruent Handle: $W = 0.934$, $P = 0.015$; Left hand, Incongruent Handle: $W = 0.920$, $P = 0.005$). RTs data were first normalized by means of a root-square transformation (recommended in cases of negative asymmetry), and after the normalization, the data looked normally distributed (Right hand, Congruent Handle: $W = 0.959$, $P = 0.124$; Right hand, Incongruent Handle: $W = 0.958$, $P = 0.108$, Left hand, Congruent Handle: $W = 0.974$, $P = 0.411$; Left hand, Incongruent Handle: $W = 0.973$, $P = 0.385$). Data were then analyzed by means of a repeated-measures $2 \times 2 \times 2$ ANOVA with "Group" (Elderly/Young) as a between-subjects factor and "Hand" (Right/Left) and "Handle Congruency" (Congruent/Incongruent with respect to the hand to be used for the grip) as within-subjects factors. The results are shown in Figure 2a.

Table 1a Descriptive statistics of the accuracy data (% correct responses) in each condition for each group

	Group	RH_Congruent	RH Not Congruent	LH_Congruent	LH_Not Congruent
Mean	Elderly	94	85.5	83.5	79.5
	Young	95.3	88	91.9	88.4
S.E.	Elderly	0.7	2.6	2.7	2.5
	Young	1.1	2.6	1.4	2.1

Table 1b Descriptive statistics of the reaction times (in milliseconds) in each condition for each group

	Group	RH_Congruent	RH Not Congruent	LH_Congruent	LH Not Congruent
Mean	Elderly	1185	1868	1758	1991
	Young	1165	1580	1465	1646
S.E.	Elderly	55.4	101	92.7	103
	Young	88.3	79.2	76.1	88.3

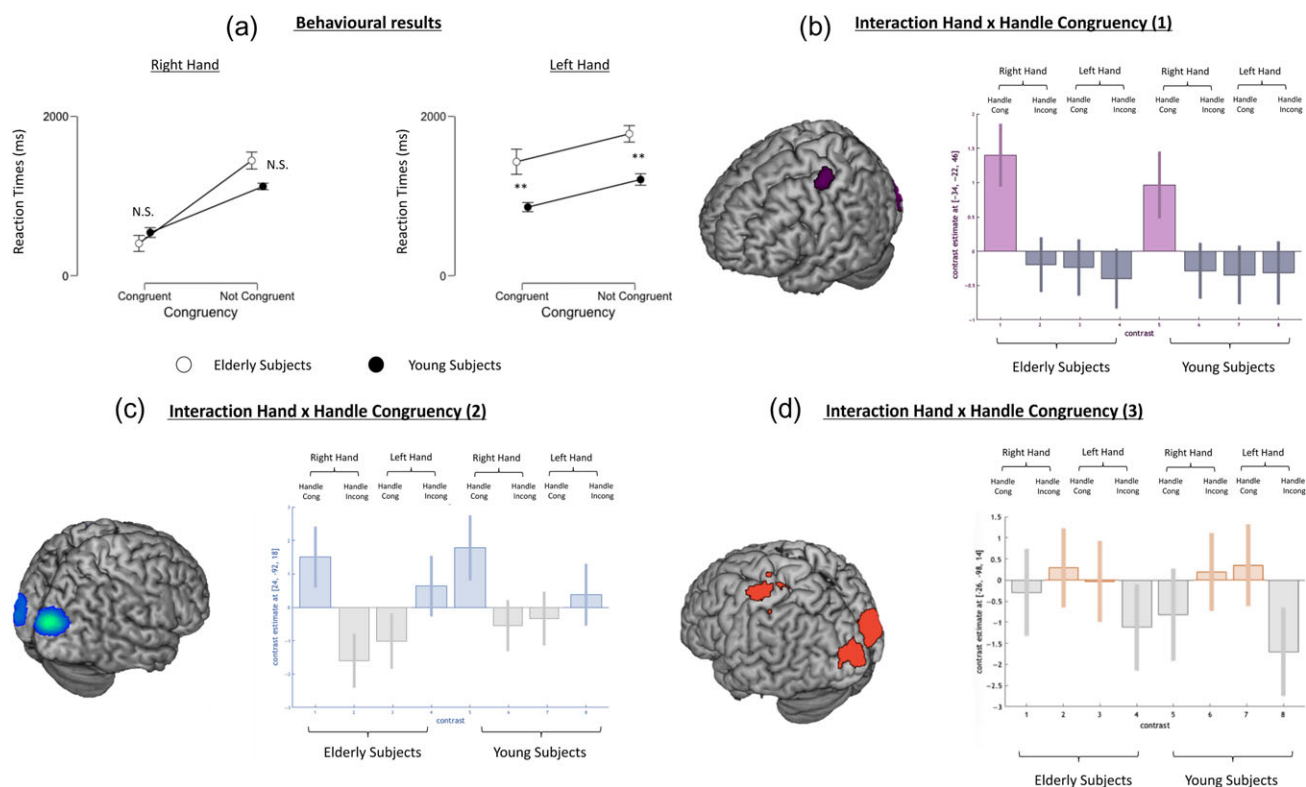


Figure 2. (a) Behavioral results: the figure shows the mean RTs (\pm SEM) for each group in each experimental condition; (b) fMRI results: interaction between the factor Hand and the factor Handle Congruency in the premotor cortex; (c) and (d) fMRI results: interaction between the factor Hand and the factor Handle Congruency in the left (on the left) and right (on the right) occipital poles.

fMRI Data Acquisition and Analysis

Before the fMRI scans, for all subjects, we collected a standard volumetric T1 MRI (flip angle 35°, TE 5 ms, TR 21 ms, FOV 256 × 192 mm², matrix 256 × 256, TI = 768 ms, for a total of 160 axial slices with 1 mm cubic voxels) using a 1.5 T Siemens Avanto scanner, equipped with gradient-echo echo-planar imaging.

fMRI scans were then performed (flip angle 90°, TE = 60 ms, TR = 3000 ms). The voxel sizes of the native fMRI images were 3.91 × 3.91 × 5 mm³. We collected 225 volumes in a single run resulting in an overall 11'15" run duration. The first 10 volumes (corresponding to the task instructions) were discarded from the analyses. 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 (MathWorks, Natick, MA, USA) using Statistical Parametric Mapping software (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 dimensions of 2 × 2 × 2 mm³. The stereotactically normalized scans were smoothed using a Gaussian filter of 10 × 10 × 10 mm³ to improve the signal-to-noise ratio.

The BOLD signal associated with each experimental condition was analyzed by a convolution with a canonical haemodynamic response function (Worsley and Friston 1995). The haemodynamic response for each event was characterized

using the event-related analysis option of SPM8 with onset centered at the time of stimulus presentation. Global differences in the fMRI signal were removed from all voxels with proportional scaling. High-pass filtering (128 s) was used to remove artefactual contributions to the fMRI signal, such as physiological noise from cardiac or respiratory cycles.

A fixed-effect analysis was performed for each subject to characterize the BOLD response associated with each of the 4 experimental and 4 baseline control conditions, all treated as separate regressors. Accordingly, the contribution of the laterality of the motor response was controlled for in the analyses of the MI task at the second level as well. The 4 control conditions were composed of the control trials matching the experimental ones: for example, trials with scrambled pictures derived from right congruent objects were grouped to generate the baseline control condition for the “right congruent” experimental trials. At the first level, we included only correct responses in the analysis.

Group level analyses were performed using a second-level full factorial design conforming to a random-effect analysis 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: Hand (Right or Left) and Handle Congruency (Congruent or Incongruent), after subtracting out the BOLD response for the events of the matched baseline control condition. Post hoc analyses to examine the direction of the aforementioned effects were performed using linear contrasts to generate SPM[t] maps. To partition and model the effect of the individual RTs on the results, these

were entered as group-specific covariates in the second-level GLM analysis.

The main pattern of activation for the GST, the effects of hand laterality and handle congruency and relevant interactions are presented in Table 2a–d and in Figure 2b–d. Here, we report shared effects across the 2 groups in the form of main effects. We also present a full conjunction of the main effect of the GST to define brain areas of “identical” activation in the 2 groups (Table 2e). Furthermore, specific group differences are described in Table 2f and in Figure 3a.

Corrections for multiple comparisons: the results are reported using the nested-taxonomy strategy recommended by Friston et al. (1996), that is regional effects meeting either a clusterwise or voxelwise FWER correction for multiple comparisons. The voxelwise threshold applied to the statistical maps, before the clusterwise correction, was $P < 0.001$ uncorrected, as recommended by Flandin and Friston (2017). For clusters significant at $P < 0.05$ FWER corrected level we also report the other peaks at $P < 0.001$.

Behavioural Results

Accuracy Data

Descriptive statistics of accuracy are reported in Table 1a.

We conducted 4 nonparametric independent samples t-tests based on Mann–Whitney U statistics that gave the following results: the mean accuracy was not different between the elderly and young subjects in the 2 conditions involving the right hand (Right hand, Congruent Handle: $U = 203$, $P = 0.323$; Right hand, Incongruent Handle: $U = 216$, $P = 0.540$), while the elderly subjects showed a worse performance in terms of accuracy for task conditions involving the left hand (Left hand, Congruent Handle: $U = 158$, $P = 0.047$; Left hand, Incongruent Handle: $U = 140$, $P = 0.016$).

RTs Data

Descriptive statistics of RTs are reported in Table 1b.

A $2 \times 2 \times 2$ repeated-measures ANOVA on RTs data with “Group” (Elderly/Young) as a between-subject factor and “Hand” (Right/Left) and “Handle Congruency” (Congruent/Incongruent) as within-subject factors revealed the following results.

Main Effects

There was an overall between-group difference ($F[1,42] = 4.23$; $P = 0.046$; $\eta^2 = 0.037$), a main effect of the factor Hand ($F[1,42] = 66.54$; $P < 0.001$; $\eta^2 = 0.116$) and a main effect of the factor Handle Congruency ($F[1,42] = 80.21$; $P < 0.001$; $\eta^2 = 0.192$).

Within-Subject Interactions

The Hand by Handle Congruency interaction was significant ($F[1,42] = 50.77$; $P < 0.001$; $\eta^2 = 0.045$).

Planned Bonferroni-corrected post hoc comparisons showed that there was a special advantage for the conditions involving the right hand, particularly when the handle was oriented in a congruent way (Right hand, Congruent Handle vs. Right hand, Incongruent Handle: $t[69.4] = -11.36$, $P < 0.001$; Right hand, Congruent Handle vs. Left hand, Congruent Handle: $t[76] = -10.78$, $P < 0.001$; Right hand, Congruent Handle vs. Left hand, Incongruent Handle: $t[81.9] = -12.11$, $P < 0.001$).

Group by Task Interactions

The Hand by Group interaction ($F[1,42] = 13.38$; $P < 0.001$; $\eta^2 = 0.023$) and the Hand by Handle Congruency by Group interaction ($F[1,42] = 7.12$; $P = 0.011$; $\eta^2 = 0.006$) were significant, while the Handle Congruency by Group interaction was not ($F[1,42] = 1.92$; $P = 0.173$; $\eta^2 = 0.005$).

However, planned post hoc comparisons, once corrected for multiple comparisons with a Bonferroni approach, showed that the differences between groups were mainly related to the hand used to solve the task, independently from the handle congruency: indeed, elderly subjects were slower with respect to their younger counterparts only in conditions involving the left hand (Left hand, Congruent Handle, Elderly vs. Young: $t[92.7] = 3.039$, $P = 0.003$; Left hand, Incongruent Handle, Elderly vs. Young: $t[92.7] = 2.839$, $P = 0.006$). No differences were reported in conditions involving the right hand (Right hand, Congruent Handle, Elderly vs. Young: $t[92.7] = -0.919$, $P = 0.36$; Right hand, Incongruent Handle, Elderly versus Young: $t[92.7] = 1.594$, $P = 0.114$).

These results are illustrated in Figure 2a.

fMRI Results

Within-Subject Effects

A vast pattern of frontoparieto-occipital and temporal activations was seen as a main effect of the task in comparison with the baseline control task (Table 2a).

We also found a significant main effect of the factor “Hand,” with greater activations for the right hand in the contralateral motor regions (precentral and postcentral gyrus) (Table 2b).

Moreover, there was a main effect of the factor “Handle Congruency.” Given the present paradigm, in spite of the subtraction of the motor response by the baseline, this was associated with the motor cortex controlling the hand used by the participants to respond with an “overhand grip” or an “underhand grip.” However, there were additional bilateral premotor and parietal regions showing a congruency effect, all reflecting a stronger response for the incongruent stimuli and the complex spatial relationship between the position in space of the imagined movement, its complexity and the position of the responding hand (Table 2c).

Finally, a significant “Hand by Handle Congruency” interaction was recorded at the level of the left precentral gyrus and bilaterally in the occipital regions. Post hoc analyses, by means of simple t-contrasts, revealed that the left precentral and postcentral gyri were mainly activated by the imagination of the right hand when the handle was presented in a congruent orientation; on the other hand, the interactions detected in the two occipital poles were driven by specific activations of the visual areas that map the hemi-space containing the relevant information needed to imagine the tool use (e.g., activation of the right occipital pole for a brush with its head falling in the left visual hemi-field). See Figure 2b–d and Table 2d for details.

Between-Group Similarities and Differences

The conjunction analysis showed “shared activations” between the two groups bilaterally in the triangular and opercular subdivisions of the inferior frontal gyrus, the precentral gyrus, the inferior parietal lobule, the superior occipital gyrus, the inferior occipital gyrus, left superior frontal gyrus, the middle frontal gyrus, the insula, the precuneus, the superior parietal lobule, the inferior occipital gyrus, the right middle frontal gyrus, the

Table 2 Brain regions showing a significant effect for each contrast of interest

Brain regions (BA)	MNI coordinates							
	Left hemisphere				Right hemisphere			
	x	y	z	Z-score	x	y	z	Z-score
a) Main effect of the factor task								
Frontal orbital gyrus (47)	-42	46	0	6.6* ^o				
Frontal inferior triangular gyrus (45)	-42	36	14	6.8* ^o	48	32	28	7.2* ^o
	-42	36	0	5.8* ^o				
	-44	28	26	Inf* ^o				
Frontal inferior opercular gyrus (44)	-52	12	6	6.7* ^o	52	14	4	5.0* ^o
	-52	14	2	6.6* ^o	48	10	30	Inf* ^o
	-46	8	28	Inf* ^o				
Frontal middle gyrus (6)	-26	0	60	Inf* ^o	32	0	56	Inf* ^o
	-26	-2	56	Inf* ^o				
Frontal superior gyrus SMA (6)	-22	-2	52	Inf* ^o	0	14	50	Inf* ^o
Precentral gyrus (6)	-38	0	52	Inf* ^o				
	-46	8	34	Inf* ^o				
	-42	4	38	Inf* ^o				
	-40	2	42	Inf* ^o				
Insula	-30	20	-4	Inf* ^o	34	22	-2	Inf* ^o
Parietal superior lobule (7)	-18	-64	56	Inf* ^o	24	-70	42	Inf* ^o
	-20	-68	44	Inf* ^o	16	-68	54	Inf* ^o
Parietal inferior lobule (40)	-38	-44	50	Inf* ^o	36	-50	52	Inf* ^o
Occipital superior gyrus (19)					28	-78	38	Inf* ^o
Occipital middle gyrus (19)	-40	-82	16	Inf* ^o				
	-32	-52	-20	Inf* ^o				
Occipital inferior gyrus (19)	-48	-68	-4	Inf* ^o	44	-68	-10	Inf* ^o
Calcarine fissure (17)	-10	-78	12	Inf* ^o	12	-76	10	Inf* ^o
Cerebellum_6					36	-44	-26	Inf* ^o
					36	-56	-20	Inf* ^o
Cerebellum_7b					30	-72	-50	4.64* ^o
Cerebellum_Crus1	-32	-60	-34	Inf* ^o				
Cerebellum_Crus2	-8	-78	-28	5.7* ^o	10	-78	-30	5.9* ^o
Pallidum	-16	8	0	5.0* ^o	14	10	0	5.2* ^o
b) Main effect of the factor hand: Right Hand > Left Hand								
Precentral gyrus (6)	-32	-26	64	4.8* ^o				
Postcentral gyrus (3)	-36	-30	58	4.7* ^o				
	-28	-26	50	4.6* ^o				
	-32	-34	68	4.6* ^o				
	-32	-28	48	4.6* ^o				
	-26	-38	56	5.1* ^o				
	-24	-40	52	4.9* ^o				
Caudate					6	6	4	5.0* ^o
Pallidum					10	6	2	4.9* ^o
c) Main effect of the factor handle congruency								
Frontal superior gyrus (6)					28	-10	70	4.8* ^o
Rolandic opercular gyrus					54	-22	22	4.7* ^o
Precentral gyrus (6)					30	-14	70	4.7* ^o
Precentral gyrus (4)	-32	-26	72	5.8* ^o	46	-18	52	6.2* ^o
	-36	-22	64	5.5* ^o	54	-20	48	5.9* ^o
	-42	-18	64	5.5* ^o				
Postcentral gyrus (3/2)	-36	-24	54	5.3* ^o	42	-42	62	6.8* ^o
	-38	-20	52	5.1* ^o	48	-20	60	6.6* ^o
	-48	-16	48	4.7* ^o	46	-36	62	6.3* ^o
	-28	-24	50	4.7* ^o	52	-28	52	5.8* ^o
	-54	-14	50	4.7* ^o	54	-24	50	5.7* ^o
					52	-20	38	4.8* ^o
					36	-24	48	4.7* ^o
Sup. parietal lobule (7)					14	-64	56	5.6* ^o
Inf. parietal lobule (40)					54	-28	56	5.9* ^o

(Continued)

Table 2 (Continued)

					32	-44	48	5.2*
Supramarginal gyrus					52	-22	26	4.6°
Cerebellum	-18	-52	-20	5.1*				
	-28	-38	-36	4.0°				
	-8	-52	-12	3.4°				
	-26	-44	-32	3.4°				
d) Interaction of Hand × Handle congruency								
Precentral gyrus (6)	-34	-24	62	3.6°				
Precentral gyrus (4)	-40	-16	60	3.9°				
	-30	-24	50	3.9°				
	-38	-22	62	3.7°				
Postcentral gyrus (3)	-34	-22	46	4.1°				
Cuneus (18)					20	-72	22	3.2°
Occipital superior gyrus (19)					22	-80	22	3.4°
Occipital superior gyrus (18)					20	-94	18	6.2*
Occipital middle gyrus (18)	-32	-94	12	3.4°				
	-32	-92	16	3.3°				
	-36	-94	6	3.2°				
Occipital middle gyrus (17)	-18	-106	8	4.1°				
	-16	-102	8	4.1°				
	-18	-98	14	3.7°				
	-18	-102	18	3.6°				
Calcarine fissure (17)					4	-92	0	3.7°
e) Conjunction between young and elderly subjects								
Frontal inferior triangular gyrus (45)	-44	28	26	6.8*	46	34	28	5.2*
	-48	24	26	6.4*	50	32	30	5.1*
Frontal inferior opercular gyrus (44)	-48	8	32	Inf*	52	10	28	5.4*
	-50	12	6	4.8*	48	8	28	5.3*
					50	8	22	5.3*
Frontal middle gyrus (6)					34	0	56	Inf*
SMA (6)					0	14	50	7.4*
Precentral gyrus (6)					46	4	38	5.0*
	-28	0	62	Inf*				
	-28	-2	58	Inf*				
Insula	-28	22	-6	6.1*	34	22	-2	6.3*
Parietal superior lobule (7)	-16	-70	54	Inf*	16	-68	54	Inf*
	-22	-68	46	Inf*				
Parietal inferior lobule (7)	-30	-54	50	Inf*				
	-32	-54	54	Inf*				
Parietal inferior lobule (40)	-38	-44	50	Inf*				
	-54	-30	40	7.5*				
Temporal inferior gyrus (37)					36	-52	50	Inf*
Precuneus (7)	-10	-70	56	Inf*	44	-60	-10	Inf*
Occipital superior gyrus (19)	-26	-78	32	Inf*				
Occipital middle gyrus (19)	-40	-82	16	7.4*	30	-80	36	Inf*
Occipital inferior gyrus (19)	-48	-68	-4	Inf*	42	-68	-10	Inf*
					42	-84	-6	7.3*
Calcarine fissure (17)	-10	-80	8	4.6*	10	-74	10	5.3*
f) Main effect of group (Young > Elderly subjects)								
Parietal superior lobule (7)	-18	-60	60	4.9*				

x, y, and z are the stereotactic coordinates of the activations in MNI space.

*FWE correction (peak level).

°FWE correction (cluster level).

Inf = z-score > 8.

SMA, the superior parietal lobule, the inferior temporal gyrus and the calcarine fissure (Table 2e).

Importantly, there were also “between-group differences”: elderly subjects showed reduced activations in the superior parietal lobules. This difference survived a correction for multiple comparisons in the left hemisphere, while there was a

substantial trend in the right mirror region ($X = +20$; $Y = -64$; $Z = +70$; Z score: 4.01; $P < 0.00003$ uncorrected; cluster size: 115 voxels; cluster size significance: $P < 0.025$ uncorrected) (see Fig. 3a and Table 2f) (In order to examine whether excluding about 20% of all trials in the elderly group may have resulted in a power problem in the current event-related design, especially

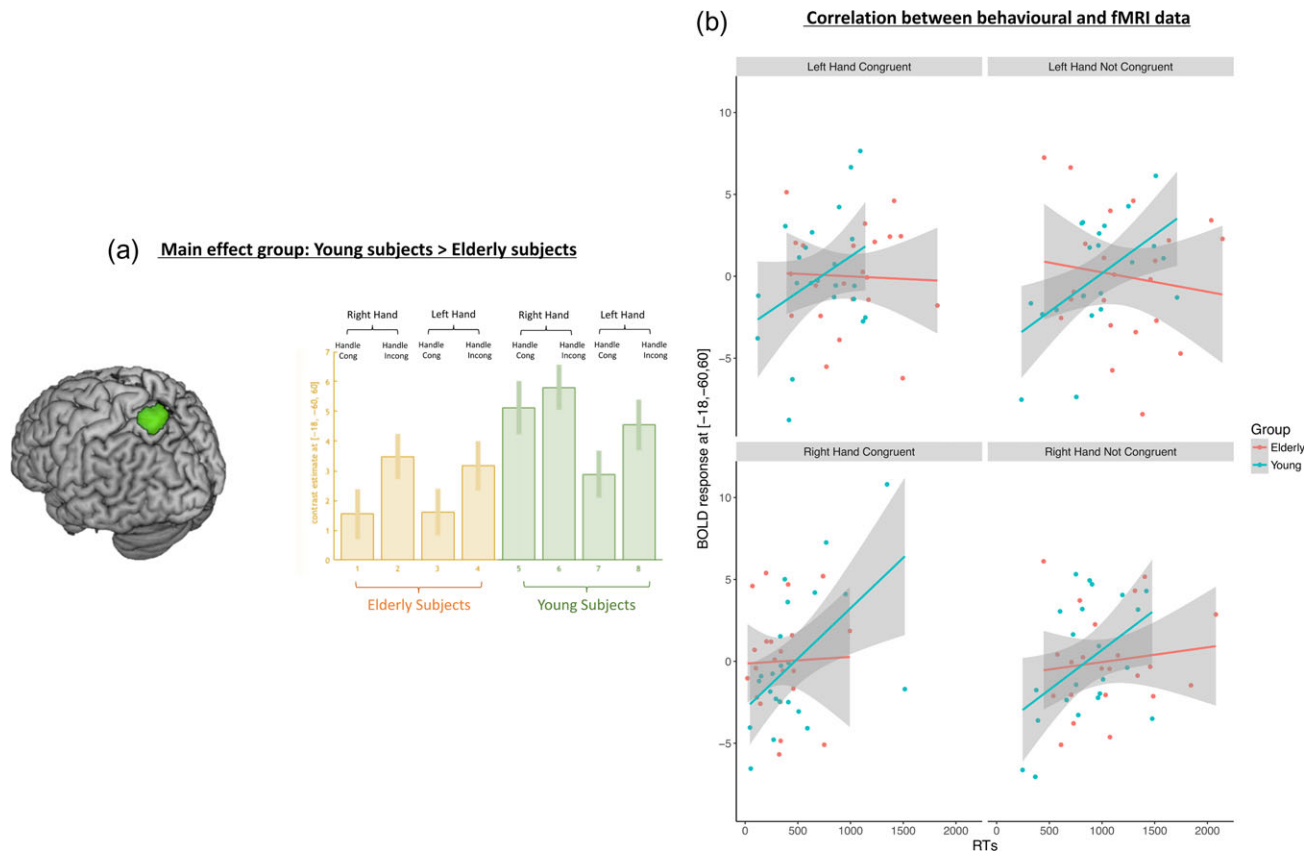


Figure 3. (a) fMRI results: main effect of the factor Group (hypoactivations recorded in elderly subjects). (b) Relationship between fMRI activity recorded in the posterior parietal cortex and reaction times recorded in the young (in blue) and elderly subjects (in red). For the younger subjects, the average brain response across the different conditions was significantly associated with the fMRI BOLD signal in the posterior parietal cortex ($P < 0.05$ FWE corrected); the same was not the case for the older subjects, where we could not observe any correlation surviving a correction for multiple comparisons.

since only about 10% of all trials were excluded in the young group, we performed a supplementary analysis and we included the same number of trials for each condition for both young and elderly subjects (80% of trials: 13 trials instead of 16 trials for each condition). The results were very similar to those originally described: the main area of significant difference in left superior parietal cortex meets a FWER correction at both the voxel and cluster level).

No significant differences were found in the opposite comparison (Elderly > Young), nor were there significant interactions with the group factor and other factors.

Relationship Between fMRI and Behavioral Data

To further explore the meaning of the fMRI data, we performed a linear regression analysis between the brain activations for different conditions and the differential RTs (the subtraction of the RTs for each condition and their matched control baseline); the brain images used for these analyses were the contrast images of the subtraction between the experimental trials minus their matched control baseline from the same GLM used for the between-group comparisons described before.

We first assessed this relationship within each group and then assessed their relative comparative strength.

For the younger subjects, the average brain response across the different conditions was significantly associated with the fMRI BOLD signal in a number of regions of the main pattern of activation (Table 3a). The same was not the case for the older

subjects, where we did not observe any correlation surviving a correction for multiple comparisons.

In addition, the comparison of the relative strength of the linear regressions proved highly significant for the very region that also discriminated the 2 groups, the left superior parietal cortex (Table 3b), which had an increased response together with the increased labor time (Fig. 3b).

Discussion

We recently provided evidence that the early stages of senescence are associated with brain compensatory processes that make implicit MI, as measured through the HLT, still possible at a quasi-juvenile level (Zapparoli et al. 2016). The aim of the present study was to investigate whether such observations could be generalized to another implicit but more ecological MI task, the GST. To date, there are no studies (behavioral or neurofunctional) that have explored this issue. Compared with the HLT, the GST involves more complex visuomotor transformations and the (mental) interaction with an external object, a daily life tool.

The involvement of MI in GST has been confirmed by several experiments showing how subjects were slower and less accurate in decisions that involved adopting awkward postures (as already seen in other MI tasks; see, e.g., Parsons et al. 1987b). Moreover, the time needed for these judgments increased as a function of the distance between the location of the subjects' hands and the orientation of the chosen posture

Table 3 Brain regions showing a significant correlation with reaction time data

Brain regions (BA)	MNI coordinates							
	Left hemisphere				Right hemisphere			
	x	y	z	Z-score	x	y	z	Z-score
a) Brain areas whose activity is related with reaction times (young subjects)								
Frontal orbital gyrus (47)	-34	40	-2	3.5°				
Frontal inferior opercular gyrus (44)	-52	22	30	4.5°				
Frontal middle gyrus (46)	-40	50	2	4.2°				
	-34	46	10	3.8°				
Parietal superior lobule (7)	-20	-70	54	4.6°				
	-20	-50	48	4.5°				
	-18	-64	60	4.2°				
Occipital middle gyrus (19)					34	-86	16	4.0°
					30	-82	34	3.5°
					34	-86	26	3.3°
Calcarine fissure (17)	-6	-98	4	3.6°	12	-102	8	4.2°
					4	-98	-2	3.6°
b) Brain areas whose activity is related with reaction times (Young > Elderly subjects)								
Parietal superior lobule (7)	-20	-64	64	4.16°				
	-28	-58	62	3.7°				
	-6	-74	58	3.6°				

x, y, and z are the stereotactic coordinates of the activations in MNI space.
°FWE correction (cluster level).

through the biomechanically defined trajectory; all these findings suggest that GST involves “on-line, analogue, simulations of movements” (Johnson 2000b).

The results of the present study demonstrated the existence of significant behavioral and neurofunctional effects of early ageing on implicit motor mechanisms involved in simulated reaching and grasping for objects; this was clearly different from what was observed with other MI tasks described in our previous experiments (Zapparoli et al. 2013, 2016).

We start this section by discussing the behavioral findings, considering both within- and between-group effects and their relative interactions. We then address the neurofunctional differences associated with ageing: the differences between younger and elderly in this case were mainly represented by hypoactivations in older subjects in the superior parietal lobules. We then discuss our findings in light of the different neurocognitive models of ageing.

Behavioural Results: Within-Group Effects

The within-group results showed better behavioral performance in terms of accuracy and RTs when the task involved the right hand; these findings are in line with the behavioral results of previous papers on HLT (Zapparoli et al. 2014, 2016). In addition, there was a special advantage for congruent stimuli that were to be mentally grasped with the right hand. This visuomotor effect can be easily explained by the hand preference of our subjects, as they were all right-handed. Conversely, our findings are different from what was observed in previous behavioral studies on GST: e.g., Johnson (2000b) described a similar performance for both the right and left hand, hypothesizing that subjects mentally simulate movements with both the hands before giving a response (Johnson 2000b). However, in that study, the stimulus was a standard dowel, an object not commonly manipulated in “real life” with affordances of a mere geometrical nature deprived of semantics. In contrast, in our study, the experimental stimuli were pictures of real tools,

which suggests that the combination of right-handedness of our subjects and the fact that we used real tools was instrumental in bringing about a hand by handle congruency interaction.

However, we are aware that for further testing this hypothesis, we should recruit a sample of subjects characterized by more variability with regard to their handedness and try out a formal correlation analysis between the handedness score obtained in formal tests and behavioral data.

The handle congruency factor was also significant: when the handle was located on the same side as the hand on which participants responded, performance was faster and more accurate than when the handle was located on the opposite side; this could be explained by the physical distance between the imagined hand’s position and the handle location suggesting that subjects also simulate the reaching component of the mentally simulated behavior: in noncongruent conditions, this distance is greater and results in longer RTs, in line with previous literature (Johnson 2000b).

Behavioural Results: Between-Group Effects

The comparison between groups showed significant differences in terms of accuracy and RTs, as the elderly subjects were less accurate and slower than the younger subjects.

There was also a significant group by hand interaction because elderly subjects were slower in conditions involving the nondominant hand.

The existence of lower accuracy and slower RTs in young elderly subjects was different to what had been found with other MI tasks, such as the HLT; it is important to observe that differences are present in conditions involving the nondominant hand: this would suggest an effect due to an intrinsic “difficulty” of certain items, particularly when the nondominant hand is involved. However, a further factor contributing to the greater difficulty of the GST might be that, while the stimuli of the HLT provide a final end-state of the motor simulation

needed to solve the problem presented by the stimuli (the hand position and view), the GST provides fewer such cues when subjects needed to simulate both the reaching and grasping movements for the manipulanda, given their affordances. Interestingly, no age effect was present for the right-hand grip simulation suggesting that such over-practised hand-tool interactions are processed normally in elderly subjects.

Neurofunctional Findings: Within-Group Effects

The main effect of the task was in line with previous findings on implicit MI and GST (Parsons et al. 1995; Johnson et al. 2002; Vingerhoets et al. 2002; Seurinck et al. 2004; de Lange et al. 2005, 2006): there was a large activation of the brain regions involved in reaching and grasping movements observed in monkeys, such as the frontal and the precentral gyrus, the inferior and superior parietal lobules and the occipital areas (Cohen and Andersen 2002). The large involvement of the parietal lobe is also consistent with several findings on the more general concept of intentional actions (Zapparoli et al. 2017, 2018).

There were also specific effects associated with the imagined hand: the mental simulation of movements with the right hand was associated with greater activation in the contralateral motor system. Most likely, the presence of daily life tools determined a greater recruitment of motor representations when the hand to be used for the task is the same that subjects usually used to manipulate them. This greater recruitment for the right hand was evident in the congruent conditions when the handle was presented in the same portion of space as the hand, resulting in a significant hand-by-handle congruency interaction (Fig. 2b): the effect was present for young and elderly participants alike.

Neurofunctional Findings: Between-Group Effects

As much as the network activated in the two groups during the GST was generally a shared one, we also found significant group differences: a highly significant decrease in activation at the level of the left superior parietal lobule in older subjects (A hypoactivation in the mirror parietal region of the right hemisphere did not survive a correction for multiple comparisons: Stereotactic coordinates: $x = -20$, $y = -64$, $z = 70$; Z score = 4.0; uncorrected P value: 0.00003).

The involvement of the posterior parietal cortex in the visuomotor integration implied by reaching and grasping behaviors was first suggested by neuropsychological studies on human neurological populations (review in Battaglia-Mayer and Caminiti 2002). fMRI studies on humans have confirmed the neuropsychological findings: for example, Hermsdörfer et al. (2007) found a posterior parietal activation associated with both planning and execution of pantomimed and actual tool use in healthy subjects using a variety of familiar tools and objects that were tested with both the left and right hand (Hermsdörfer et al. 2007). More specific details about the posterior parietal lobule involvement during tool interactions were found by Brandi et al. (2014): they developed a “tool-carousel” to test in fMRI the actual manipulation of different objects to plan and execute different goal-directed actions; the authors found that the posterior parietal cortex was particularly activated for the online monitoring of the grip of objects during complex actions (Brandi et al. 2014).

Of crucial importance for our interpretation of the present imaging data in ageing would be some evidence that connects the domain of MI with that of actual motor control for the region identified here for the specific behavior that was tested.

Such evidence is present both in the monkey and in the human literature.

In monkeys, it has been found that populations of neurons in the posterior parietal cortex represent high-level aspects of action planning and combine visual information of the external object with motor information about the acting effector (e.g., the limb position, see, e.g., Cohen and Andersen 2002). More importantly, Hauschild et al. (2012) showed that a monkey, after some practice, was able to move a cursor and reach targets on a computer screen without moving his own limbs, supposedly by MI. This was made possible by online decoding of the electrical activity of the monkey’s posterior superior parietal cortex, the monkey analogue for the region found in our experiment (Hauschild et al. 2012).

The same basic finding has been shown in humans by studies on a tetraplegic patient (Aflalo et al. 2015): the authors first identified with MI tasks and fMRI a candidate region of the superior parietal lobule for their invasive electrophysiological recordings. This was the same region hypoactivated in our elderly group (Talairach coordinates from Aflalo et al. (2015) converted to MNI space: $x = -17$, $y = -65$, $z = 56$) (see Supplementary Fig. S1). Furthermore, they deciphered the recordings from that region and demonstrated that the paralyzed patient was able to move a prosthetic limb in reaching behavior. These findings indicated that this portion of the parietal cortex represents high-level, cognitive aspects of reaching behavior (Aflalo et al. 2015).

It is interesting to note that the recordings made by Aflalo et al. (2015) covered 2 subdivisions of the intraparietal sulcus: the anterior intraparietal region (AIP) and the medial intraparietal region (MIP). These were both activated as a main effect of our task, with the data of the young and elderly averaged. However, the between-group difference was located in the more dorsal component of the region.

The selective hypoactivation of the more dorsal parietal cortex provides a strong clue about the specific components that might become less efficient in implicit MI for the elderly, namely, the reaching component. This conclusion is consistent with the finer-grained characterization of the brain networks involved in tool manipulation: according to Binkofski and Buxbaum (2013), there are 2 distinct dorsal routes in the human brain: a “grasp” and “use” system. Of these 2 dorsal routes, a left-lateralized ventrodorsal system most likely subserves manipulation of knowledge that contributes to the generation of specific object-oriented motor plans: damage in this system has been associated with limb apraxia (review in Binkofski and Buxbaum 2013). A bilateral dorsodorsal system, needed for sensory-motor mapping, has been more associated with the task of reaching: lesions here have been associated with optic ataxia (see reviews in Buxbaum 2017).

Given the location of the areas of hypoactivation in our elderly subjects and the presence of a substantial trend of hypoactivation in the right superior parietal cortex, we conclude that elderly subjects have initial signs of malfunction within the bilaterally distributed dorsodorsal system.

Of course, reaching and grasping are not entirely independent behaviors (but see also Gallese et al. 1994): the two interact dynamically with changes of the grip from its initial preshaping to the final configuration when landing on target (Hoff and Arbib 1993).

Previous behavioral findings have documented the vulnerability of these interactions later in life. It has been found that elderly subjects may generally rely on visual control when they act, more than younger people (Coats and Wann 2011). In that study, young and elderly subjects performed a reaching and

grasping task using an apparatus that eventually obscured the target and the approaching hand, after allowing for initial visual exploration. For the elderly subjects, both reaching and grasping were selectively affected when visualization of the hand was prevented; they produced additional reaching movements and had longer adjustment times for the grasping phase of the movement. Of course, the GST, in the format adopted in this experiment, is not sufficiently specific to permit subtle distinctions between the reaching and grasping phases of the mental behavior and their dynamic interactions.

Before summarizing all the above, it is worth mentioning that [Nedelko et al. \(2010\)](#) reported hyperactivation in the superior posterior parietal cortex during the imagining of reaching and grasping movements triggered by the observations of the same movements performed by others while keeping their eyes open (see Fig. 4 in [Nedelko et al. 2010](#)). This finding is at variance with our own, and it is worth a comment. After careful examination of their paradigm, we came to the conclusion that there were sufficient differences between our protocol and the one adopted by [Nedelko et al. \(2010\)](#), primarily because their task seems easier than our GST: indeed, there was a dynamic model upon which subjects could produce their imagined movements. If seen in the framework of the CRUNCH hypothesis, an easier version of an imaginary reaching and grasping task should be accompanied with stronger activations in elderly subjects to maintain good behavioral performance. Unfortunately, [Nedelko et al. \(2010\)](#) did not collect behavioral data to further confirm this hypothesis.

To summarize, given the paradigm adopted here and the distribution of the parietal areas of hypoactivation identified, these results suggest a specific behavioral and neurofunctional decline in mental representations of reaching, and possibly grasping, movements associated with early ageing for the demanding GST.

This is somewhat different from what has been observed in other MI tasks described in our previous work ([Zapparoli et al. 2013, 2016](#)) that engaged simpler movements and did not involve any kind of mental interaction with external objects. One possible explanation of this difference is, as mentioned in the introduction, that during the GST, subjects cannot revert to alternative strategies to deal with the task, perhaps with the only exception of canonical presentations for the right hand. This is similar to saying that for other MI tasks, there are more degrees of freedom as far as the strategy of choice than for the more demanding GST.

It remains to be seen whether other components of the functional information processing flow are impaired in elderly people. For example, it is well known that the simple observation of an object automatically activates motor representations (something similar to the “visuomotor priming” described by [Craighero et al. 1996](#)). Whether access to these is fully preserved in ageing people remains to be demonstrated.

The present results have another methodological implication because, contrary to what was observed in the previous experiments, that is, preserved performance and compensatory hyperactivations, here we observed a reduced performance that was accompanied by a reduced activation of specific brain areas. This is consistent with current models of the ageing brain, which we discuss below ([Reuter-Lorenz and Cappell 2008](#); [Berlinger et al. 2010](#)) However, there was one limitation in this set of findings in that the group by hand interaction seen in the behavioral data was not mirrored by the fMRI data using the present paradigm. Why this was the

case remains a matter open for discussion and for future experimentation.

Interpretation of the Data in the Light of Neurocognitive Models of Ageing

Taken together with the results of our previous experiments ([Zapparoli et al. 2013, 2016](#)), this study permits a more general discussion about neurocognitive models of ageing in the domain of MI and motor representations.

Modifications of fMRI patterns in the elderly have been interpreted as evidence of compensatory processes of graceful ageing by a number of authors ([Grady et al. 1994](#); [Cabeza et al. 2002](#); [Buckner 2004](#)). If performance remained unaffected, compensatory processes manifest themselves in the recruitment of additional brain regions. These patterns have been documented in several cognitive domains (e.g., working memory, episodic memory retrieval, perception, inhibitory control). The phenomenon was initially observed in the prefrontal cortex ([Cabeza 2002](#)); moreover, compensatory processes have been described as reduced inter-hemispheric asymmetries for tasks that are associated with strongly lateralized fMRI patterns in younger participants while also involving regions outside the frontal lobes ([Berlinger et al. 2010](#)).

Our results showed that, at relatively low levels of task demand, region-specific hyperactivations in older subjects are associated with good performance ([Zapparoli et al. 2016](#)). With the increase of the cognitive load, the attempt at compensation becomes less successful ([Zapparoli et al. 2013](#)), and beyond a certain level of task demands, the elderly brain does not show sufficient activation levels, and performance declines relative to the younger group (the present study).

In our exploration of these phenomena, the first case was represented by the HLT task, where older subjects had a behavioral performance comparable with the younger subjects in terms of accuracy and normalized RTs, mirrored by overactivations in the occipital cortices, whose response was positively correlated with behavior ([Zapparoli et al. 2016](#)). One possibility was that the HLT requires little explicit action monitoring as the “desired state” of the system (the hand position that one mimics with imagination to solve the task) is readily and visually available.

In the case of explicit MI processes, we found what we define as a “partially successful” compensation, represented by the occipital hyperactivations associated with the loss of temporal congruency between real and imagined movements ([Zapparoli et al. 2013](#)). This finding suggested an initial decrease in MI abilities for this explicit MI behavior.

Finally, the GST brought about a more evident decline in performance, possibly because of the limited degrees of freedom of the task in permitting alternative strategies together with specific hypoactivations. In the range of possibilities predicted by current models of ageing (e.g., the CRUNCH hypothesis), this represents the final scenario when both behavior and neural response decline, at variance with successful compensation or compensatory attempts.

A word of caution is needed here: while the results of our three MI experiments seem to support the CRUNCH hypothesis ([Reuter-Lorenz and Cappell 2008](#)), we are aware that to further confirm our speculations and fully support the model, we would need to formally test the model with an ad hoc constructed experiment (e.g., by parametrically varying the level of

cognitive load within a common task in the same sample of subjects; see, [Vergallito et al. 2018](#)), which remains to be done.

How Early is the Motor Decline?

As anticipated in our introduction, it would be good to know how early a decline of motor representations for imagined behaviors, such as those necessary for the GST, takes place. Admittedly, we did not explore a population covering all the decades between early adulthood and clear-cut senescence. This is a limitation that we should acknowledge. However, by having studied subjects with an average age of 60 years, we can now at least claim that some relevant changes have already occurred by a time when people are still active and possibly still working. This evidence suggests that something could/should be done in terms of physiotherapy or mental practice to prevent further decline.

Another aspect that deserves a discussion is the possible “protective” effect of being actively involved in sport or motor-related activities in a constant manner; we did not directly assess this in our protocol, and we only made sure that our subjects reported any kind of specific motor-related diseases in the recruitment phase. However, in future studies, it might be interesting to formally assess the level of engagement of subjects in physical activities to see whether it might have a modulatory effect on the behavioral and fMRI data, as expected from the literature on ageing and dementia (see, e.g., [Rolland et al. 2010](#)).

Conclusions

Explorations of ageing-related changes in cognitive functions and their neural underpinnings are increasingly showing that these are not confined to memory functions. As clearly shown here, motor cognition is affected by ageing even at its earliest onset. In the particular case of the GST, it was possible to demonstrate a breakdown of performance accompanied by a reduced activation of superior parietal cortex normally involved in actual visuomotor transformations needed in reaching and grasping movements. It will be most interesting to test whether specific training of the explored behaviors can return the behavioral performance to a juvenile-like level together with functional plasticity of the crucial regions involved. This seems a class of empirical questions worth testing given the increasing number of people living well beyond their seventh decade.

Supplementary Material

Supplementary material is available at *Cerebral Cortex* online.

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